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# Réponse des communautés végétales aquatiques des Iles Kerguelen (Subantarctique) au réchauffement climatique.

Pauline Douce

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# THESE de DOCTORAT DE L'UNIVERSITE CLAUDE BERNARD LYON 1

**Ecole Doctorale 341  
Evolution Ecosystèmes Microbiologie Modélisation**

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**Pauline Douce**

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## **Réponse des communautés de plantes aquatiques des Iles Kerguelen (Subantarctique) face au changement climatique.**

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**Réponse des communautés de plantes aquatiques  
des Iles Kerguelen (Subantarctique) face  
au changement climatique.**

**Response of aquatic plant communities  
of the Iles Kerguelen (sub-Antarctic)  
to climate change.**

## Résumé

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Les effets de l'augmentation de la température s'avèrent particulièrement marqués chez les plantes aquatiques, qui constituent une ressource et un habitat pour une grande diversité d'organismes. Pourtant, la dynamique des communautés de plantes aquatiques (macrophytes) en contexte de changement climatique reste peu étudiée. Dans la littérature, les réponses fonctionnelles des espèces végétales au stress thermique et aux interactions plantes-plantes sont généralement étudiées séparément alors qu'elles y sont soumises simultanément dans leur habitat. Ces variations de composition fonctionnelle des communautés pourraient impacter les mécanismes de coexistence entre les espèces végétales ainsi que la productivité et les cycles biogéochimiques à l'échelle de l'écosystème, avec des rétroactions possibles sur l'évolution phénotypique des espèces.

Dans ce contexte, cette thèse vise à évaluer comment l'augmentation des températures modifie la dynamique des communautés de macrophytes et en conséquence, le fonctionnement de l'écosystème aquatique, en prenant en compte le rôle de la variabilité intraspécifique des traits de réponse et d'effet des espèces. Les questions de recherche de cette thèse ont été traitées à travers des approches *in situ* et en conditions contrôlées, sur le modèle des mares d'eau douce du littoral des Iles Kerguelen dans la région Subantarctique.

Nos résultats montrent qu'il existe une hétérogénéité d'habitat entre les mares en lien avec les variations de température et de disponibilité en nutriments. Ces paramètres d'habitats sont les plus structurants pour les communautés de macrophytes, et déterminent leurs performances au travers de leurs effets directs, ou *via* la modulation des interactions plantes-plantes et des paramètres biotiques tels que les patrons spatiaux. A l'échelle spécifique, nous avons montré un effet interactif de la température et des interactions plantes-plantes sur les traits fonctionnels chez l'une des espèces étudiées. Par ailleurs, les modifications de phénotype des individus, particulièrement au niveau foliaire, impactent le processus écosystémique de décomposition de la litière. Par rétroaction, ces modifications écosystémiques affectent le phénotype des individus, mettant en évidence l'existence d'une boucle éco-évolutive reposant sur les espèces végétales au sein de l'écosystème aquatique.

Pour conclure, les changements climatiques en cours dans la région Subantarctique impactent la biologie des mares, et ce sur plusieurs niveaux d'intégration écologique, questionnant ainsi le devenir de ces systèmes aquatiques d'eau douce, particulièrement adaptés à des conditions de températures froides.

### **Mots-clés :**

Variabilité intraspécifique des traits, patrons spatiaux, mésocosme, dynamiques éco-évolutives, structures des communautés, mécanismes d'assemblage des communautés, systèmes aquatiques, macrophytes, Iles Kerguelen.

## Abstract

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The effects of increasing temperatures are especially severe in aquatic plants, which are a resource and a habitat for a large variety of organisms. However, the dynamics of aquatic plant (macrophytes) communities in the context of climate change remain poorly studied. In the literature, the functional responses of plant species to thermal stress and plant-plant interactions are generally studied separately, while these species are subjected to them simultaneously in their habitat. These variations in the functional composition of communities could impact the coexistence mechanisms between plant species, as well as productivity and biogeochemical cycles at the ecosystem scale, with possible feedbacks on the phenotypic evolution of species.

In this context, this thesis aims to assess how increasing temperatures modify macrophyte community dynamics and consequently aquatic ecosystem functioning, taking the role of intraspecific variability in species response and effect traits into account. The research questions of this thesis were addressed through *in situ* and controlled condition approaches, on the model of freshwater ponds of the Iles Kerguelen, located along the coast, in the sub-Antarctic region.

Our results show that there is habitat heterogeneity between ponds in relationship with variations in temperature and nutrient availability. These habitat parameters are the most structuring for macrophyte communities, and determine their performance through their direct effects, or through the modulation of plant-plant interactions and biotic parameters such as spatial patterns. At the species scale, we showed an interactive effect of temperature and plant-plant interactions on functional traits in one of the studied species. Furthermore, changes in the phenotype of individuals, particularly at the foliar level, impact the ecosystem process of litter decomposition. By feedback, these ecosystem modifications affect the phenotype of the individuals, highlighting the existence of an eco-evolutionary loop based on plant species within the aquatic ecosystem.

As a conclusion, the current climate changes in the sub-Antarctic region are impacting the biology of ponds at several levels of ecological integration, thus questioning the future of these freshwater aquatic systems, which are particularly adapted to cold temperature conditions.

### **Keywords:**

Intraspecific trait variability, spatial patterns, mesocosm, eco-evolutionary dynamics, community structure, community assembly mechanisms, aquatic systems, macrophytes, Iles Kerguelen.

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---

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## Liste des papiers

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- Article I** Douce P., Mermillod-Blondin F., Simon L., Dolédec S., Eymar-Dauphin P., Renault D., Sulmon C., Vallier F., Bittebiere A.-K. 2023. Biotic and abiotic drivers of aquatic plant communities within the sub-Antarctic region. *Polar Biology*.
- Article II** Douce P., Renault D., Simon L., Mermillod-Blondin F., Vallier F., Bittebiere A.-K. How does trait variance partitioning help us to understand plant community assembly? The example of pond communities at the Kerguelen Islands. *Soumis à Journal of Vegetation Science*.
- Article III** Douce P., Saiz H., Benot M.-L., Mermillod-Blondin F., Simon L., Renault D., Vallier F., Oury. Y., Fontaine M., Bittebiere A.-K. 2023. Functional characteristics rather than co-occurrences determine the outcome of interactions between neighbouring plants in sub-Antarctic ponds: consequences for macrophyte community biomass. *Freshwater Biology*.
- Article IV** Douce P.\*, Eymar-Dauphin P.\*, Saiz H., Renault D., Mermillod-Blondin F., Simon L., Vallier F., Bittebiere A.-K. Using multidimensional trait space to study responses in aquatic plant community to modifications of abiotic filtering in the sub-Antarctic ponds. *En préparation*. (\*contributions égales des auteurs).
- Article V** Douce P., Renault D., Sulmon C., Mermillod-Blondin F., Simon L., Fontaine M., Oury Y., Bittebiere A.-K. Macrophyte strategies and performance in response to thermal constraints in a context of plant-plant interactions. The example of the plant species from the Iles Kerguelen. *En préparation*.
- Article VI** Douce P., Simon L., Colas F., Mermillod-Blondin F., Renault D., Sulmon C., Dubreucque R., Bittebiere A.-K. Temperature drives eco-evolutionary feedbacks within sub-Antarctic ponds: evidence from an experiment conducted at the community and ecosystem levels. *En préparation*.

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## INTRODUCTION GENERALE

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## Structure de la thèse

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### 1. Cadre général et enjeux

Le changement global affecte les écosystèmes et entraîne aujourd'hui une crise majeure pour la biodiversité (Khare et al., 2020 ; Harrison, 2020). Ce manuscrit de thèse se focalise sur la composante du changement climatique, avec en particulier, l'élévation des températures. Conditions thermiques et interactions plantes-plantes constituent respectivement des filtres abiotiques et biotiques qui affectent simultanément l'assemblage des espèces végétales (Keddy, 1992). Cependant, tout changement environnemental, dont l'augmentation des températures, pourrait renforcer ou modifier ces filtres, affectant *in fine* la richesse et l'abondance des espèces au sein des communautés (Zhu et al., 2020 ; Chaudhry & Sidhu, 2022). Des approches basées sur les traits permettent de caractériser les patrons de réponses à des changements environnementaux et d'en comprendre les mécanismes sous-jacents (McGill et al., 2006). En particulier, l'augmentation des températures est susceptible d'affecter la morphologie/physiologie des individus végétaux (Moles et al., 2014 ; Bjorkman et al., 2018 ; Myers-Smith et al., 2019), ainsi que les équilibres de coexistence des espèces végétales, notamment au travers de modifications des interactions plantes-plantes (compétition, facilitation) (Ploughe et al., 2019 ; Souza et al., 2021).

Les écosystèmes d'eau douce comptent parmi les habitats les plus abiotiquement contraints (Santamaría, 2002), abritant généralement des communautés végétales de plantes aquatiques (*i.e.* macrophytes). Les effets de l'augmentation de la température s'avèrent particulièrement marqués chez les macrophytes, qui constituent une ressource et abritent une grande diversité d'organismes (Keddy, 2010). Pourtant, la dynamique des communautés de macrophytes en contexte de changement climatique reste peu étudiée. Les espèces végétales (dont les macrophytes) sont sessiles et donc soumises simultanément aux contraintes thermiques et aux interactions plantes-plantes de leur habitat. Il semblerait notamment qu'elles y répondent de façon antagoniste. Par exemple, compétition et stress thermique induisent respectivement une augmentation (Novoplansky, 2009 ; Bittebiere et al., 2012) et une diminution (Shah & Paulsen, 2003 ; Chalanika De Silva & Asaeda, 2017) des valeurs moyennes de taux de croissance, de hauteur et de surface foliaire. Ces réponses antagonistes suggèrent alors l'existence d'un compromis entre résistance à la contrainte thermique et aptitude compétitive. Étonnamment, les réponses des communautés végétales à ces deux types de

contraintes sont généralement étudiées séparément (*e.g.* Greulich & Bornette, 1999 ; Riis et al., 2012), limitant ainsi le pouvoir explicatif des études quant aux effets combinés de ces variables sur les assemblages de macrophytes. Cette thèse se démarque ainsi des études menées jusqu'à présent, en proposant une approche innovante afin de déterminer la réponse des espèces de communautés végétales aquatiques à une augmentation des contraintes thermiques de leur habitat, en contexte d'interactions plantes-plantes. La prise en compte des interactions plantes-plantes, qui renforcent les pressions de sélection exercées sur les plantes, permettra d'affiner les prédictions des conséquences des changements climatiques sur la coexistence des espèces de macrophytes et le fonctionnement de l'écosystème aquatique.

Dans un contexte d'augmentation des températures, la variabilité intraspécifique assurerait la pérennité des espèces végétales (Ghalambor et al., 2007) en leur permettant de résister conjointement aux filtres biotiques et abiotiques. Cette variabilité serait la résultante d'une variabilité génétique et/ou de la plasticité phénotypique (Ghalambor et al., 2007 ; Byars et al., 2007 ; Albert et al., 2011). Des études récentes ont quantifié un fort taux de variabilité intraspécifique, pouvant compter jusqu'à 40% de la variabilité totale d'un trait au sein d'une communauté (Jung et al., 2010 ; Albert et al., 2010a). Pourtant, celle-ci reste faiblement prise en compte dans les scénarios actuels de réponses des espèces végétales face aux changements climatiques dans un contexte d'interactions plantes-plantes. Une méthode par partition de variance des traits permettrait de quantifier la part de variabilité attribuée aux différentes échelles (intra- vs. interspécifiques), et pourrait notamment apporter des réponses quant aux rôles des différents traits dans cette réponse aux facteurs biotiques et/ou abiotiques (Le Bagousse-Pinguet et al., 2017 ; Liu et al., 2018). Par ailleurs, les traits co-varient au sein d'un même individu pour coordonner plusieurs fonctions souvent énergivores, tout en maximisant la performance d'un individu (*i.e.* production de biomasse végétative et taux de reproduction) (Murren, 2002 ; De Kroon et al., 2005). Aussi, ces co-variations sont susceptibles d'être modifiées par l'intensification des filtres biotiques et abiotiques, impactant en retour la performance des individus et leur devenir dans les communautés (Wright et al., 2004, 2005).

Le filtre abiotique dans les écosystèmes aquatiques est reconnu pour être intense (Santamaría, 2002), et a une incidence sur la composition fonctionnelle et la diversité des communautés de macrophytes (Bornette & Puijalon, 2011 ; Fu et al., 2014 ; Zhang et al., 2019), qui ensemble pourraient jouer un rôle important dans les interactions plantes-plantes (Suzuki et al., 2014). En effet, la direction et l'intensité de ces interactions seraient la résultante non

seulement des traits fonctionnels des individus qui déterminent leur compétitivité (Gaudet & Keddy, 1988), mais aussi de la différence avec les valeurs des traits fonctionnels des individus voisins (Kraft et al., 2015b ; Cadotte & Tucker, 2017). Ainsi, les interactions plantes-plantes et donc la coexistence des espèces au sein d'une communauté pourraient se voir modifiées par l'intensification des processus de filtrage suite aux changements environnementaux. Par ailleurs, les interactions plantes-plantes, de même que l'hétérogénéité environnementale ou la dispersion peuvent impacter à leur tour la distribution spatiale des individus (patrons spatiaux : agrégation/ségrégation des individus) au sein d'une communauté (Herben & Hara, 2003). Par conséquent, les patrons spatiaux à l'échelle locale seraient modulés par le filtrage abiotique et les interactions plantes-plantes (Blanchet et al., 2020).

Les espèces végétales sont des producteurs primaires qui jouent un rôle crucial dans le fonctionnement des écosystèmes puisqu'elles sont à la base de multiples processus écosystémiques (Lavorel & Garnier, 2002). Les réponses des individus végétaux aux interactions plantes-plantes, ou bien à une élévation de la température, incluent un changement de valeurs de traits foliaires (Shah & Paulsen, 2003 ; Bittebiere et al., 2012), et d'allocation de nutriments et de biomasse au sein de l'individu (Reich & Oleksyn, 2004). Ces traits de réponse aux contraintes biotiques et thermiques de leur habitat pourraient constituer des traits d'effet (Díaz & Cabido, 2001 ; Lavorel & Garnier, 2002), c'est-à-dire influencer le fonctionnement de l'écosystème aquatique (Violle et al., 2007) *via* les cycles des nutriments et la productivité primaire. Par phénomène de rétroaction à l'échelle de l'écosystème, la modification des propriétés écosystémiques entraînerait des modifications de la composition fonctionnelle et de la productivité de la communauté végétale (Peñuelas et al., 2013 ; Barbe et al., 2017). Par conséquent, des changements évolutifs dans le temps et l'espace peuvent affecter les processus et patrons écologiques, de même que les modifications de patrons écologiques peuvent impacter en retour les dynamiques évolutives des espèces, créant ainsi des boucles de rétroaction entre les deux dynamiques, autrement appelées « boucles éco-évolutives » (Hairston et al., 2005 ; Urban & Skelly, 2006 ; Fussmann et al., 2007 ; Ellner et al., 2011 ; Schoener, 2011 ; Matthews et al., 2011 ; Shefferson & Salguero-Gómez, 2015 ; De Meester et al., 2016, 2019).

Dans les écosystèmes tempérés, l'empreinte anthropique est devenue si forte qu'il est devenu difficile de cerner avec certitude le(s) facteur(s) à l'origine des réponses observées. Les systèmes de type mésocosme apportent quant à eux des réponses convaincantes en écologie, mais ils ne peuvent reproduire parfaitement la complexité des variations et des interactions des

facteurs abiotiques. Au cours des dernières décennies, un nombre croissant de théories et de concepts en écologie ont été testés dans les régions polaires, écosystèmes sentinelles, fréquemment définies comme des laboratoires à ciel ouvert (Bergstrom & Chown, 1999). Le réchauffement climatique y est particulièrement rapide (Walther et al., 2002) alors que les communautés animales et végétales autochtones, pauvres en termes de nombres d'espèces, sont remarquablement adaptées à des températures fraîches (4,6°C en moyenne) (Frenot et al., 2006). Elles seraient donc particulièrement sensibles aux modifications thermiques actuelles (Bergstrom & Chown, 1999). Les questions de recherche de cette thèse sont traitées à travers des approches *in situ* et en conditions contrôlées, sur le modèle des mares d'eau douce, localisées en bordure de littoral sur l'archipel des Iles Kerguelen. Ces mares constituent l'habitat des communautés locales des espèces macrophytes, dont la richesse spécifique est très pauvre (six espèces répertoriées au total). Ces espèces présentent une aire de répartition limitée à la région Subantarctique, voire même aux Iles Kerguelen (espèce endémique). Il y a donc un enjeu de conservation fort sur ces espèces. Ce modèle d'étude est particulièrement pertinent pour aborder les questions théoriques développées dans cette thèse. En effet, il s'agit d'un système écologique simple (Frenot et al., 2001 ; Van der Putten et al., 2010), dont les espèces sont adaptées à des températures froides mais soumises à des changements climatiques rapides (Lebouvier et al., 2011). Par ailleurs, ce sont des systèmes peu connus et qui ont fait l'objet dans le cadre de cette thèse, d'une description spatio-temporelle de la structure des communautés de macrophytes qu'ils abritent, ainsi que d'une étude des facteurs biotiques et/ou abiotiques qui expliquent ces variations.



## 2. Objectifs de la thèse

Cette thèse vise à évaluer comment l'augmentation des températures modifie les mécanismes de coexistence des macrophytes et en conséquence, le fonctionnement d'un écosystème aquatique. Il s'agit en particulier de déterminer le rôle de la variabilité intraspécifique, au travers de l'étude de la réponse des traits fonctionnels aux contraintes thermiques de leur habitat, combinées aux interactions plantes-plantes. Une approche méthodologique basée sur la partition de variance est proposée afin d'évaluer le rôle de plusieurs traits dans les réponses aux filtres biotiques et/ou abiotiques. Toujours dans un contexte méthodologique, les systèmes étudiés sont présentés *via* la description spatio-temporelle des conditions abiotiques des mares et de la composition des communautés de macrophytes qu'elles abritent. Les conséquences des variations de conditions abiotiques et de composition fonctionnelle de la communauté végétale pour les interactions plantes-plantes et les patrons spatiaux associés sont également étudiées à l'échelle de la communauté. Enfin, les dynamiques Eco-Evo de ces systèmes aquatiques sont explorées, avec les impacts des changements évolutifs des phénotypes sur la productivité et les cycles biogéochimiques, ainsi que les rétroactions possibles sur les traits des individus. Cette thèse repose sur une approche intégrative (espèce, communauté, écosystème) afin d'identifier d'éventuels processus « bottom-up » et « top-down » (Figure 1), et vise à répondre aux questions suivantes :

- (i) Chapitre 1 : comment la structuration spatiale des communautés de macrophytes et les conditions du milieu affectent le sens et l'intensité des interactions plantes-plantes ? Comment les paramètres biotiques et abiotiques se modulent entre eux et quelles sont les conséquences sur la performance (*i.e.* biomasse totale) des communautés à l'échelle des mares ?
- (ii) Chapitre 2 : à l'échelle des communautés, quelles réponses sont mises en place à moyen terme (4 ans) ? Et quels sont les mécanismes sous-jacents à ces patrons de réponses ? A l'échelle spécifique, quelles sont les réponses fonctionnelles des macrophytes à la combinaison des contraintes abiotiques (dont la température) et des interactions plantes-plantes au sein de leur habitat ?
- (iii) Chapitre 3 : quelles sont les conséquences de la réponse fonctionnelle des macrophytes aux interactions plantes-plantes  $\times$  hausse des températures sur la

décomposition de litière, et donc sur la productivité et les cycles biogéochimiques de l'écosystème aquatique ? Par phénomène de rétroaction, quelles sont les réponses fonctionnelles des macrophytes aux modifications de ce processus écosystémique (dynamique Eco-Evo) ?

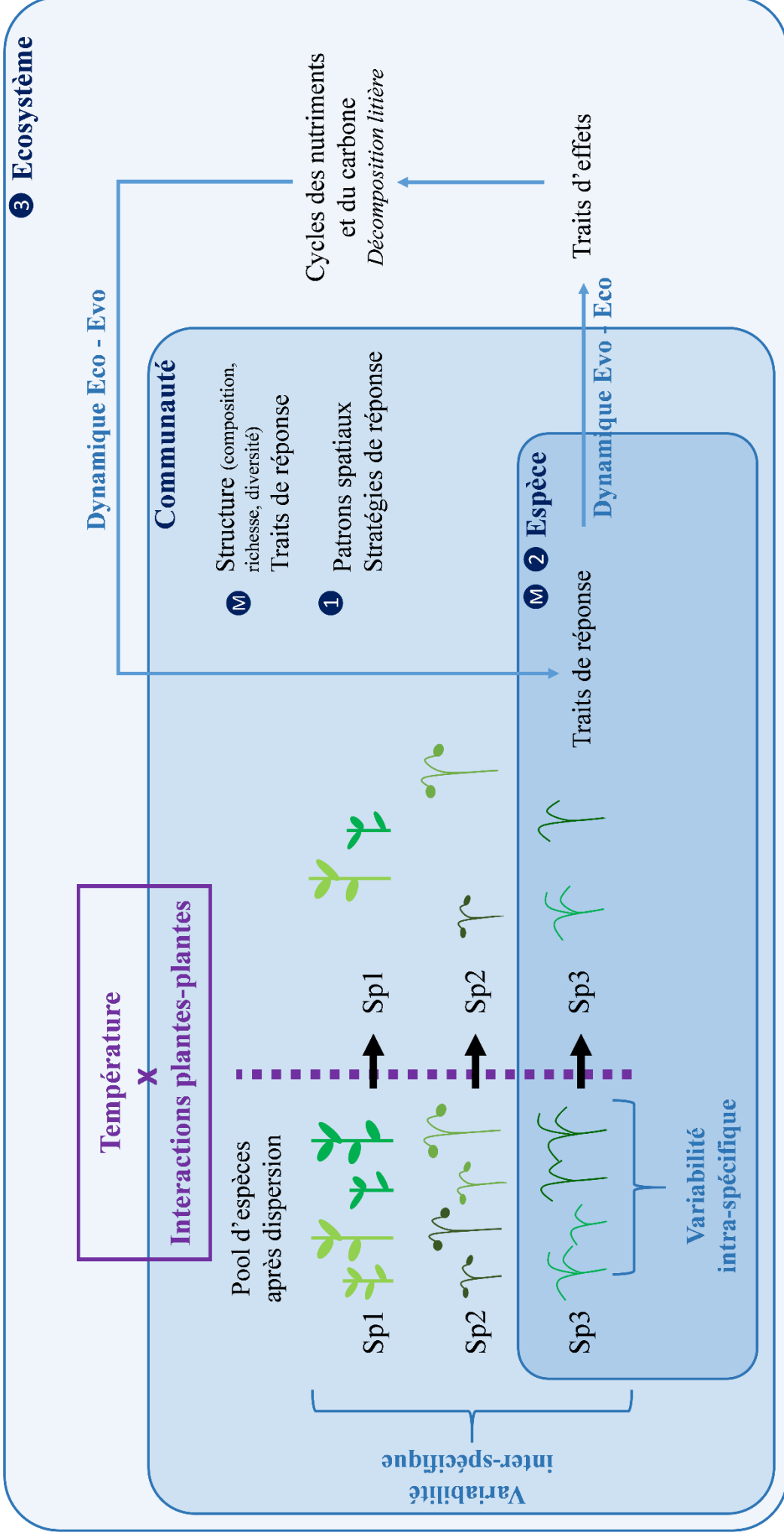


Figure 1. Structure de la thèse. 'sp' espèce. **(M)** : méthodologie, **(1)** **(2)** **(3)** : chapitres.

- M** Les mécanismes d'assemblage de la communauté aquatique ont été étudiés (**article I**), de même que le rôle de plusieurs traits dans les réponses aux filtres biotiques et/ou abiotiques à travers une approche méthodologique basée sur la partition de variance (**article II**).
- 1** Comment les conditions abiotiques du milieu, les caractéristiques fonctionnelles du voisinage et la structuration spatiale des communautés de macrophytes affectent le sens et l'intensité des interactions plantes-plantes ? Quelles sont les conséquences sur la biomasse des communautés à l'échelle des mares ? (**article III**)
- 2** Face à des conditions environnementales changeantes, observe-t-on une convergence de stratégies de réponse à l'échelle des communautés à moyen terme (4 ans) ? Quels traits participent à la mise en place de ces patrons de réponses et quels sont les facteurs abiotiques qui conduisent à une modification des stratégies à l'échelle des communautés ? (**article IV**)  
Quelle sont les réponses fonctionnelles des espèces de macrophytes à la combinaison des contraintes thermiques et des interactions plantes-plantes ? (**article V**)
- 3** Quelles sont les dynamiques Eco-Evo mises en place au sein de l'écosystème aquatique ? Comment la réponse fonctionnelle des macrophytes aux interactions plantes-plantes × hausse des températures affecte les processus de décomposition de litière et comment, par phénomène de rétroaction, la modification de ce processus écosystémique impacte le phénotype des individus macrophytes ? (**article VI**)

### 3. Organisation de la thèse

Tout d'abord, une revue de la littérature est proposée afin de dresser un état de l'art sur les mécanismes de réponse à la combinaison des filtres biotiques et abiotiques, à l'échelle de l'espèce et de la communauté, et leurs effets sur le fonctionnement de l'écosystème. En particulier, l'accent est porté sur la réponse des espèces de macrophytes à l'élévation des températures dans un contexte d'interactions plantes-plantes, et les conséquences possibles sur les cycles biogéochimiques des nutriments et du carbone de l'écosystème aquatique. Cette revue bibliographique permet d'énoncer les mécanismes théoriques sous-jacents de réponses à ces filtres, nécessaires à la discussion des résultats.

La seconde partie comprend les approches méthodologiques complémentaires qui ont été utilisées dans cette thèse, avec une description détaillée des suivis *in situ* et des designs expérimentaux en conditions contrôlées mis en œuvre pour répondre aux différentes questions posées. Deux articles ont été intégrés dans cette partie : le premier article permet de décrire les conditions biotiques et abiotiques qui caractérisent le système aquatique des mares (**article I**), le deuxième article présente une approche méthodologique basée sur la partition de variance pour quantifier les réponses des traits des espèces à plusieurs facteurs environnementaux (**article II**).

Les résultats sont organisés en trois chapitres, chacun répondant à l'un des objectifs de la thèse (Figure 1). Au début de chaque chapitre, les questions abordées et les hypothèses testées sont rapidement présentées. Le chapitre 1 se positionne à l'échelle de la communauté pour étudier l'impact de la structuration spatiale des communautés de macrophytes et des conditions du milieu sur les interactions plantes-plantes et la performance (*i.e.* biomasse totale) des communautés (**article III**). Le chapitre 2 s'articule autour de deux articles (**article IV, V**) qui s'intéressent à la réponse des traits fonctionnels aux contraintes abiotiques (notamment l'élévation des températures) dans un contexte d'interactions plantes-plantes. Enfin, le chapitre 3 se place à l'échelle de l'écosystème pour déterminer les dynamiques Eco-Evo en jeu face à une augmentation de la température dans un contexte de communauté (**article VI**).

## Revue bibliographique

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Les systèmes aquatiques d'eau douce sont définis comme tout système dont la formation, les processus et les caractéristiques sont contrôlés par l'eau, temporairement ou en permanence (Desta et al., 2012). Parmi ces systèmes, on compte les lacs, mares, marais, et tourbières qui totalisent un recouvrement de près de 2 à 6% de la surface terrestre (Downing et al., 2006). Ensemble, ils offrent des habitats pour une grande variété de plantes, invertébrés, poissons, mammifères et oiseaux. Toutes les interactions entre les compartiments végétaux, animaux, eau, sédiments et sol des terres voisines permettent aux systèmes aquatiques de remplir de nombreuses fonctions comme des fonctions hydrologiques, climatiques ou de qualité de l'eau, et de maintenir une certaine biodiversité (Bardecki, 1991 ; Lambert, 2003). Aussi, ils offrent de nombreux services aux sociétés humaines (Dixon & Wood, 2003 ; Desta et al., 2012), notamment la fourniture en eau potable et un service de régulation du micro-climat, puisqu'ils régulent la température, les précipitations et autres processus climatiques à échelle locale (Kayranli et al., 2010 ; Desta et al., 2012 ; Mitsch et al., 2013). Cependant, ces systèmes et les communautés qu'ils abritent restent peu étudiés alors qu'ils sont soumis fortement à de nouvelles contraintes environnementales liées aux changements climatiques (Parker et al., 2008 ; Reid et al., 2019 ; Cantonati et al., 2020).

### 1. L'assemblage des communautés en fonction des filtres biotiques et abiotiques

Un habitat peut se définir par un ensemble de facteurs biotiques et abiotiques. Les espèces qui y sont observées sont celles capables de survivre et de se reproduire au sein de ces conditions. Toutefois, le changement climatique est susceptible de modifier les caractéristiques biotiques et abiotiques des habitats, perturbant ainsi l'équilibre des communautés (Komatsu et al., 2019 ; Harrison, 2020).

## a. Règles d'assemblage des communautés

### i. Les communautés végétales de milieux aquatiques

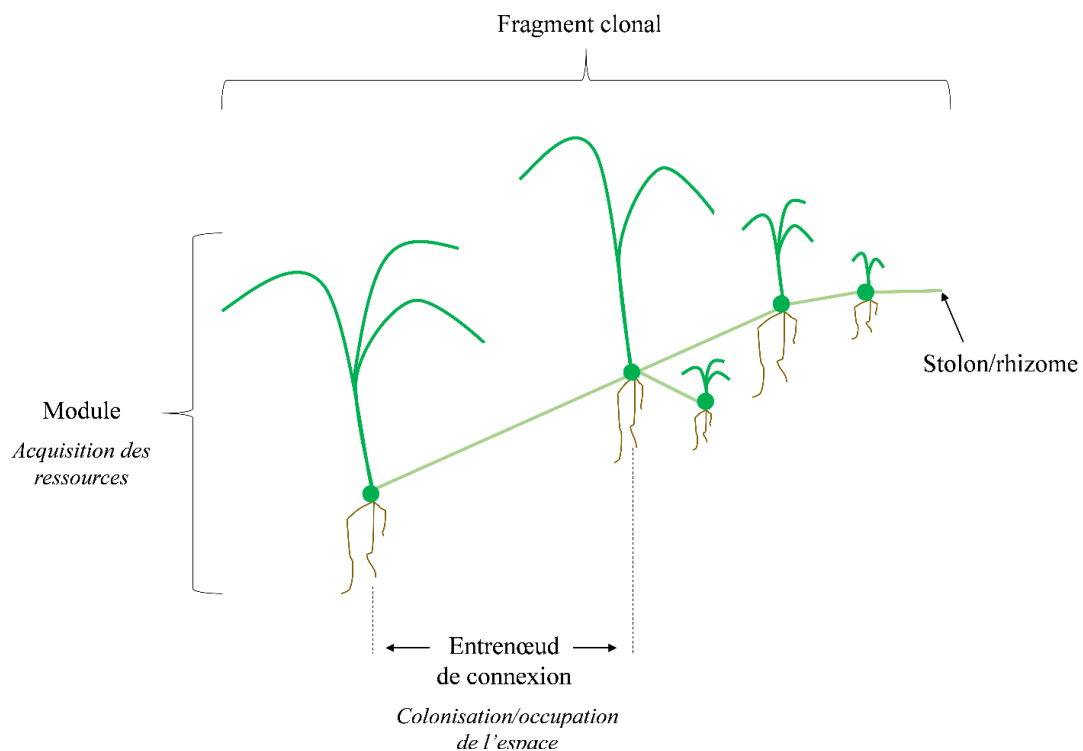
La végétation des zones aquatiques temporaires ou permanentes est essentiellement dominée par des macrophytes. Ces dernières sont définies comme des « organismes aquatiques photosynthétiques, assez grands pour être observés à l'œil nu, qui poussent en permanence ou périodiquement sous la surface de l'eau, pouvant flotter, ou se développant au moins en partie au-dessus de la surface de l'eau » (Chambers et al., 2008). Elles sont soit totalement immergées (strictement aquatiques : **hydrophytes**) ou partiellement immergées (**hélophytes**) (Cronk & Fennessy, 2001), et interagissent avec une multitude d'organismes, des microorganismes aux vertébrés, en leur procurant des habitats et des nutriments (Sand-jensen, 1998 ; Engelhardt & Ritchie, 2001 ; Wood et al., 2017).

Parmi les plantes Eudicotylédones et Monocotylédones, respectivement 7.5% et 11% d'entre elles sont aquatiques (Les & Schneider, 1995). Bien qu'elles soient réparties mondialement, de nombreuses espèces ont une aire de distribution très restreinte avec un fort taux d'endémisme (Murphy et al., 2019), ce qui les rend particulièrement sensibles aux extinctions. Aussi, près de 1% des espèces de macrophytes sont classées comme à risque par l'IUCN (Murphy et al., 2019), étant donné le fort impact des changements globaux sur la physiologie, les aires de répartitions ou encore le métabolisme des communautés de macrophytes (Lloréns & Lucas, 2008).

Même si la plupart des espèces de macrophytes produisent des graines, leur reproduction par voie sexuée est moins fréquente que chez les espèces végétales terrestres (Grace, 1993) car la mosaïque de micro-conditions aquatiques réduit grandement les succès de pollinisation, de maturation de graines ou d'établissement des juvéniles (Li, 2014). La majorité d'entre elles sont cependant capables de se multiplier de façon clonale *i.e.* par multiplication végétative. La clonalité se définit comme « la capacité à se propager et à produire des descendants par voie végétative » à partir d'une seule graine (Bell, 1984). Cette croissance se construit par organisation modulaire, c'est-à-dire par une suite de sous-unités multicellulaires génétiquement identiques, appelées **modules** (Harper, 1977). L'ensemble des modules connectés constitue un **fragment clonal** (Figure 2). Ces modules possèdent leur propre système racinaire et aérien, et peuvent donc survivre en cas de séparation du reste du fragment clonal et

se multiplier à leur tour par voie végétative (Herben et al., 1994 ; Dong et al., 2010). Aussi, plusieurs fragments clonaux peuvent avoir la même identité génétique *i.e.* constituer le genet (ou **clone**). Par conséquent, l'identification *in situ* d'un clone et de l'ensemble des modules qui le compose reste difficile, à moins de trouver des modules physiquement connectés entre eux. Bien souvent, ces stratégies de croissance clonale sont rencontrées au sein de systèmes pauvres en nutriments, humides, peu lumineux ou sous de faibles températures (van Groenendael et al., 1996 ; Klimeš et al., 1997 ; Ye et al., 2014).

La croissance clonale est rendue possible par diverses structures et organes. Dans le présent manuscrit, les macrophytes étudiés ne réalisent que de la croissance clonale en réseau, qui s'opère *via* des organes d'origine caulinaire. Ces derniers correspondent à des tiges modifiées, à développement horizontal (plagiotope) souterrain (**rhizomes**) ou aérien (**stolons**). Elles assurent alors la connexion entre les modules. Ces connexions sont constituées d'une succession d'**entrenœuds** et définissent la distance de dispersion clonale (de Kroon & Hutchings, 1995) (Figure 2).



**Figure 2.** Croissance clonale en réseau, avec des modules reliés entre eux par des entrenœuds de connexion.



## ii. Des processus stochastiques vs. déterministes dans l'assemblage des communautés

Les processus d'assemblage des espèces au sein d'une communauté occasionnent des débats depuis des décennies. Deux principales théories s'opposent, à savoir que la structure des communautés végétales observée à un instant  $t$  serait la résultante de processus soit stochastiques, soit déterministes (Lortie et al., 2004 ; Kembel, 2009 ; Vergnon et al., 2009). Dans le cas de processus déterministes, les règles d'assemblage font référence à tout processus écologique sélectionnant certaines espèces capables de survivre dans un habitat local donné, à partir d'un pool régional d'espèces (Keddy, 1992 ; Chase, 2003), et s'opposent ainsi à une organisation aléatoire des espèces au sein d'une communauté (Chave, 2004 ; Alonso et al., 2006 ; Chase, 2007 ; Hubbell, 2011). Trois processus sont alors communément considérés. Ils opèrent successivement à des échelles spatio-temporelles différentes (Götzenberger et al., 2012) : (1) la dispersion, (2) les **filtres abiotiques** (physico-chimiques) et (3) les **filtres biotiques** (résultant des interactions entre individus). Ainsi, sont sélectionnées dans un premier temps les espèces capables de disperser vers l'habitat considéré, puis entrent en jeu les filtres abiotiques et biotiques sur une échelle spatiale plus fine (Figure 3). Les individus présentant des phénotypes non adéquats et ne leur permettant pas de se maintenir dans les conditions biotiques et abiotiques de l'habitat sont éliminés.

## iii. Filtres abiotiques

Les individus issus des propagules subissent tout d'abord les filtres abiotiques qui influencent leur recrutement (capacité à s'établir) et leur taux de croissance (capacité à se maintenir). En effet, des conditions abiotiques non idéales pour la plante peuvent entraîner un ralentissement de croissance, des dommages physiques ou physiologiques permanents ou temporaires, voire une mortalité si ces conditions dépassent les limites de tolérances de l'espèce (Mosa et al., 2017). Ainsi, ne subsistent que les espèces physiologiquement capables de se maintenir durablement au sein de toutes les conditions physico-chimiques du milieu. L'ensemble des conditions biophysiques permettant à un organisme d'exister localement est alors défini comme la « niche fondamentale » de l'espèce (Hutchinson, 1957 ; Austin, 1999 ; Kearney & Porter, 2004).

Les filtres abiotiques incluent plusieurs types de contraintes physico-chimiques, qui diffèrent en termes de durée et de récurrence, et qui peuvent éliminer les espèces non adaptées : des contraintes chroniques (stress), ponctuelles et prévisibles (saisonnalité), ou ponctuelles et imprévisibles (perturbation) (Grime, 1979 ; Keddy, 1992 ; Chapin et al., 1993 ; Lavorel & Garnier, 2002 ; Ackerly, 2004). Par exemple, les fluctuations de précipitation, de température, de nutriment disponible ou de salinité peuvent intervenir dans le cadre d'un stress, d'une perturbation ou d'un changement de saison. Pourtant, certaines espèces ont développé des stratégies de résistance pour minimiser l'impact négatif des contraintes environnementales : des stratégies de tolérance ou d'évitement, qui confèrent aux individus un meilleur taux de survie (Schulze et al., 2005 ; Pujalon et al., 2011 ; Fitter & Hay, 2012).

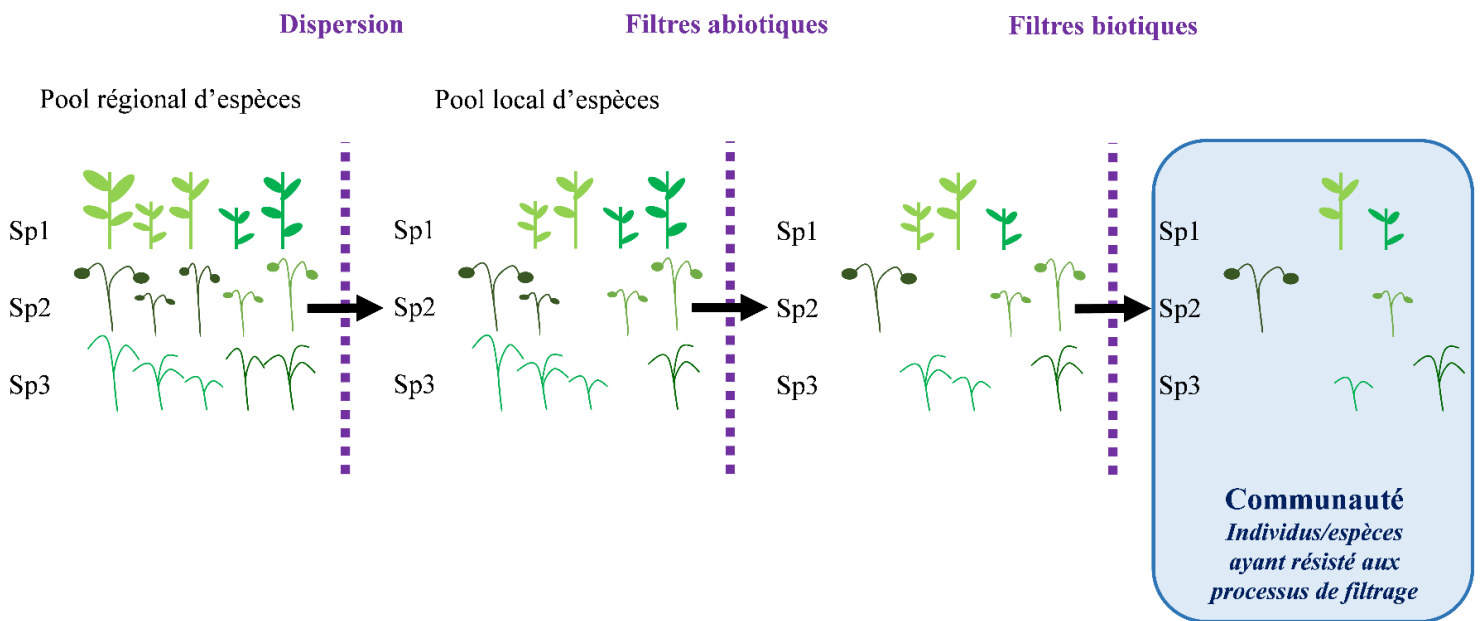
Cette thèse s'appuie en particulier sur la notion de **stress**, décrit comme « une contrainte externe limitant les taux d'acquisition de ressources, de croissance ou de reproduction des organismes » (Grime, 1989), ou comme « des conditions extraordinairement défavorables » (Larcher, 2003) qui provoquent à terme un « changement aberrant dans les processus physiologiques de l'organisme entraînant finalement une blessure » (Nilsen & Orcutt, 1996). A titre d'exemple, seules des espèces capables de survivre sous une faible luminosité sont sélectionnées dans les sous-bois forestiers (Niinemets, 2010). Au sein de systèmes aquatiques, l'intensité lumineuse, la température ainsi que les apports en carbone inorganique sont d'importants facteurs limitants qui peuvent être à l'origine de stress pour les plantes. En effet, ils peuvent affecter la germination des graines, le taux de croissance et la mise en dormance, ou encore les processus physiologiques en jeu dans la photosynthèse (Lacoul & Freedman, 2006 ; Li, 2014). Les caractéristiques chimiques (alcalinité, pH, substances dissoutes, conductivité) et physiques de l'eau (température, profondeur, quantité et qualité de la luminosité, vitesse des courants, substrat) peuvent être très variables, multipliant les possibilités de conditions stressantes pour les macrophytes mais pouvant parallèlement offrir une multitude de conditions physico-chimiques viables.

#### iv. Filtres biotiques

Faisant suite aux filtres abiotiques, les filtres biotiques opèrent à une échelle de quelques centimètres. Ils désignent les interactions « plante-plante » au sein de la communauté végétale. A l'issue de l'action du filtre biotique, la niche fondamentale d'une espèce se restreint finalement à une niche dite « réalisée », correspondant à l'ensemble des conditions biotiques et

abiotiques qui conviennent à la survie des individus de cette espèce (Hutchinson, 1957 ; Austin, 1999 ; Kearney & Porter, 2004).

Dans le cas particulier des végétaux qui sont sessiles, les individus expérimentent en permanence des interactions avec leur voisinage végétal immédiat, composé d'individus appartenant à la même espèce (interactions intra-spécifiques) ou non (interactions inter-spécifiques). Ces interactions plante-plante peuvent avoir deux effets opposés. Les interactions négatives, *i.e.* la compétition, réduisent la croissance, la survie et/ou la reproduction d'un moins l'un des deux individus (Grime, 1973). Elles résultent de la concurrence entre individus pour une même ressource limitée (*e.g.* eau, lumière, espace, nutriments - Naeem et al., 1999). Inversement les interactions positives, *i.e.* la facilitation, procurent des bénéfices aux individus quand une espèce favorise la croissance et le développement d'une autre espèce (Callaway, 1995). Elles améliorent l'établissement, la croissance et la survie des individus grâce au partage des quelques ressources disponibles, à l'amélioration des conditions abiotiques à très fine échelle (microclimat, propriétés physiques et chimiques du sol) ou *via* les effets indirects sur l'herbivorie (Callaghan & Emanuelsson, 1985 ; Bertness & Callaway, 1994 ; Brooker et al., 2008 ; Maestre et al., 2009 ; Bonanomi et al., 2011). Ces interactions facilitatrices ont été mises en évidence au sein de nombreux environnements contrains, tels que les déserts (Yeaton, 1978), les montagnes méditerranéennes, les écosystèmes alpins (Callaway et al., 2002), les zones humides et salines (Bertness & Callaway, 1994 ; Bertness & Ewanchuk, 2002), ou encore les systèmes aquatiques (Gopal & Goel, 1993 ; Souza et al., 2021). Facilitation et compétition peuvent agir simultanément au sein d'une communauté, créant ainsi un réseau complexe d'interactions biotiques (Walker, 1997).



**Figure 3.** Succession des processus de filtrage depuis un pool régional d'espèces. Schéma adapté depuis Violle et al. (2012). 'sp' espèce.

#### v. La balance entre compétition et facilitation dépend du niveau de stress de l'habitat

Les filtres biotiques et abiotiques ne peuvent pas être considérés comme des phénomènes distincts du fait de leur modulation réciproque. Par exemple, [Le Bagousse-Pinguet et al. \(2015\)](#) décrivent que tout changement environnemental peut modifier, altérer voire même inhiber des interactions biotiques entre espèces végétales, affectant la diversité et l'abondance des espèces au sein des communautés. En effet, plusieurs études ont montré que la balance entre facilitation et compétition dépend fortement des conditions d'habitats notamment de l'intensité du stress ([Choler et al., 2001](#) ; [Callaway et al., 2002](#) ; [Maestre & Cortina, 2004](#), en systèmes aquatiques : [Martin & Coetzee, 2014](#) ; [Shields & Moore, 2016](#) ; [Souza et al., 2021](#)). « The Stress Gradient Hypothesis » (SGH) prévoit d'ailleurs que l'importance relative de la facilitation par rapport à la compétition augmenterait le long d'un gradient de stress croissant et de productivité décroissante ([Bertness & Callaway, 1994](#) ; [Callaway, 2007](#) ; [Brooker et al., 2008](#) ; [He et al., 2014](#) ; [Shields & Moore, 2016](#)). Les interactions facilitatrices joueraient ainsi un important rôle dans des environnements contraints, en réduisant le stress environnemental au sein d'un micro-site, augmentant ainsi la niche réalisée d'une espèce, et lui permettant d'occuper un site qu'elle n'aurait normalement pas atteint ([Bruno et al., 2003](#) ; [Callaway, 2007](#)).

L'hypothèse du SGH a été souvent étudiée au sein d'habitats subalpins et alpins. [Callaway et al. \(2002\)](#) ont montré que la biomasse, la croissance et la reproduction d'espèces dans les étages alpins (avec de fortes contraintes abiotiques : faibles températures, vents forts et sols instables) diminuaient quand les individus étaient isolés de tous voisins, témoignant de l'importance de la facilitation à l'extrémité du gradient de stress *via* une légère augmentation de la température et la protection contre le vent ([Callaway et al., 2002](#)). Au contraire, la compétition dominait au sein des étages subalpins qui sont abiotiquement moins contraints.

Concernant les milieux aquatiques, les compétitions interspécifiques impliquent en grande partie l'acquisition de la lumière, du carbone inorganique et des nutriments. L'hypothèse du SGH a été notamment validée en réponse à un stress nutritif (excès), correspondant à une eutrophisation du milieu, qui mène généralement à un bloom de phytoplancton et donc un blocage de la pénétration lumineuse. Dans ce cas, une augmentation de l'intensité des interactions facilitatrices a été relevée, *via* le prélèvement des nutriments dissous dans l'eau par les macrophytes, diminuant ainsi la quantité de phytoplancton et augmentant la pénétration de la lumière dans le système, maintenant alors une haute biodiversité ([Scheffer, 2004](#) ; [Le Bagousse-Pinguet et al., 2012](#)). De plus, il a été montré en système lotique, que l'organisation spatiale des macrophytes en patchs d'individus soutient la coexistence des espèces en créant des interactions facilitatrices ([Cornacchia et al., 2018](#)). En particulier, la présence de macrophytes permet de diminuer localement le débit de l'eau au sein de leur patchs et favorise le dépôt de sédiments ([Sand-Jensen & Mebus, 1996](#) ; [Sand-jensen, 1998](#) ; [Wharton et al., 2006](#)), la pénétration de la lumière à travers la diminution de la concentration des particules en suspension ([Horppila & Nurminen, 2003](#)) et la disponibilité des nutriments ([Brock et al., 1985](#) ; [Webster & Benfield, 1986](#)), créant ainsi une rétroaction positive sur leur propre croissance et survie. L'hypothèse du SGH a été également validée suite à des épisodes d'inondations chez des espèces de marais, grâce à des espèces facilitantes qui réduisent l'anoxie du sol en libérant de l'oxygène dans les sols des habitats inondés ([Luo et al., 2010](#) ; [Li et al., 2018](#)).

Toutefois, dans certaines situations, les interactions compétitives domineraient également aux deux extrémités des gradients de productivité d'un système ([Maestre & Cortina, 2004](#)). En effet, au sein d'habitats extrêmement contraints, les potentielles espèces facilitatrices ne peuvent augmenter les ressources pour le voisinage au-delà de leurs propres besoins. Des exemples ont été donnés dans les systèmes arides et semi-arides ([Maestre & Cortina, 2004](#) ; [Maestre et al., 2005, 2006](#) ; [Butterfield et al., 2016](#)) où la compétition domine pour l'eau qui est

une ressource très rare. De la même façon dans les systèmes aquatiques, la compétition a été mise en évidence en réponse à un stress hydrique (Bu et al., 2013), ou à un phénomène d'eutrophisation [où la compétition pour les nutriments laisse place à la compétition pour la lumière, amenant à une exclusion compétitive de certains individus (Suding et al., 2005 ; Sand-Jensen et al., 2008)].

Ce réseau complexe d'interactions joue un rôle important dans les réponses aux changements climatiques (Brooker, 2006 ; Suttle et al., 2007 ; van der Putten et al., 2010 ; HilleRisLambers et al., 2013 ; Michalet et al., 2014), par des mécanismes maintenant la biodiversité (Bascompte et al., 2006), ou agissant sur les aires de répartition et l'abondance des espèces (Tylianakis et al., 2008 ; Hellmann et al., 2012). Par ailleurs, les interactions plantes-plantes deviennent imprévisibles avec les changements climatiques et les conséquences associées à ces changements, aussi bien dans des systèmes terrestres (réponse à la sécheresse : Ploughe et al., 2019) qu'aquatiques (réponse à l'élévation des températures et du taux de CO<sub>2</sub> : Souza et al., 2021). Dans des régions où la croissance des individus est limitée par les faibles températures, un climat plus chaud dans les limites de tolérance thermique pourrait diminuer le stress thermique « froid », et la balance entre compétition et facilitation évoluerait vers une augmentation de l'intensité de la compétition (Brooker, 2006), comme observé par des relevés le long d'un gradient climatique (Callaway et al., 2002 ; Kikvidze et al., 2005 ; Olsen et al., 2016) ou par des expériences de réchauffement artificiel (Dunnett & Grime, 1999 ; Klanderud, 2005 ; Olsen & Klanderud, 2014). Cependant, si l'élévation des températures dépasse les limites hautes de tolérance thermique des espèces, alors un stress thermique « chaud » peut se mettre en place avec une augmentation de l'intensité des interactions facilitatrices, comme montré au sein des systèmes alpins. Les espèces facilitatrices peuvent alors améliorer la dispersion et l'établissement d'autres espèces en tamponnant les élévations de température (Anthelme et al., 2014 ; Cavieres et al., 2014).

## b. Structuration spatiale des communautés

Les communautés végétales sont organisées selon des patrons de co-occurrences spécifiques non aléatoires (Gotelli & McCabe, 2002). En d'autres termes, les individus montrent souvent un arrangement spatial horizontal non homogène entre les espèces ou au sein d'une même

espèce, avec des patrons de ségrégation ou d'agrégation. Ces patrons spatiaux peuvent être étudiés à plusieurs échelles : celle de la communauté, ou encore de la population.

Ces patrons hétérogènes peuvent être aléatoires ou être la conséquence de plusieurs facteurs déterministes (Herben & Hara, 2003). Tout d'abord le type de dispersion, *i.e.* par voie clonale ou par reproduction sexuée *via* les graines, peuvent déterminer les aires potentielles de recrutement des plantules et donc expliquer les répartitions horizontale et spatiale des espèces (Nathan & Muller-Landau, 2000). Ensuite, les variations abiotiques induites par une hétérogénéité de l'habitat à très fine échelle (propriétés du sol, microclimat, topographie...) peuvent également affecter les répartitions spatiales des individus. Quelques études ont été menées pour lier les hétérogénéités d'habitat et les patrons spatiaux des macrophytes par exemple (Schoelynck et al., 2012 ; Cornacchia et al., 2018 dans les systèmes riverains, Joye et al., 2006 ; Jeffries, 2008 ; Manzo et al., 2020 dans des mares). Cette hétérogénéité des conditions abiotiques peut être inhérente à l'habitat, et être notamment expliquée par des événements historiques (perturbations). Elle peut aussi être induite par la végétation elle-même, qui peut améliorer les micro-conditions locales par phénomène de facilitation (Herben & Hara, 2003), mais qui peut à l'inverse diminuer localement la qualité de l'habitat par le prélèvement des ressources (lumière, nutriments et eau). Par exemple, dans des milieux fortement contraints et abiotiquement homogènes, tels que les systèmes arides (Rietkerk et al., 2002 ; Drezner, 2006) ou les tourbes sibériennes (Eppinga et al., 2008), les individus s'agrègent, diminuant ainsi les contraintes abiotiques locales et augmentant leurs chances de survie. Par conséquent, les interactions biotiques participent également à la structuration spatiale, qui peut alors les refléter. En effet, les agrégations spatiales entre individus mettent souvent en évidence de la facilitation, qui permet un meilleur établissement et maintien en améliorant les micro-conditions abiotiques (Choler et al., 2001 ; Kikvidze et al., 2005 ; Tirado & Pugnaire, 2005). A l'inverse, une ségrégation des individus résulte généralement de l'effet d'un groupe d'espèces compétitrices qui excluent spatialement des espèces moins compétitives (Seabloom et al., 2005 ; Pottier et al., 2007 ; Schöb et al., 2008). Ces relations entre patrons spatiaux et interactions plante-plante ont été souvent étudiées dans des milieux alpins (Kikvidze & Nakhutsrishvili, 1998 ; Choler et al., 2001) ou désertiques (Phillips & MacMahon, 1981 ; Anderson & Bliss, 1998), mais rarement au sein de zones aquatiques (mais voir Boschilia et al., 2008 ; Cornacchia et al., 2018). Cependant, ces associations binaires « agrégation/facilitation » et « ségrégation/compétition » s'avèrent parfois trop simplistes et dénotent une réalité plus complexe qui dépend notamment de l'échelle étudiée (Blanchet et al., 2020). Par exemple, la résolution d'échantillonnage est à

prendre en compte puisque les interactions négatives seraient plus difficilement discernables sur de larges échelles, à l'inverse des interactions positives (Araújo & Rozenfeld, 2014 ; Thuiller et al., 2015 ; Bar-Massada et al., 2018). Enfin, Herben et Hara (2003) précisent que les facteurs biotiques et abiotiques peuvent conjointement expliquer les répartitions spatiales des individus, et distinguer leurs effets respectifs s'avère nécessaire pour une meilleure compréhension des formations de patrons spatiaux.

Les patrons spatiaux ont en retour de fortes implications dans les interactions plantes-plantes qui dépendent des individus présents dans le voisinage de la plante cible (Bolker & Pacala, 1999 ; Uriarte et al., 2010 ; Detto & Muller-Landau, 2016 ; Wiegand et al., 2017). En effet, ils déterminent la probabilité pour un individu de rencontrer ou non un meilleur compétiteur, ou bien des individus facilitants, conditionnant alors son maintien ou son exclusion de la communauté.

### c. Vers une modification des filtres par les changements climatiques

#### i. Intensification et modification des filtres

Les changements environnementaux peuvent être à l'origine de modification des processus de filtrage biotiques et abiotiques, créant des bouleversements au sein de la structuration des communautés. Les changements climatiques par exemple, pourraient mener à des phénomènes de stress pour les communautés végétales (Franklin et al., 2016 ; Komatsu et al., 2019), en particulier l'élévation des températures (Chaudhry & Sidhu, 2022). Les modèles simulant l'évolution des températures prévoient une augmentation des températures moyennes globales de 1.1 à 6.4°C au 21<sup>ème</sup> siècle, par rapport aux températures enregistrées entre 1980-1999 (Bernstein et al., 2008). Dans des milieux froids notamment, les pics de chaleur estivale mais aussi hivernale entraînent la fonte de la neige, exposant la végétation au gel qui peut causer d'important dégâts et avoir des conséquences majeures sur la productivité et diversité des communautés végétales adaptées à des températures fraîches (Bokhorst et al., 2009).

Les filtres biotiques tels que les interactions plantes-plantes, sont également susceptibles d'être modifiés face aux changements climatiques (McCluney et al., 2012) étant donné leur sensibilité à la phénologie, physiologie, performance ou abondance relative des espèces (Parmesan, 2006 ; Stiling & Cornelissen, 2007 ; Suttle et al., 2007 ; Tylianakis et al., 2008),



mais également aux conditions environnementales (modification de la balance compétition/facilitation). Par exemple, des variations prononcées ou une diminution d'eau disponible dans des systèmes arides (McCluney et al., 2012), ou encore une élévation des températures et de la disponibilité en nutriments (Klanderud, 2005), affecteraient les directions ou intensités des interactions biotiques à échelle individuelle.

## ii. Cas particulier des systèmes d'eau douce

Les prévisions suggèrent une hausse des températures aériennes de 1.5°C à 5.8°C d'ici 2100 (Houghton et al., 2001), affectant directement les températures d'eau de surface des systèmes aquatiques. Les eaux surfaciques de lacs se sont déjà réchauffées de 0.3°C par décennies ces dernières années à l'échelle mondiale (O'Reilly et al., 2015). De plus, la durée annuelle des épisodes de réchauffement extrême de ces eaux de surface, qui est généralement plus élevée aux basses latitudes, devrait augmenter considérablement (Woolway et al., 2021). Selon Wrona et al. (2006), l'ampleur des conséquences écologiques des changements climatiques sur les écosystèmes d'eau douce dépend de la fréquence et de l'intensité de trois principaux facteurs environnementaux : la température, le régime de précipitations et les altérations de la chimie de l'eau telles que les concentrations en éléments nutritifs, l'oxygène dissous et les chargements de matières organiques particulières. Ces systèmes sont ainsi tristement devenus les habitats les plus vulnérables au changement climatique mondial à travers les variations de température aérienne et de précipitations, impactant *in fine* la température et la hauteur d'eau (Bates et al., 2008 ; Jin et al., 2009). Les menaces qui pèsent sur les écosystèmes d'eau douce seraient devenues plus intenses encore que celles auxquelles sont soumis les écosystèmes terrestres (Strayer & Dudgeon, 2010).

Les changements climatiques jouent un rôle prépondérant dans l'hydrologie des systèmes aquatiques d'eau douce puisqu'ils déterminent entre autre le niveau et le temps de résidence de l'eau qui fluctuent selon les taux de précipitation et la hausse des températures, perturbant en retour, la qualité et la biogéochimie des eaux (Waddington et al., 2015 ; Stefanidis et al., 2016) de même que les émissions de gaz (Maljanen et al., 2001 ; Clark et al., 2007 ; Lafleur, 2009 ; Kasak et al., 2016). Une baisse des niveaux d'eau peut menacer les connectivités entre les différents corps d'eau douce, souvent essentielles à leur bon fonctionnement et à la reproduction des espèces aquatiques (Kling et al., 2003). De même, les macrophytes qui co-occurrent *via* une distribution des différentes espèces le long de la colonne d'eau peuvent voir

leur niche écologique se chevaucher, impactant leur coexistence (Bates et al., 2008). Par ailleurs, une sécheresse des terres peut certes diminuer les intrants polluants dans les systèmes aquatiques mais peut aussi augmenter la concentration et la rétention de ces substances dans les corps d'eau devenus peu profonds (Kling et al., 2003). Des perturbations hydrologiques extrêmes telles que des exondations, devraient survenir plus fréquemment, menaçant grandement les espèces de macrophytes non résistantes à la dessiccation en été, et non résistantes au gel et aux épisodes venteux en hiver. A l'inverse, des épisodes pluvieux extrêmes devraient élever le niveau d'eau, ce qui diminue la pénétration de l'énergie lumineuse pourtant nécessaire à la croissance et la survie des macrophytes (Coops et al., 2003). Quant à la hausse des températures, elle peut conduire à de nombreuses conséquences sur les processus écosystémiques. L'élévation des températures peut amplifier les invasions biologiques et stimuler la croissance algale (Poff et al., 2002 ; Parker et al., 2008), qui mène souvent à une eutrophisation des milieux, et donc au déclin de la qualité de l'eau et une modification de la composition spécifique des communautés végétales (Watts et al., 2015).

Malheureusement, la capacité des systèmes aquatiques à s'adapter à ces variations environnementales reste limitée. Les changements environnementaux ont de fortes répercussions sur la biodiversité rencontrée dans les zones aquatiques d'eau douce, puisque les abondances et les aires de répartition diminuent considérablement chez de nombreuses espèces (Weltzin et al., 2000 ; Kosten et al., 2009 ; Strayer & Dudgeon, 2010 ; Dieleman et al., 2015 ; Lind et al., 2022). Les écosystèmes d'eau douce en zones froides sont particulièrement menacés par les changements climatiques, notamment les espèces aquatiques dont les populations sont peu abondantes et/ou ont une niche environnementale très restreinte (Wrona et al., 2006).

## 2. Des mécanismes de réponse aux filtres environnementaux basés sur les traits fonctionnels des individus

L'étude de la réponse des espèces à des facteurs environnementaux en fonction de leur identité taxonomique a laissé place depuis deux décennies à une nouvelle méthode plus pertinente : (i) d'une part car elle définit nouvellement les espèces par des caractéristiques physiques et physiologiques qui les rendent apte à survivre dans un environnement plutôt que par une simple appartenance à un taxon (Lavorel et al., 1997), (ii) et d'autre part car elle affine les observations jusqu'à l'échelle de l'individu, ouvrant un regard nouveau sur la variabilité des caractéristiques individuelles au sein d'une même espèce (Jung et al., 2010 ; Albert et al., 2011 ; Violle et al., 2012). L'approche fonctionnelle est apparue comme un tournant majeur dans le domaine de l'écologie des communautés, permettant l'étude des réponses ciblées à un facteur environnemental donné, et ce à plusieurs échelles possibles : individu, population, communauté ou même écosystème.

### a. Définition : le concept de trait fonctionnel

Un trait est défini comme toute caractéristique morphologique, physiologique ou phénologique mesurable à l'échelle d'un individu depuis la cellule jusqu'à l'organisme tout entier, sans référence à l'environnement ou à tout autre niveau d'organisation (Lavorel et al., 1997 ; Violle et al., 2007). Les traits permettent de comparer et de classer les espèces selon les valeurs. Un trait est considéré comme fonctionnel s'il impacte *in fine* la performance de l'individu (*i.e.* biomasse, taux de reproduction et survie) (Geber & Griffen, 2003 ; McGill et al., 2006). La surface des feuilles, la hauteur d'un individu, la longueur des racines, la biomasse d'un organe, la teneur en azote foliaire ou encore la concentration en molécules de défenses sont des exemples de traits fonctionnels au sein des espèces végétales. Les valeurs de traits sont évidemment liées au génotype, mais également à l'environnement. Aussi une gamme de valeurs de traits dans un type d'habitat est peut-être défavorable dans un autre (Grime & Pierce, 2012).

Les traits morphologiques sont les plus couramment utilisés dans la littérature et renseignent sur les stratégies mises en place par les individus pour répondre à des facteurs biotiques et/ou abiotiques. Chez les plantes clonales, deux types de traits sont mesurables : les traits verticaux (*i.e.* aériens et racinaires) et les traits horizontaux (*i.e.* clonaux). Les traits aériens (hauteur de la plante, Specific Leaf Area, Leaf Dry Matter Content) et racinaires

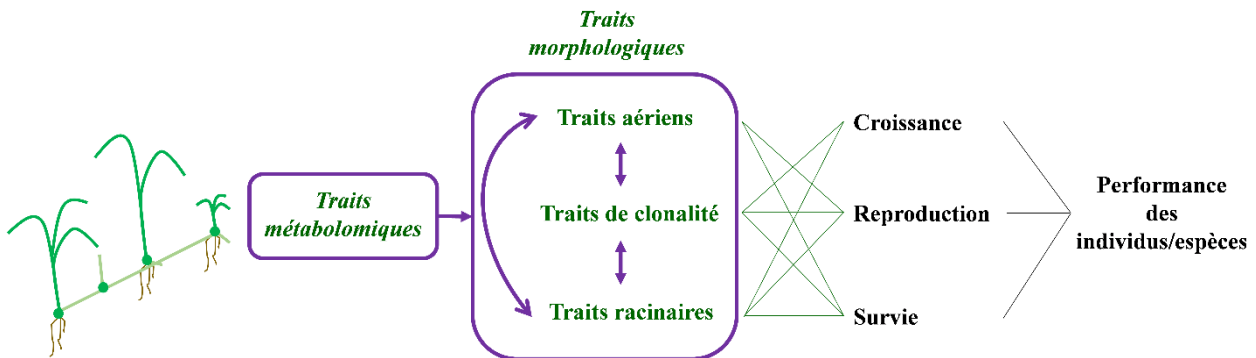
(longueur racines, masse spécifique des racines...) renseignent sur la compétitivité et la résistance des individus *via* l'acquisition et la conservation des ressources (nutriments, lumière, eau...). Les traits clonaux (longueur de l'entrenœud, masse spécifique de l'entrenœud, nombre de branches...) caractérisent l'architecture du fragment clonal et renseignent sur la colonisation de l'espace par croissance clonale et sur la mise en réserve (Suzuki & Stuefer, 1999 ; Lavorel & Garnier, 2002 ; Cornelissen et al., 2003). Du fait de l'organisation d'un fragment clonal en succession de modules, la réponse de ces plantes à leur environnement s'exprime à différents niveaux : à l'échelle du clone *via* l'exploration et l'occupation de l'espace (déterminées à travers la mesure des traits clonaux), et à l'échelle du module *via* l'acquisition des ressources (à travers les traits aériens et racinaires).

Si les traits morphologiques sont les plus couramment utilisés, les traits métabolomiques permettent quant à eux d'apporter des précisions dans les réponses des plantes aux modifications environnementales, cette fois-ci à une échelle physiologique. Ils permettent de qualifier et quantifier les molécules (*i.e.* les métabolites) synthétisées par les plantes leur conférant une certaine résistance/résilience face des agressions extérieures : herbivores, sécheresse, froid, carence en nutriments... (Croteau et al., 2000 ; Wahid & Ghazanfar, 2006 ; Groppa & Benavides, 2007 ; Wink, 2013). Le métabolome (ensemble des métabolites au sein d'un organisme) se place à l'interface entre la perception des signaux environnementaux et leur traduction au niveau des traits fonctionnels, jouant ainsi un rôle majeur dans les réponses aux contraintes environnementales. Les métabolites primaires (acides aminés, carbohydrates) sont essentiels à la physiologie de la plante et peu nombreux, tandis que les métabolites secondaires sont particulièrement divers (Croteau et al., 2000). Ces métabolites secondaires sont impliqués dans la protection contre les stress environnementaux et la compétition (Croteau et al., 2000 ; Wahid & Ghazanfar, 2006 ; Groppa & Benavides, 2007 ; Wink, 2013). La composition du métabolome peut être ajustée à court terme (sur une échelle horaire) suite à des changements abiotiques subits, voire à long terme pour s'adapter aux nouvelles conditions (Smirnoff, 1995).

Les traits ne sont pas indépendants les uns des autres. Ils sont connus pour co-varier ensemble au sein d'un individu, et de nombreuses corrélations entre traits ont été mises en évidence permettant de coordonner différentes fonctions pour maximiser la performance de l'individu avec un minimum d'investissement possible (Murren, 2002 ; De Kroon et al., 2005) (Figure 4). Ces corrélations inter-traits peuvent être positives ou négatives (compromis). Les compromis résultent souvent de la nécessité pour les individus d'investir à la fois dans la

résistance (mesurée par la longévité) et dans la performance (mesurée par la capacité photosynthétique) (Wright et al., 2004 ; Koehler et al., 2012 ; Molina-Montenegro et al., 2012 ; Reich, 2014 ; Díaz et al., 2016 ; Bucher et al., 2019). Des stratégies d'investissement dans certaines fonctions sont alors mises en place par les individus, au dépend d'autres fonctions. Ces co-variations peuvent s'appliquer au sein d'un même organe et sont particulièrement étudiées au sein des feuilles. Un exemple bien connu réside dans le compromis mis en place chez les plantes pour la construction de feuilles, soit denses et épaisses (corrélées à une longévité plus importante), soit d'une grande surface pour une bonne capacité photosynthétique (qui nécessite une forte concentration en azote foliaire pour le bon fonctionnement de la photosynthèse), pour limiter le coût de construction (Wright et al., 2004). Des inter-relations entre traits morphologiques et métabolomiques ont également été montrées. Par exemple, les populations adaptées à des climats alpins froids investissent dans la production de métabolites en réponse au stress thermique, à défaut d'investir dans une croissance rapide (Walker et al., 2019, 2022). Des compromis existent également entre les fractions de biomasses différemment allouées aux compartiments pour assurer au mieux la survie d'une espèce dans un environnement donné. Dans des systèmes aquatiques profonds, la fraction de biomasse allouée aux parties aériennes serait relativement plus importante que celle allouée aux parties racinaires chez des individus héliophytes, avec des tiges moins nombreuses mais plus hautes afin d'accélérer l'émergence pour optimiser le métabolisme (Vretare et al., 2001). Sous des conditions peu lumineuses, Chen et al. (2020) ont montré que certaines espèces de macrophytes trouvent des compromis entre une croissance en hauteur et un développement de la surface foliaire pour une meilleure capture de l'énergie lumineuse. De la même façon, des co-variations positives sont possibles entre traits appartenant à des organes différents. Par exemple, la quantité d'azote foliaire co-varie avec la quantité d'azote dans les tiges et racines (Kerckhoff et al., 2006 ; Freschet et al., 2010 ; Liu et al., 2010), de même que la SLA co-varie avec la longueur spécifique des racines (Withington et al., 2006 ; Liu et al., 2010).

Cependant, le sens et l'intensité des co-variations entre traits sont susceptibles de changer en fonction des conditions environnementales, notamment en relation avec le changement climatique (Wright et al., 2004, 2005). Par conséquent, une approche multi-traits prenant en compte ces relations inter-traits est souvent nécessaire pour évaluer l'ampleur des réponses face à des changements de conditions environnementales.



**Figure 4.** Effets des traits fonctionnels (métabolomiques et morphologiques), et de leurs co-variations, sur la performance des individus et donc des espèces. Schéma adapté de Violle et al. (2007).

## b. La variabilité intraspécifique des traits

### i. Importance de la variabilité des traits pour la résistance aux filtres

Historiquement, la réponse des traits face à des conditions environnementales changeantes a été abordée à l'échelle interspécifique, c'est-à-dire en comparant les réponses entre espèces et en portant une plus grande attention à leurs variations interspécifiques. Plusieurs auteurs affirment que la coexistence de plusieurs espèces au sein d'un même habitat est possible si les traits diffèrent plus entre espèces qu'au sein de celles-ci (McGill et al., 2006). Les travaux de comparaisons inter-espèces se sont alors multipliés, privilégiant des métriques comme les moyennes de traits à l'échelle des communautés (trait agrégés) (Garnier et al., 2004, 2007 ; Louault et al., 2005 ; Choler, 2005 ; Quétier et al., 2007).

Pourtant, chaque espèce présente une variabilité de valeurs de traits qui lui est propre, appelée variabilité intraspécifique des traits (ITV). Cette dernière peut être considérée à plusieurs niveaux : des différences de valeurs moyennes de traits entre des populations vivant dans des conditions environnementales différentes, des différences entre individus au sein d'une même population, ou encore des différences entre feuilles, tiges et racines au sein d'un

même individu (Shiple, 1995). Cette variabilité est communément issue de deux mécanismes complémentaires en réponse à des variations d'habitats : l'expression de la diversité génétique résultant de l'adaptation locale et de la dérive génétique, et la plasticité phénotypique des différents génotypes. La diversité génétique au sein d'une espèce résulte en une multiplicité de génotypes individuels qui aboutissent à des valeurs moyennes de traits différentes, condition nécessaire pour s'adapter aux changements environnementaux (Crozier, 1997 ; Barrett & Schluter, 2008). La plasticité phénotypique quant à elle se définit comme la capacité d'un seul génotype à produire plusieurs phénotypes sous des conditions environnementales différentes (DeWitt et al., 1998 ; Albert et al., 2010b). Cette dernière permet à un organisme de répondre rapidement à une contrainte environnementale, en permettant l'ajustement de ses valeurs de traits pour optimiser sa performance à court terme (Sultan, 2000), au contraire de l'adaptation locale qui est un processus plus lent car il nécessite l'apparition d'une mutation aléatoire conduisant éventuellement à l'expression d'un phénotype adapté aux conditions.

De nombreux travaux ont prouvé l'importance de la variabilité intraspécifique (Nicotra et al., 2010), puisqu'elle participerait largement au maintien de la biodiversité en permettant aux espèces de mieux résister aux filtres environnementaux (Jung et al., 2010 ; Albert et al., 2011 ; Violle et al., 2012). Aussi, une espèce plus diverse aura plus de chance de se maintenir face à des changements environnementaux importants. En effet, plusieurs publications ont démontré l'importance du rôle de l'ITV dans les mécanismes d'assemblage et de réponse, et ce dans plusieurs milieux (Gross et al., 2009 ; Jung et al., 2010 ; Siefert, 2012 ; Fu et al., 2013 ; Fu, 2020). Au sein de prairies, Jung et al. (2010) ont montré que la prise en compte de l'ITV dans les modèles permettait d'améliorer la détection des mécanismes d'assemblage de communautés non aléatoires. Plus particulièrement, l'ITV compterait pour 19 à 49% et pour 8 à 25% de la part de variabilité totale de la hauteur des individus et du LDMC respectivement, chez 16 espèces terrestres (Albert et al., 2010b). Messier et al. (2010) ont prouvé que deux traits foliaires (LDMC et SLA) variaient autant au sein des espèces, qu'entre espèces d'arbres dans les forêts tropicales. De la même façon, les espèces de macrophytes ont montré d'important taux d'ITV le long de gradients environnementaux impliquant la hauteur d'eau, la luminosité et la disponibilité en nutriments (Ni, 2001 ; Yang et al., 2004 ; Li et al., 2007 ; Fu et al., 2012, 2013).

Ces variations permettent aux espèces de répondre à des processus biologiques opérant à différentes échelles spatio-temporelles. La variation temporelle des traits a été montrée, par exemple, dans le cadre des stratégies saisonnières des plantes leur permettant d'ajuster en permanence les performances des traits pour faire face aux stress externes. Un ajustement des caractéristiques physiologiques (capacité photosynthétique, p. ex. [Grassi et al., 2005](#) ; [Muraoka et al., 2010](#)) ou morphologiques (épaisseur des feuilles, p. ex. [Fullana-Pericas et al., 2017](#)) est fréquemment signalé chez les espèces végétales. Les échelles spatiales, en raison de la diversité des conditions environnementales qu'elles englobent et des divers processus de filtrage associés, façonnent également les variations globales des traits. En effet, il a été constaté que les traits aériens ([Reich & Oleksyn, 2004](#)) et racinaires ([Zadworny et al., 2016](#)) varient dans l'espace par rapport à la température ([Reich & Oleksyn, 2004](#)). Ainsi, les variations intraspécifiques de traits sont de toute importance dans la mise en place de stratégies de réponse des espèces face à l'intensification des filtres par le changement climatique.

#### ii. La plasticité chez les plantes clonales

La plasticité est un phénomène bien connu chez les plantes clonales. Tous les modules d'un fragment clonal sont dotés du même génotype (sauf cas de mutations somatiques), mais celui-ci peut s'exprimer différemment en fonction du module et de l'environnement local dans lequel il vit ([De Kroon et al., 2005](#)). Aussi, un module peut acquérir des valeurs de traits fonctionnels différentes de ses modules frères. Cette plasticité a été montrée au niveau de plusieurs traits fonctionnels tels que les traits aériens (SLA, contenu en chlorophylle, longueur de pétiole, hauteur aérienne : [Slade & Hutchings, 1987a](#) ; [van Kleunen et al., 2000, 2007](#) ; [Wang et al., 2022](#)), racinaires ([Keser et al., 2014](#) ; [Li et al., 2021](#)) et clonaux (masse spécifique et longueur des entrenœuds : [Slade & Hutchings, 1987b](#) ; [van Kleunen et al., 2000, 2002, 2007](#) ; [Louâpre et al., 2012](#) ; [Wang et al., 2022](#)). Notamment, le « foraging » est l'une des réponses plastiques observée à l'échelle du clone. Elle correspond à la capacité des clones à percevoir l'hétérogénéité de leur environnement, à modifier la morphologie des modules nouvellement produits en conséquence, et à les positionner au sein de micro-sites favorables à leur croissance et leur survie ([Hutchings & de Kroon, 1994](#)). Grâce à cette réponse plastique, le clone explore efficacement son habitat, lui permettant d'augmenter l'exploitation et l'acquisition des ressources ([de Kroon & Hutchings, 1995](#)). Par exemple, en cas de stress lié à la disponibilité en nutriments, les fragments clonaux sont capables de fuir cet environnement défavorable en allongeant les entrenœuds et en réduisant les ramifications, traduisant une stratégie d'évitement.



En effet, des entrenœuds plus courts et une forte ramification du réseau clonal permettent l'installation d'un grand nombre de modules au sein de micro-sites riches en nutriments, et inversement au sein de micro-sites pauvres en nutriments (Slade & Hutchings, 1987b ; López et al., 1994). Le « foraging » peut aussi s'exprimer dans la direction verticale avec un allongement des pétioles et des feuilles plus larges en réponse à un manque de lumière (Wijesinghe & Hutchings, 1996).

### c. Ce que nous apprend l'étude de la distribution des valeurs de traits sur les mécanismes d'assemblage

La réponse aux différents filtres et la coexistence de plusieurs espèces au sein d'un habitat est rendue possible par l'ajustement de valeurs de traits fonctionnels (moyenne et variabilité) entre espèces et au sein des espèces, en fonction des paramètres environnementaux (Petchey & Gaston, 2006). Ces traits sont alors qualifiés de « traits de réponse » (Lavorel & Garnier, 2002 ; Hooper et al., 2006). Il a été montré par exemple que les hydrophytes ont la capacité de modifier leurs valeurs de traits foliaires, de croissance ou de biomasse pour faire face à des variations environnementales, comme des modifications de hauteur d'eau et/ou de luminosité (Strydom et al., 2018 ; Fu et al., 2018 ; Liu et al., 2020).

Pour quantifier au mieux l'intensité et la direction des effets des filtres, il a été proposé d'étudier la distribution des valeurs de ces traits (Freschet et al., 2011 ; Violle et al., 2012). Premièrement, la métrique la plus utilisée est la valeur moyenne d'un trait en réponse à des conditions environnementales données. Deuxièmement, la réponse à un filtre peut être étudiée à travers la variance d'un trait, en comparant la variance observée à celle attendue sous un modèle neutre, c'est-à-dire sous une distribution aléatoire sans l'action d'un quelconque filtre (Connor & Simberloff, 1979). Pour une gamme donnée de valeurs de traits, si leur variabilité est plus grande ou petite qu'attendue sous modèle nul, alors la distribution des valeurs de traits est dite respectivement divergente ou convergente (Weiher & Keddy, 1995 ; Weiher et al., 1999 ; McGill et al., 2006). Dans les deux cas, ces patrons de dispersion de traits ne supportent pas la théorie neutre qui assure que l'assemblage des communautés suit un processus de sélection aléatoire depuis un pool régional d'espèce (Hubbell, 2011). Dernièrement, il est possible d'aller plus loin encore avec l'utilisation de deux métriques : la « skewness » et la « kurtosis » d'une gamme de valeurs. La « skewness » et la « kurtosis » (Enquist et al., 2015 ; Gross et al., 2017) sont des compléments aux métriques très souvent utilisées (moyenne et variance), et reflètent

respectivement l'asymétrie et l'uniformité de la distribution des traits. Les distributions asymétriques des traits, qui indiquent que les distributions de l'abondance des traits sont fortement décalées vers la gauche ou vers la droite, sont le résultat d'une compétition asymétrique (Schamp et al., 2007 ; Gross et al., 2009) ou d'un changement environnemental rapide (Enquist et al., 2015 ; Le Bagousse-Pinguet et al., 2017). Des valeurs élevées de kurtosis indiquent des distributions étroites, c'est-à-dire une faible diversité de traits, et reflètent un fort filtrage environnemental (Le Bagousse-Pinguet et al., 2017), tandis que des valeurs faibles de kurtosis reflètent des distributions plus étalées, donc une grande diversité de traits par exemple dans le cas de la « limiting similarity » (MacArthur & Levins, 1967).

#### d. Mécanismes et patrons de réponses aux filtres abiotiques

##### i. Echelle individuelle

A l'échelle individuelle, un déplacement des valeurs moyennes de traits est observé en réponse à une augmentation de la température, aussi bien sur des traits morphologiques que métabolomiques.

Une augmentation de température dans la gamme de tolérance des espèces peut induire des changements morphologiques et d'allocation de biomasse, stimulant la photosynthèse et la croissance (Barko et al., 1986 ; Rooney & Kalff, 2000 ; Pilon & Santamaría, 2002 ; Feuchtmayr et al., 2009 ; Riis et al., 2012 ; Silveira & Thiébaud, 2017). De même, la plasticité de traits morphologiques et physiologiques permettent aux individus de produire une biomasse similaire (et donc de maintenir leur performance) le long d'un gradient croissant de température et/ou de sécheresse, rendant les individus tolérants à ces facteurs (Pilon & Santamaría, 2002 ; Nicotra et al., 2010). Par ailleurs, au sein de systèmes aquatiques, un important réchauffement, de fortes précipitations ou au contraire de fortes sécheresses peuvent induire une intense fluctuation du niveau d'eau (Woolway et al., 2021). Des espèces de macrophytes ont montré en conséquence une plasticité foliaire en réponse aux variations d'intensité lumineuse induites par les variations de profondeurs de l'eau (stratégie d'acquisition/conservation de ressources dans des eaux profondes ou non, Gao et al., 2021). De plus, face à des phénomènes d'exondations extrêmes, certaines espèces de macrophytes hydrophytes ont développé des phénotypes adaptés aux assecs par plasticité, avec une plus forte valeur moyenne de LDMC, permettant un meilleur port

terrestre et une surface foliaire moyenne réduite avec une cuticule plus épaisse afin de réduire les pertes en eau (De Wilde et al., 2014 ; Han et al., 2021).

Cette plasticité morphologique intra-individuelle a également été montrée en réponse à d'autres facteurs abiotiques, tels que la disponibilité en nutriments (Louâpre et al., 2012 ; Wang et al., 2022), la disponibilité en lumière (Slade & Hutchings, 1987a ; Wang et al., 2022), ou bien la durée des inondations (van Kleunen et al., 2007).

Concernant la plasticité physiologique, les amines et flavonoïdes sont les deux grandes catégories de métabolites secondaires impliqués dans la protection des plantes contre les stress (Levine et al., 2008 ; Lasky et al., 2012 ; Agati et al., 2012 ; Tiburcio et al., 2014 ; Reudler & Elzinga, 2015 ; Hennion et al., 2016 ; Sardans et al., 2020), tels que l'augmentation des températures (Jochum et al., 2007 ; Ramakrishna & Ravishankar, 2011). En effet, la température influence fortement l'activité métabolique des plantes, car le carbone fixé par la photosynthèse est d'avantage alloué à la production de métabolites secondaires pour répondre à un stress, plutôt qu'à la production de biomasse (Mooney, 1991), résultant ainsi en une augmentation de leur concentration (Litvak et al., 2002 ; Yu et al., 2005 ; Jochum et al., 2007).

## ii. Echelle de la communauté

A l'échelle de la communauté végétale, la théorie de *l'habitat filtering* prévoit que seules les espèces fonctionnellement adaptées aux contraintes abiotiques d'un milieu donné peuvent survivre et assurer leur reproduction. En d'autres termes, les contraintes abiotiques filtrent les combinaisons de traits permettant aux individus de se maintenir dans le milieu à échelle locale, induisant une convergence des valeurs de traits vers une valeur optimale, ce qui se traduit par une grande similarité fonctionnelle entre espèces sélectionnées (Grime, 2006). Par exemple, Cornwell et Ackerly (2009) ont montré que six des 11 traits foliaires et de tiges étudiés présentaient un patron de convergence vers des valeurs qui assurent la survie des individus le long d'un gradient de teneur en eau dans le sol, témoignant de l'effet d'un filtre d'habitat sur l'assemblage local des espèces.

Plusieurs études sont venues moduler cette hypothèse de convergence des traits suite à un processus de filtrage abiotique et ont montré que certains facteurs abiotiques pouvaient induire au contraire une distribution divergente des traits. C'est le cas notamment dans des

milieux sujets à des perturbations, où les espèces ont acquis des stratégies différentes de régénération, conduisant à une dispersion des valeurs de traits liés à la régénération (Grime, 2006 ; Grime & Pierce, 2012). De plus, une hétérogénéité d'habitats à échelle très locale peut également induire une dispersion des valeurs de traits (Bergholz et al., 2017), comme une divergence de hauteur, SLA et LDMC en réponse à des conditions hétérogènes de profondeur de sol et de luminosité (Siefert, 2012).

## e. Mécanismes et patrons de réponses aux filtres biotiques

### i. Echelle individuelle

Les valeurs moyennes de certains traits morphologiques, connus pour leur sensibilité aux facteurs biotiques, répondent aux interactions plantes-plantes. La plasticité de la structure aérienne des plantes est bien documentée, avec notamment la perception des individus voisins qui est possible *via* l'ombre produite, influençant l'architecture aérienne pour augmenter la performance des individus (Tucić et al., 2006 ; Bell & Galloway, 2007). En effet, une plasticité des traits morphologiques comme une augmentation des valeurs moyennes de la hauteur, de la longueur des pétioles et des entrenœuds, ou de la surface foliaire, permet de maximiser la performance des individus en situation de compétition pour la lumière, et donc joue un rôle dans leur compétitivité (Sultan & Bazzaz, 1993 ; van Kleunen & Fischer, 2003 ; Callaway et al., 2003 ; Bell & Galloway, 2007). La plasticité racinaire a également été mise en évidence, minimisant ainsi le chevauchement de rhizosphère entre individus et diminuant la compétition intraspécifique (longueur des racines, Schiffers et al., 2011) ou interspécifique (prolifération racinaires et prélèvement des nutriments : D'Antonio & Mahall, 1991 ; Jackson & Caldwell, 1996). Chez des espèces de plantes clonales, une plasticité dans la morphologie aérienne et clonale a été mise en évidence en réponse à la présence de compétiteurs (van Kleunen et al., 2000, 2007) pour augmenter la probabilité de coexistence des espèces (Chesson & Rosenzweig, 1991), voire même en réponse à l'identité spécifique du voisinage (Turkington et al., 1991).

Concernant les traits métaboliques, peu d'études se sont penchées sur les effets de la composition d'une communauté sur le métabolome d'espèces cibles (mais voir Scherling et al., 2010 ; Mraja et al., 2011 ; Walter et al., 2012), bien que certains amines sont connus pour répondre à des facteurs biotiques comme la diversité et l'identité des espèces végétales voisines

(Hennion et al., 2016), ou encore la présence de communautés d’herbivores et de pathogènes (Molgaard, 1986 ; Agrawal, 2011 ; Züst et al., 2012).

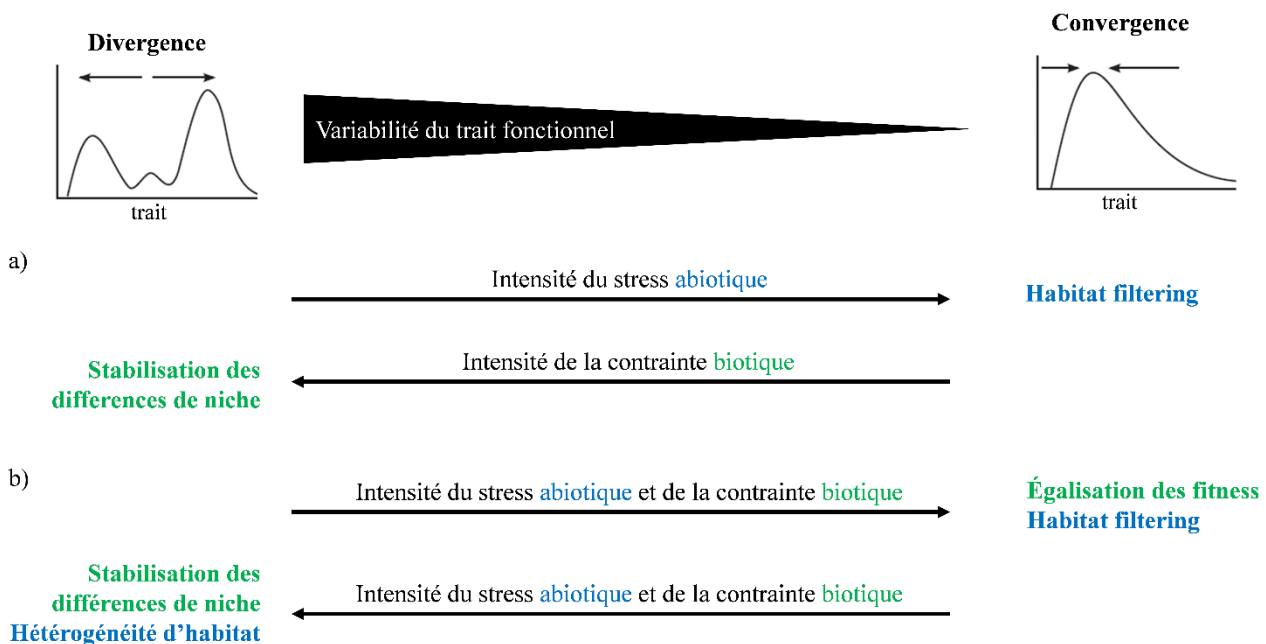
## ii. Echelle de la communauté

Les filtres biotiques peuvent induire de la convergence ou de la divergence des valeurs de traits à l’échelle de la communauté, en lien avec deux mécanismes de réponse favorisant la coexistence des espèces : l’égalisation des fitness et la stabilisation de niche. La stabilisation de niche se traduit par une dispersion des valeurs de traits permettant aux différentes espèces d’occuper des niches différentes (Chesson, 2000 ; Kraft et al., 2015a). L’égalisation des fitness conduit au contraire à une convergence vers les valeurs de traits permettant de maximiser l’aptitude compétitive des espèces. Les espèces qui ne parviennent pas à atteindre ces gammes de traits sont exclues par compétition, tandis que les espèces survivantes présentent de fortes valeurs de traits associés à la croissance et à l’acquisition des ressources (Chesson, 2000 ; Grime, 2006 ; Nagashima & Hikosaka, 2011 ; Kraft et al., 2015b). Ces deux types de réponses peuvent exister au sein des mêmes individus pour différents traits. En effet, les traits clonaux associés à l’occupation de l’espace (*e.g.* nombre de branches, longueurs des entrenœuds...) tendent à diverger quand les traits associés à la croissance et l’acquisition des ressources (*e.g.* hauteur, surface foliaire...) tendent à converger vers les valeurs de trait les plus compétitives (Herben & Goldberg, 2014). Ces résultats soulignent l’importance d’une approche multi-traits pour améliorer la compréhension des mécanismes déterminant l’issue des interactions biotiques (Kraft et al., 2015b).

## f. Réponses à la combinaison des filtres biotiques et abiotiques

Les patrons de divergence et convergence étaient historiquement décrits comme issus des mécanismes de stabilisation de niche et d’« *habitat filtering* » (Figure 5 a). Pourtant, ces deux patrons peuvent chacun résulter d’un filtre biotique ou abiotique, menant à des confusions. En effet, un filtre abiotique et un mécanisme d’égalisation des fitness peuvent chacun générer une convergence de valeurs de traits (Kraft et al., 2015a ; Cadotte & Tucker, 2017), de même qu’une hétérogénéité de micro-conditions abiotiques et un mécanisme de stabilisation de niche peuvent générer une divergence de valeurs (Grime, 2006) (Figure 5 b). Ainsi, les patrons de dispersion

de traits sont à étudiés avec précaution, pour mieux affiner les interprétations des mécanismes sous-jacents à l'échelle des communautés.



**Figure 5.** Vision a) historique et b) actuelle des patrons de dispersion des traits et des mécanismes associés en lien avec les intensités respectives du stress abiotique et de la contrainte biotique.

La réponse des plantes à une augmentation de la température est bien documentée dans la littérature, de même que leur réponse aux interactions biotiques. Cependant, peu de travaux étudient ensemble stress thermique et interactions biotiques, bien que les espèces végétales y soient simultanément soumises dans un contexte de changements climatiques. Pourtant, des actions simultanées de filtres biotique et abiotique ont été montrées à l'échelle des individus. En effet, les réponses contraires de patrons de dispersion de leurs valeurs peuvent exister au sein d'un même individu pour différents traits, suggérant que certains mécanismes de coexistence opèrent simultanément sur les individus mais sur des traits différents, et que la direction et intensité de leurs effets sont trait-dépendants. Par exemple, à travers la prise en compte de l'ITV, [Cornwell et Ackerly \(2009\)](#) ont démontré l'action simultanée du filtre abiotique et de la *limiting similarity*. De la même façon, le long de gradients de hauteur d'eau dans les milieux aquatiques, les intervalles de valeurs de SLA et du carbone foliaire sont contraints (filtre abiotique) par la profondeur d'eau, au contraire du diamètre de tige (*limiting similarity*) ([Fu et al., 2014](#)). Aussi, cela suggère l'existence de stratégies intermédiaires pour répondre au mieux à l'action simultanée des filtres biotiques et abiotiques.

### 3. Effets sur les écosystèmes

Les plantes sont des producteurs primaires et se situent à la base des chaînes trophiques. Elles jouent donc un rôle crucial dans le fonctionnement des écosystèmes. Ainsi, toute variation de traits à l'échelle individuelle peut conduire à des modifications de structure ou de composition des communautés végétales, pouvant à leur tour impacter de nombreux processus à plus large échelle, notamment celle de l'écosystème.

#### a. Fonctions et processus écosystémiques

##### i. Définitions

L'écosystème est le siège de nombreuses fonctions essentielles qui garantissent ensemble son bon fonctionnement et assurent la survie et le maintien des organismes qu'il abrite. Parmi ces fonctions, on distingue notamment les cycles biogéochimiques aux interfaces air, eau, sédiments (*i.e.* cycles du carbone, de l'azote, de l'hydrogène/oxygène), ainsi que les composantes de ces cycles comme la rétention de nutriments et la séquestration de carbone. Les productivités primaires et secondaires sont également des fonctions écosystémiques. La productivité primaire nette est quantifiée par la production de carbone organique résultant de la photosynthèse, à laquelle est soustraite la perte simultanée de carbone par respiration. Des valeurs positives indiquent un puits de carbone tandis que des valeurs négatives indiquent une source de carbone. Les processus écosystémiques sont quant à eux des processus qui participent au maintien de ces fonctions écosystémiques. Ils sont définis comme tous les processus physiques, chimiques ou biologiques qui lient les organismes et leur environnement, c'est-à-dire comme tout type de transfert d'énergie, de matériel ou d'organismes au sein d'un écosystème (Lovett, 2005). La décomposition et minéralisation de matières organiques sont par exemple des processus bien étudiés qui transforment les substances organiques, relâchent le carbone et les nutriments, et constituent donc une composante des cycles biogéochimiques (Wardle, 2002 ; De Deyn et al., 2008 ; Zhang et al., 2010).

ii. Vers une modification des processus écosystémiques par le changement climatique, particulièrement au sein des systèmes aquatiques

Le réchauffement climatique perturbe les processus écosystémiques et les fonctions qui leur sont associées (Gutt et al., 2021). Il est particulièrement intense dans les régions de hautes latitudes (Chapman & Walsh, 1993 ; Serreze et al., 2000 ; Hansen et al., 2001), pouvant altérer les couvertures neigeuses, les épisodes de dégel, ainsi que la durée des saisons de croissance végétative. A leur tour, ces modifications ont des impacts sur les taux photosynthétiques et le dégel de l'horizon organique des sols, influençant en retour la productivité des systèmes terrestres et la balance carbone source/séquestration, notamment au sein des forêts boréales (Myneni et al., 1997 ; Black et al., 2000 ; Euskirchen et al., 2006 ; Piao et al., 2008 ; Arain et al., 2011).

De plus, les zones humides font partie des systèmes les plus productifs sur Terre et ont le plus fort taux de séquestration de carbone dans le sol (Battin et al., 2009 ; Kayranli et al., 2010 ; Aufdenkampe et al., 2011 ; Zeng et al., 2014 ; Villa & Bernal, 2018 ; Were et al., 2019). En effet, ils contiendraient 20 à 30% du carbone mondial (Mitsch et al., 2013) à travers l'accumulation de biomasse végétale et de matière organique dans les sédiments qui se décomposent très mal en raison des conditions anoxiques de ces systèmes (Laiho, 2006). Par conséquent, les systèmes aquatiques d'eau douce sont des sources/puits de gaz à effets de serre (Whiting & Chanton, 2001 ; Kayranli et al., 2010 ; Mitsch et al., 2013), notamment les zones humides qui seraient les principaux contributeurs des flux de méthane mondiaux (Bridgham et al., 1995). Ils ont donc la capacité de moduler les concentrations atmosphériques du CH<sub>4</sub>, CO<sub>2</sub> et même du N<sub>2</sub>O qui contribuent respectivement à 60%, 20% et 6% du réchauffement global (Bernstein et al., 2008). De nombreuses études ont prouvé que la hauteur de colonne d'eau et la température contrôlent les taux de séquestration de carbone à travers la balance entre les taux de photosynthèse et de respiration (Flanagan & Syed, 2011 ; Salimi et al., 2021), la décomposition de matière organique (Mitsch et al., 2013 ; Olsson et al., 2015 ; Villa & Bernal, 2018 ; Salimi et al., 2021) et la minéralisation des éléments organiques (Gudasz et al., 2010, 2012). Par exemple, il a été montré que le cycle de l'azote a été impacté suite aux hausses de températures dans des lacs boréaux (MacKay et al., 2009), avec une augmentation de l'activité microbienne conduisant à une accélération des processus de nitrification et de dénitrification, et donc à des émissions plus intenses d'oxyde d'azote (Coops et al., 2003 ; Weyhenmeyer et al., 2007 ; Huang et al., 2013). De même, une augmentation des températures combinée à une



baisse de disponibilité en eau seraient responsables d'une hausse de décomposition de matière organique et d'une accélération du relargage de CO<sub>2</sub> et CH<sub>4</sub> dans l'atmosphère, conduisant à une diminution de séquestration de carbone et nutriments (Bardecki, 1991 ; Mulholland et al., 1997 ; Updegraff et al., 2001 ; Laiho, 2006 ; Bates et al., 2008 ; Kayranli et al., 2010 ; Flanagan & Syed, 2011).

Les macrophytes interagissent également avec les processus hydrologiques, géomorphologiques et physico-chimiques de l'environnement aquatique, en régulant plusieurs paramètres : vitesse du flux, pH, conductivité, disponibilité en nutriments, suspension de particules et clarté de l'eau sont les facteurs les plus connus (Scheffer et al., 1993 ; Vermaat et al., 2000 ; Madsen et al., 2001 ; Engelhardt & Ritchie, 2001 ; Horppila & Nurminen, 2003 ; Hadad et al., 2006 ; Wharton et al., 2006 ; Hilt & Gross, 2008 ; Jeppesen et al., 2012 ; Blindow et al., 2014 ; Rolland et al., 2015 ; Bowden et al., 2017 ; Reitsema et al., 2018 ; Su et al., 2019 ; Manolaki et al., 2020 ; Lürig et al., 2021). Ils ont donc un rôle important dans le cycle de la matière et les transferts d'énergie au sein des systèmes aquatiques (Asaeda et al., 2000). Aussi, le changement climatique peut impacter les écosystèmes indirectement *via* son effet sur les communautés végétales.

## b. Traits d'effet

La richesse spécifique a été la première métrique de diversité à être reliée au fonctionnement des écosystèmes. Les premières expériences menées au sein de prairies ont montré un effet positif de la richesse spécifique sur le fonctionnement de l'écosystème (Tilman et al., 1996 ; Hooper et al., 2005 ; Cardinale et al., 2012), ce qui a été confirmé plus tard au sein de plusieurs autres écosystèmes (Gamfeldt et al., 2008, 2015 ; Maestre et al., 2012 ; Grace et al., 2016), dont les systèmes aquatiques qui restent toutefois peu étudiés (*e.g.* Engelhardt & Ritchie, 2001 ; Bouchard et al., 2007). Cependant, de nouvelles études ont démontré que les traits fonctionnels jouent également un rôle prépondérant dans les fonctions écosystémiques. En effet, une modification des valeurs de certains traits fonctionnels à échelle individuelle ou spécifique peut affecter la performance des individus et l'assemblage des espèces, impactant en retour les niveaux trophiques supérieurs jusqu'aux écosystèmes. Ainsi, les valeurs de ces traits dits « d'effet », ainsi que leur diversité au sein d'une communauté, peuvent impacter certaines

fonctions (Lavorel & Garnier, 2002 ; Naeem & Wright, 2003 ; Diaz et al., 2007), parfois même plus intensément que le nombre d'espèce *per se*.

Un exemple bien étudié est l'effet des traits foliaires sur le processus de décomposition de la litière végétale, entraînant des conséquences sur le transfert de carbone et de nutriments depuis le compartiment plante vers l'écosystème, et donc sur les cycles biogéochimiques associés. En effet, la décomposabilité de la litière serait étroitement liée à la qualité initiale de litière (Fortunel et al., 2009), elle-même liée aux valeurs de traits foliaires (Cortez et al., 2007 ; Quested et al., 2007 ; Cornwell et al., 2008). Plus précisément, une forte teneur en matière sèche combinée à une faible surface spécifique foliaire (Garnier et al., 2004 ; Quested et al., 2007 ; Fortunel et al., 2009), ainsi que des faibles ratios carbone/azote et lignine/azote (Aerts, 1997 ; Chapin et al., 2002 ; Wardle, 2002 ; Lan et al., 2012) seraient des critères importants pour une bonne qualité de litière. Celle-ci serait alors corrélée à une rapide décomposition de la matière végétale, participant alors au maintien de cycles biogéochimiques fonctionnels (Aerts, 1997 ; Chapin et al., 2002 ; Wardle, 2002 ; Korol et al., 2016). Les traits racinaires ont aussi une incidence sur la décomposition de la litière. Par exemple, des racines courtes avec une forte densité de tissus produisent une litière qui se décompose plus lentement (Personeni & Loiseau, 2005), augmentant le taux de séquestration de carbone dans le sol (Klumpp & Soussana, 2009).

Deux hypothèses majeures relient composition fonctionnelle de la communauté végétale et les propriétés écosystémiques. L'hypothèse de dominance proposée par Grime (1998) postule que les traits fonctionnels des espèces les plus abondantes influencent le plus les processus écosystémiques. Cette hypothèse tend à être vérifiée pour certains processus comme la productivité primaire, la décomposition de la litière et certaines composantes des cycles du carbone et de l'eau (Garnier et al., 2004 ; Quétier et al., 2007 ; Quested et al., 2007 ; Mokany et al., 2008 ; Cornwell et al., 2008 ; Fortunel et al., 2009). Cependant, la dominance fonctionnelle de certaines espèces n'est pas le seul indice à modifier les propriétés des écosystèmes. Une grande diversité fonctionnelle est aussi associée à un bon fonctionnement écosystémique, car les espèces avec des valeurs contrastées de traits fonctionnels exploitent des ressources différentes, ou exploitent les mêmes ressources à des échelles spatiales et temporelles différentes (Hooper et al., 2005), ce qui augmente alors l'utilisation globale des ressources (Naeem et al., 1994), et la productivité d'un écosystème (Tilman et al., 1996 ; Hooper et al., 2005 ; Wright et al., 2006 ; von Felten et al., 2009). Cette hypothèse a été testée

par des expériences en mésocosmes (Loreau et al., 2001 ; Hooper et al., 2005 ; Cardinale et al., 2006) mais aussi à travers d'observations *in situ* (Gross et al., 2007 ; Diaz et al., 2007 ; Mouillot et al., 2011).

### c. Effets indirects des facteurs environnementaux biotiques et abiotiques sur les processus écosystémiques *via* la réponse des traits fonctionnels des végétaux

Un trait peut être à la fois un trait de réponse et un trait d'effet (Lavorel & Garnier, 2002). L'utilisation des traits fonctionnels permet donc de réaliser un changement d'échelle depuis la communauté végétale vers l'écosystème.

Dans un contexte de changement climatique, les modifications de valeurs de traits fonctionnels en réponse aux variations climatiques pourraient donc impacter certaines fonctions écosystémiques. En effet, la température et les paramètres hydrologiques s'avèrent impacter le plus les fonctions écosystémiques des zones humides (Bridgham et al., 1995 ; Bubier et al., 1998 ; Lafleur et al., 2005 ; Chivers et al., 2009 ; Laine et al., 2014), non seulement en modifiant directement les paramètres biogéochimiques des systèmes (Kløve et al., 2010 ; Song et al., 2013 ; Laine et al., 2014), mais aussi en modifiant les valeurs de traits associés à la production primaire (Chagas et al., 2012 ; Gutt et al., 2021) ou la composition chimique des individus (Swan & Kominoski, 2012). En retour, ces modifications morphologiques et/ou physiologiques affectent certains processus écosystémiques (Weltzin et al., 2000 ; Bragazza et al., 2013 ; Kuiper et al., 2014 ; Dieleman et al., 2015).

Les processus de décomposition en particulier peuvent être influencés directement par la température *via* ses effets sur les activités enzymatiques microbiennes et indirectement *via* la qualité de litière qui serait la meilleure variable pour prédire les taux de décomposition. Suite à une élévation de température, les propriétés chimiques de la litière et donc sa décomposition se voient modifiées par les réponses phénotypiques des plantes à court terme, puis à long terme suite aux changements de composition de communautés végétales. Par exemple, il a été montré que la hausse des températures provoquait un changement dans les couvertures relatives des espèces poussant dans les tourbières initialement dominées par des mousses, avec une expansion des espèces vasculaires, menant à une modification des teneurs stœchiométriques du carbone et nutriments dans la litière et impactant ultérieurement sa dégradation et sa minéralisation (Bragazza et al., 2013). De la même façon, au sein de systèmes aquatiques

dominés par des macrophytes, une hausse des températures induit une modification des valeurs de plusieurs traits, dont la SLA ou encore les ratios C:nutriments (Zhang et al., 2020), connus pour impacter la décomposition du matériel végétal (Wedderburn & Carter, 1999 ; Santiago, 2007). Par conséquent, étant donné la forte capacité des macrophytes à répondre aux variations environnementales (Bornette & Puijalon, 2011 ; Lauridsen et al., 2020), les processus écosystémiques associés aux macrophytes seraient d'autant plus affectés par les changements climatiques.

De la même façon, les interactions biotiques sont capables d'induire des modifications des valeurs de traits fonctionnels, comme une hausse de la SLA, un ratio C:N plus faible et une faible LDMC en situation de compétition (Violle et al., 2007, 2009 ; Barbe et al., 2017), influençant *in fine* les taux de décomposition. Cependant, peu d'études à ce jour traitent des effets des interactions plantes-plantes sur les processus de décomposition à travers la modification des valeurs de traits (mais voir Barbe et al., 2017).

#### 4. Les dynamiques Eco-Evo : des pistes de réflexions sur les réponses des communautés végétales et des écosystèmes face à des changements environnementaux rapides

Jusqu'à récemment, les processus évolutifs et écologiques étaient étudiés séparément, sans évoquer leurs possibles rétroactions. Pourtant, des recherches intégratives ont récemment reconnu que les dynamiques écologiques et évolutives co-occurrent, voire même interagissent. Des changements évolutifs dans le temps et l'espace pourraient affecter les processus et patrons écologiques, de même que les modifications de patrons écologiques impacteraient en retour les dynamiques évolutives des espèces, créant ainsi des boucles de rétroaction entre les deux dynamiques, appelées « boucles éco-évolutives » (Hairston Jr et al., 2005 ; Urban & Skelly, 2006 ; Fussmann et al., 2007 ; Urban et al., 2008 ; Ellner et al., 2011 ; Schoener, 2011 ; Matthews et al., 2011 ; Shefferson & Salguero-Gómez, 2015 ; De Meester et al., 2016, 2019). Ainsi, le champ disciplinaire d'étude des boucles éco-évolutives progresse depuis quelques années, avec un nombre croissant de théories et d'expérimentations (De Meester et al., 2019).

Plus précisément, un phénotype observé résulte à la fois du génotype exprimé, de l'influence de l'environnement et de leur interaction (Via et al., 1995 ; Nelson & Crone, 1999 ; Govaert et al., 2016). Cependant, certains facteurs abiotiques de même que les interactions biotiques sont des pressions de sélection opérant sur les phénotypes. Ils peuvent conduire à de l'évolution si ces derniers ont une base génétique, c'est-à-dire si les variations phénotypiques sont héréditaires. Ainsi, les dynamiques écologiques peuvent moduler les dynamiques évolutives, un phénomène déjà bien connu et défini comme la composante « Eco vers Evo » de la boucle éco-évolutive. Cette sélection et cette évolution phénotypique peuvent en retour impacter certaines propriétés écologiques, définissant ainsi une rétroaction des dynamiques évolutives sur les dynamiques écologiques, c'est alors la composante « Evo vers Eco ». Le champ disciplinaire des boucles éco-évolutives s'inscrit parfaitement dans la compréhension des réponses des communautés et du fonctionnement des écosystèmes face aux changements environnementaux rapides telle que l'élévation des températures (De Meester et al., 2011 ; Urban et al., 2012 ; Merilä & Hendry, 2014). L'approche fonctionnelle s'est révélée particulièrement pertinente dans ce champ disciplinaire, puisque les variations inter- et intraspécifiques des traits fonctionnels traduisent une potentielle source de différenciation génétique et donc de changements évolutifs, permettant de lier les dynamiques écologiques et évolutives.

La stricte définition d'une boucle éco-évolutive implique les mêmes espèces et traits au sein des deux dynamiques (Hendry, 2016). L'évolution d'une espèce cible impacte les processus écologiques, qui impacte à son tour l'évolution future de cette même espèce (Bull et al., 2006 ; Becks et al., 2012 ; Brunner et al., 2017). Pourtant, dans des contextes naturels et réalistes, les individus végétaux co-évoent et s'influencent au sein d'un système multi-espèces. Ainsi, les boucles éco-évolutives ont été étendues aux dynamiques éco-évolutives impliquant l'ensemble des espèces au sein des communautés (Hendry, 2016). Par conséquent, les rétroactions éco-évo ne nécessitent pas de cibler une espèce et quelques traits, mais autorisent à l'inverse une vision plus complète des mécanismes écosystémiques et évolutifs impliquant l'ensemble des communautés, avec cependant toute la complexité engendrée. En effet, les individus sont constamment contraints par des facteurs abiotiques et par les interactions avec leur voisinage, ce qui complexifie les conséquences possibles et les dynamiques associées. Entre autres, de fortes interactions interspécifiques peuvent modifier les patrons évolutifs de plusieurs façons, et donc engendrer des conséquences sur les processus écosystémiques (Barracough, 2015). Par exemple, une augmentation de la richesse spécifique induit généralement une réduction de la taille des populations qui entrent en compétition pour les mêmes ressources, réduisant la diversité génétique des espèces, les taux de mutation bénéfiques et donc le potentiel évolutif (Johansson, 2008). Par ailleurs, augmenter le nombre d'interactions possibles et leur intensité (mutualistes, parasites, prédateurs...) peut rapidement accroître les pressions de sélection sur les individus, et donc complexifier les conséquences évolutives (Benkman, 2013). En parallèle, les réponses évolutives à un facteur abiotique donné peuvent dépendre du contexte communautaire. Par exemple, une fitness moins élevée face à l'augmentation du taux de CO<sub>2</sub> au sein de cultures multi-génotypiques d'algues par rapport à des monocultures a été attribuée à un compromis entre l'énergie allouée à la réponse au stress abiotique et la capacité compétitive (Collins, 2011). De la même façon, des compromis ont été montrés entre les traits de croissance et de défense chez des plantes tropicales (Fine et al., 2006).

Cependant, peu de recherches prennent en compte la réalité complexe d'un contexte communautaire qui permettrait de limiter les biais d'études (Barracough, 2015 ; De Meester et al., 2019). Il a pourtant été montré que la co-évolution entre espèces permet d'améliorer le fonctionnement des écosystèmes : l'apparition de nouvelles stratégies, ou la spécialisation et la partition de niche qui amènent les espèces à un meilleur partage des ressources, augmentent la productivité de l'écosystème (Lawrence et al., 2012 ; Barracough, 2015). La prise en compte

des co-évolutions entre espèces est d'autant plus importante dans des systèmes paucispécifiques (Urban et al., 2008) ou isolés (Vanoverbeke et al., 2016 ; De Meester et al., 2016) au sein desquels les dynamiques évolutives seraient plus intenses. Par ailleurs, il semblerait que la boucle éco-évolutive complète, c'est-à-dire les composantes simultanées Eco vers Evo et Evo vers Eco, n'ait jamais été étudiée au sein d'une communauté végétale à ce jour (De Meester et al., 2019).

## METHODOLOGIE

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Cette partie méthodologie présente le milieu d'étude de ce manuscrit, *i.e.* les mares d'eau douces des Iles Kerguelen, leurs conditions particulières par rapport aux milieux aquatiques communément rencontrés dans les milieux tempérés, et les macrophytes à croissance clonale qu'elles abritent. Par ailleurs, les deux approches complémentaires qui ont été réalisées, *i.e.* des relevés *in situ* ainsi que des expérimentations en conditions contrôlées, sont présentées dans leur globalité, puisque les designs expérimentaux et de suivis sont communs à l'ensemble des articles proposés dans cette thèse. Ces derniers sont cités dans les sections « Approche *in situ* » ou « Approche en conditions contrôlées » pour replacer le contexte de leurs conditions expérimentales, ainsi que dans la section « Approche fonctionnelle » pour présenter les questions scientifiques qu'ils abordent.

Deux articles sont insérés dans cette section « Méthodologie » : (i) l'**article I** décrit la structure des communautés de macrophytes ainsi que les paramètres abiotiques des systèmes mares, pour une vision plus précise des conditions environnementales rencontrées sur le terrain, et (ii) l'**article II** repose sur l'utilisation de la partition de variance pour inférer les mécanismes d'assemblage des communautés.

## 1. Sites et objets d'études

### a. Iles Kerguelen

#### i. Présentation des Iles Kerguelen

L'archipel des Iles Kerguelen (7200 km<sup>2</sup> de terres comprises entre 48°30' et 50°00'S, 68°27' et 70°35'E) est situé au sein de l'océan Indien Austral dans la zone subantarctique (Lebouvier, 2007). Il fait partie du territoire français des Terres Australes et Antarctiques Françaises (TAAF) et s'inscrit dans la Réserve Naturelle Nationale des Terres Australes Françaises depuis 2006. Il est très isolé des continents, avec une distance de 3500 km environ des côtes africaines et australiennes. Les Iles Kerguelen sont d'origine volcanique et ont émergé au Tertiaire il y a 115 millions d'années (Nicolaysen et al., 2000). L'archipel est constitué d'une île principale appelée Grande Terre (6500 km<sup>2</sup>) entourée de près de 300 petites îles et îlots. Le littoral se découpe en de nombreux fjords avec une baie abritée au sud de la Grande Terre. Des dénivelés assez importants sont observés au sein de l'archipel, avec notamment le Mont Ross qui culmine à 1850 m à l'ouest de l'île principale et qui est partiellement recouvert par une calotte glaciaire (glacier Cook).

Les communautés végétales au sein de cet archipel sont très pauvres (Frenot et al., 2001 ; Pansu et al., 2015), avec 22 espèces de phanérogames autochtones (Van der Putten et al., 2010 ; Lebouvier et al., 2011) dont une espèce strictement endémique aux Iles Kerguelen (*Lyallia kerguelensis*), le reste étant d'origine magellanique et australo-néozélandaise (Hennion & Walton, 1997a). La végétation est dépourvue d'arbre et est définie comme de type toundra. La présence de l'Homme remonte à la fin du XVIIIème siècle (Frenot et al., 2006), et bien que sa présence demeure assez faible, de nombreux impacts ont été recensés avec l'introduction d'espèces végétales et animales exotiques, surtout depuis la construction d'une base permanente à Port-aux-Français au sud de la Grande Terre dans les années 1950 : 86 espèces végétales ont ainsi été introduites (Frenot et al., 2005, 2006). La faune locale participe également à façonner le paysage, avec la présence d'éléphants de mer et d'otaries Antarctique à fourrure, et une avifaune diverse (35 espèces de nicheurs) (Smith, 2008 ; Lebouvier et al., 2011). Les chaînes trophiques sont très simples, et les communautés microbiennes et détritivores assurent une grande partie des cycles des nutriments (Smith, 1985).

Les types d'habitats sont très limités (Bergstrom & Chown, 1999 ; Chown et al., 2008) et deux d'entre eux sont souvent rencontrés dans l'archipel : les prairies herbacées de basse altitude qui se caractérisent par des zones humides et sont partiellement protégées du vent, et les fell-fields qui se définissent comme des plateaux en hauteur, exposés aux vents avec des sols pauvres qui accueillent majoritairement des plantes en coussin (Hennion et al., 2006).

Les Iles Kerguelen sont caractérisées par un climat froid (4.6°C : moyenne annuelle), avec de fortes précipitations (500 à 3200 mm annuels d'Est en Ouest) et des vents violents (Frenot et al., 2006 ; Lebouvier, 2007) qui modèlent les communautés végétales. Cependant, depuis plusieurs décennies, ces îles font face à des changements climatiques rapides et intenses (Lebouvier et al., 2011), qui se caractérisent par une augmentation moyenne des températures annuelles de 1.3°C depuis 1960, une baisse du nombre de jours de gel annuels (20 à 30 jours perdus en 20 ans, Frenot et al., 2006 ; Lebouvier et al., 2011), et une baisse importante de la quantité et de la fréquence des précipitations (diminution de 100 à 250mm annuels en 20 ans - Chapuis et al., 2004 ; Frenot et al., 2006). Sur l'île Marion voisine à l'archipel des Kerguelen, une augmentation de la vitesse du vent a également été enregistrée, pouvant accélérer l'évaporation et donc amplifier la salinité des milieux côtiers (le Roux & McGeoch, 2008). Des épisodes de sécheresse estivale ont d'ailleurs été notés (Chapuis et al., 2004 ; Frenot et al., 2006 ; Lebouvier et al., 2011). Ainsi, pour des communautés adaptées à un climat froid et humide, ces changements rapides et intenses peuvent avoir d'importantes conséquences (Frenot et al., 2006 ; Lebouvier et al., 2011).

## ii. Présentation des systèmes étudiés

Les mares sont définies comme des petits bassins aquatiques permanents ou temporaires, dépourvus de poissons et donc de leur pression de prédation. Ces systèmes sont très hétérogènes et cette variabilité inter-mares est due à une multitude de variables physiques, chimiques et biologiques à large gamme de valeurs (pH, conductivité, salinité, turbidité, concentrations des éléments nutritifs, taux de précipitations/évaporation, temps de résidence des eaux, richesse et couverture des espèces de macrophytes...) (Cantonati et al., 2020). Du fait de leur petite taille et de leurs eaux peu profondes, les mares sont étroitement connectées aux processus terrestres (Pienitz et al., 1997). Par ailleurs, leur grand nombre font de ces petits systèmes des composants essentiels dans les processus écosystémiques. Downing et al. (2006) ont d'ailleurs conclu que les petits bassins de moins de 1km<sup>2</sup> dominaient la surface totale des lacs à l'échelle mondiale.

Les mares ont de forts potentiels de réactivité biogéochimique (Downing, 2009), du fait de leur grande zone de contact par unité de volume entre sédiment/eau, terre/eau et eau/air, en comparaison avec les lacs par exemple. De plus, ces zones aquatiques joueraient un important rôle dans les cycles biogéochimiques (Sobek et al., 2003 ; Walter et al., 2006 ; Tranvik et al., 2009 ; Laurion et al., 2010).



**Figure 6.** Mares d'eau douce en bordure de littoral, sur la Grande Terre.

Les mares d'eau douce des Iles Kerguelen constituent le système modèle de cette thèse. Elles sont rencontrées en bordure de littoral le long des côtes de la Grande Terre (Figure 6). Elles sont alimentées en eau essentiellement par les eaux de pluie et sont peu profondes (jusqu'à maximum 60 cm de profondeur). Les rares études qui portent sur les dynamiques des nutriments au sein de ces systèmes datent des années 1970-1980 dans les Iles Marion, Macquarie et Signy. Du fait de leur proximité avec le bord de mer, les mares sont alimentées en éléments nutritifs par les déjections d'animaux marins (Figures 6, 7) (Smith, 2008), faisant de ces systèmes des milieux mésotrophes à eutrophes en comparaison de ceux rencontrés dans les terres, avec de fortes concentrations en nitrate, ammonium et phosphore dissous (Smith, 1985). De plus, ces systèmes peu profonds peuvent expérimenter de fortes concentration en phytoplancton et algues benthiques (Smith, 1985). Enfin, le « système côtier » a été défini au sein des Iles Kerguelen comme un système regroupant les milieux terrestres, d'eau douce et marins en bordure de littoral du fait de leurs interactions très étroites (Hureau, 1985). Aussi, les communautés côtières de macro et micro-invertébrés ont été inventoriées et identifiées comme étant très pauvres, essentiellement dominées par des espèces terrestres d'acariens et d'insectes, et intégrant également des espèces marines (tardigrades, annélides, amphipodes et isopodes, Hureau, 1985).

Ainsi, bien que les processus de décomposition de la matière organique ne sont pas très efficaces, il seraient assurés par les espèces d'invertébrés citées précédemment, et par voie microbienne (bactéries et levures, [Smith, 1985](#)).



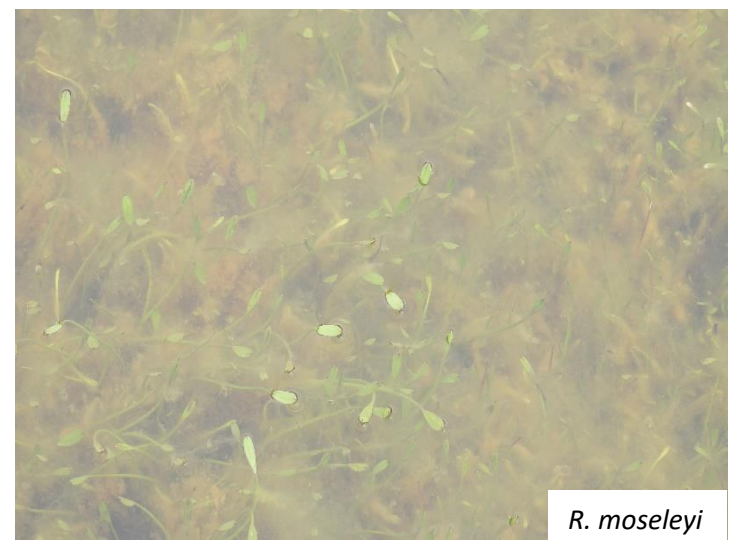
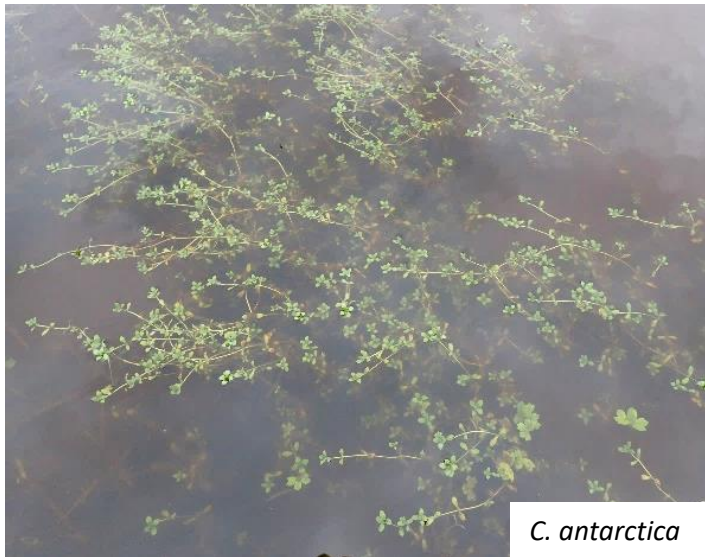
**Figure 7.** Les mares, terrain de jeu ou de repos pour de nombreux animaux marins, sont donc alimentées en éléments nutritifs par leurs déjections.

### b. Présentation des espèces étudiées de macrophytes

Les mares constituent l'habitat des populations locales des espèces de macrophytes et ne comptent pas d'espèces exotiques aquatiques. L'archipel des Kerguelen ne compte que six espèces de macrophytes (Figure 8) : *Limosella australis* R.Br. (Scrophulariacée), *Callitriche antarctica* Engelm (Plantaginacée), *Juncus scheuchzerioides* Gaudich. (Joncacée), ainsi que

trois espèces de la famille des Renonculacées : *Ranunculus biternatus* Smith, *R. pseudotrullifolius* Skottsbo., et *R. moseleyi* Hook.f. Ces espèces se répartissent dans la région subantarctique, avec *R. moseleyi* qui serait endémique des Iles Kerguelen (van der Putten et al., 2010 ; Lehnebach et al., 2017 ; Chau et al., 2021). Elles ne connaissent aucune pression de prédation. Ce sont toutes des plantes aquatiques pérennes et clonales, qui s'articulent en réseau de modules connectés entre eux par des tiges aériennes ou souterraines. *C. antarctica*, *L. australis*, *R. pseudotrullifolius* et *R. moseleyi* sont des hydrophytes (strictement aquatiques). *R. biternatus* et *J. scheuchzerioides* sont des héliophytes, que l'on retrouve dans des habitats strictement aquatiques ou humides (Hennion & Walton, 1997b). Toutes les espèces sont enracinées dans les sédiments, et *C. antarctica* se structure en canopée flottante, tandis que les cinq autres possèdent un port en rosette généralement submergée, en lien avec les variations du niveau d'eau de la mare.

Ces communautés végétales, pauvres en termes de nombres d'espèces, sont remarquablement adaptées à des températures fraîches (température aérienne de 4.6°C en moyenne) (Frenot et al., 2006). Elles seraient donc particulièrement sensibles aux modifications thermiques actuelles (Bergstrom & Chown, 1999). Une baisse d'abondance des espèces *R. biternatus* et *J. scheuchzerioides* a déjà été observée en réponse à la hausse des températures et des épisodes de sécheresse durant les saisons de croissance végétative et de reproduction (Chapuis et al., 2004). Par ailleurs, l'isolement géographique empêche les processus de migration et de colonisation vers et à partir d'autres régions du monde. Il y a donc un enjeu de conservation fort sur ces espèces.



**Figure 8.** Photos *in situ* des six espèces de macrophytes étudiées.

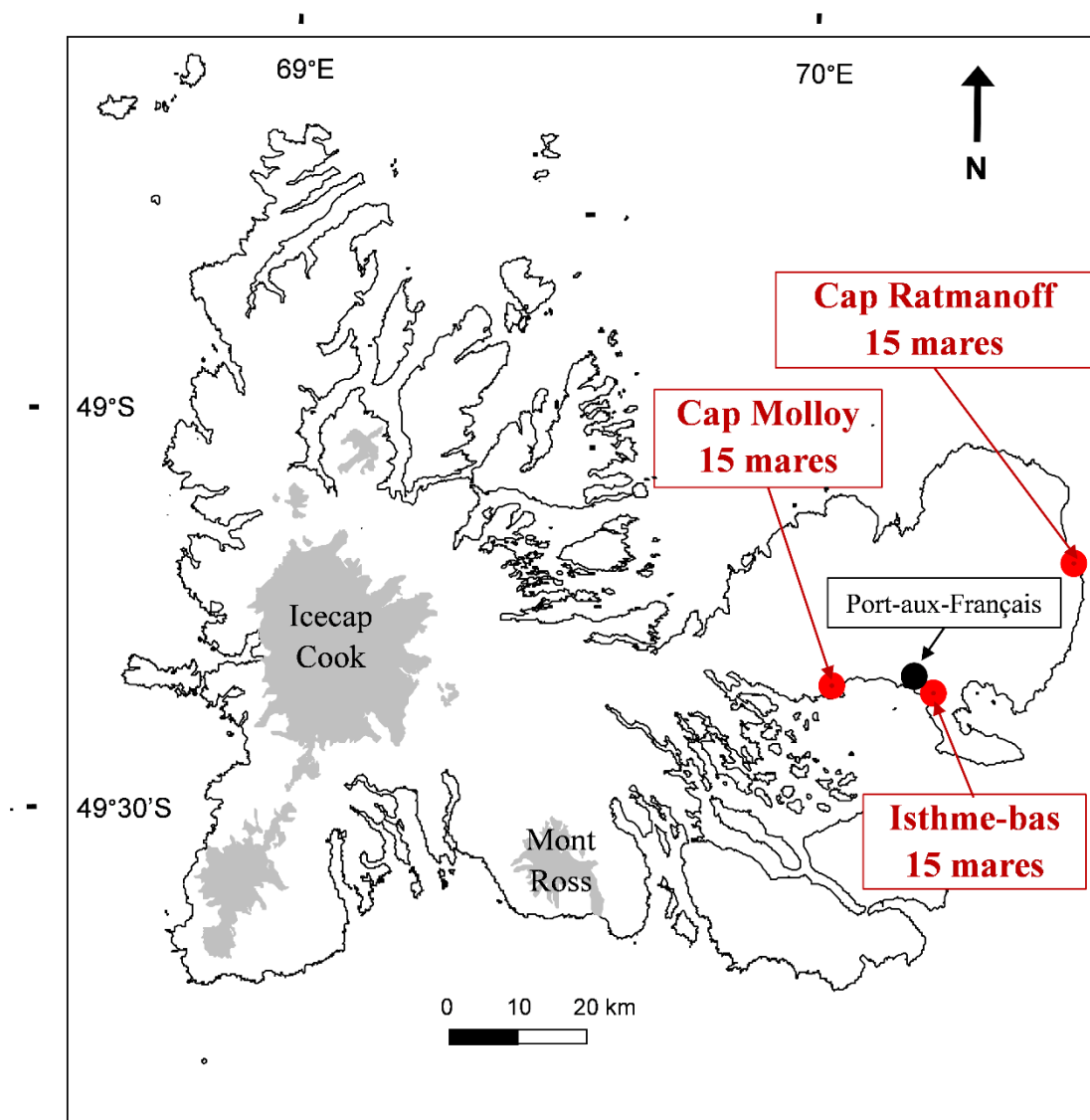
## 2. Deux approches complémentaires

### a. Approche *in situ*

Au cours des dernières décennies, un nombre croissant de théories et de concepts en écologie ont été testés dans les régions polaires, écosystèmes sentinelles, fréquemment définis comme des laboratoires à ciel ouvert (Bergstrom & Chown, 1999). Les mares constituent un système écologique simple (six espèces de macrophytes) et sont soumises à des changements climatiques rapides. Ce modèle d'étude est donc particulièrement pertinent pour aborder les questions développées dans cette thèse. De plus, les relevés *in situ* permettent de prendre en compte la réalité du terrain, avec toutes les conditions biotiques et abiotiques en jeu qui ne peuvent pas être récréées en conditions contrôlées.

Lors d'une prospection conduite pendant l'été austral 2016-2017, trois sites d'étude ont été sélectionnés sur la Grande Terre, en bordure de littoral et à basse altitude : Cap Molloy, Isthme-Bas et Cap Ratmanoff (Figure 9). La distance d'Ouest en Est entre Cap Molloy et Cap Ratmanoff est de 40km environ. Au sein de ces trois sites, 15 mares ont été sélectionnées de façon à décrire un gradient de surfaces (Figure 10), permettant d'affranchir les résultats obtenus de la taille des systèmes qui influence la température de l'eau (Bornette & Puijalon, 2011).

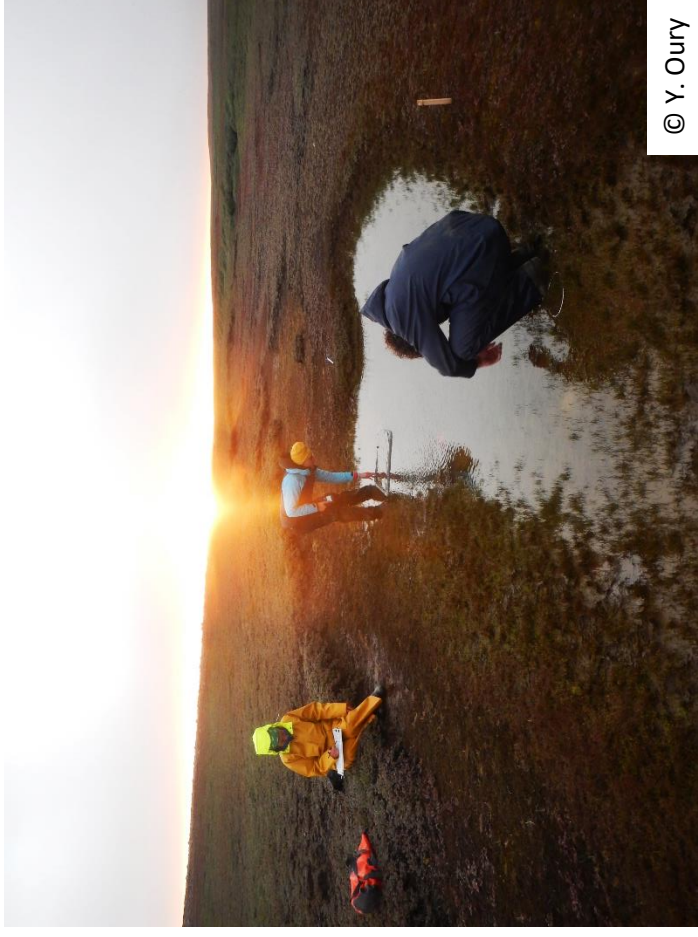




**Figure 9.** Localisations des trois sites étudiés (en rouge), situés en bordure de littoral sur la Grande Terre. 15 mares ont été échantillonnées au sein de chaque site. Port-aux-Français indique la localisation de la base scientifique.



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Figure 10. Illustration de la variabilité de la taille des mares étudiées.

Nous disposons à ce jour de cinq ans de suivis, nous permettant une étude temporelle et spatiale des communautés végétales et du fonctionnement des mares. Depuis 2017, un suivi de plusieurs paramètres biotiques et abiotiques de chacune des mares est réalisé, afin de prendre en compte au mieux la multitude des variables qui caractérisent ces systèmes et qui peuvent avoir des effets directs ou indirects sur les communautés de macrophytes et les fonctions écosystémiques associées. Ainsi, la prise en compte de ces multiples paramètres, qui bien souvent se modulent entre eux, peut éviter des biais d'interprétations.

Plus précisément, les abondances moyennes et les traits fonctionnels des espèces ont été mesurés respectivement deux fois par an (en début et fin de saison de végétation *i.e.* novembre et mai) et une fois par an (novembre). Les conditions physico-chimiques de chaque mare ont également été caractérisées tous les trois mois (novembre/février/mai/août). Pour chaque date d'échantillonnage et chaque mare, les paramètres suivants ont été mesurés : les nutriments (N-NH<sub>4</sub><sup>+</sup>, N-NO<sub>3</sub><sup>-</sup>, P-PO<sub>4</sub><sup>3-</sup>) dans l'eau, les nutriments dans les sédiments (C:N et phosphore biodisponible), la profondeur moyenne de l'eau, ainsi que le pH, la conductivité électrique (EC) et la concentration et saturation en oxygène dissous (DO) à l'aide d'une sonde multiparamètres HQ40D HACH sensor. La température de l'eau au sein de chaque mare a également été enregistrée toutes les demi-heures à l'aide d'enregistreurs (Hobo MX2202) placés au milieu de la colonne d'eau (à partir de Septembre 2020). De plus, la concentration en chlorophylle-a a été mesurée en novembre 2020 pour évaluer la quantité de phytoplancton dans l'eau. La superficie de chaque mare (longueur × largeur) a été mesurée une fois par an pour tenir compte de l'effet de la taille des systèmes sur les autres paramètres. Enfin, les positions précises de chaque mare ont été déterminées via un GPS (précision de 1m) afin de calculer les distances entre mares voisines et leur distance à la mer par Système d'Information Géographique (QGis 3.20.3).

Ce design *in situ* nous a permis : (i) d'aborder la question du lien entre la structuration spatiale des communautés de macrophytes, les paramètres abiotiques des mares, les interactions biotiques entre espèces et leurs traits fonctionnels et d'évaluer les conséquences de ces paramètres sur la performance (approchée par la biomasse totale) des communautés (**article III**) ; (ii) de déterminer comment varient les stratégies des communautés de macrophytes en réponse aux modifications des paramètres abiotiques de leur habitat, sur quatre ans (**article IV**), et (iii) d'étudier les réponses fonctionnelles des espèces de macrophytes à la combinaison des

paramètres biotiques et abiotiques des mares et leurs effets potentiels sur la performance (biomasse totale) des individus (**article II**).

De plus, ce suivi *in situ* nous a permis une description spatio-temporelle de la structure des communautés de macrophytes, ainsi qu'une identification des facteurs biotiques et/ou abiotiques qui expliquent ses variations. Cette étude fait l'objet de l'article présenté ci-après (**article I**).

**Biotic and abiotic drivers of aquatic plant communities in shallow  
pools and wallows on the sub-Antarctic Iles Kerguelen**

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C. Sulmon<sup>2</sup>, F. Vallier<sup>1</sup>, A.-K. Bittebiere<sup>1</sup>

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Article Informations	Abstract
<p><i>Article history:</i></p> <p>In revision for Polar Biology</p> <hr/> <p><i>Keywords:</i></p> <p>Aquatic plants</p> <p>Ponds</p> <p>Seasonality</p> <p>Plant community structure</p> <p>Habitat</p> <p>Spatio- temporal variability</p>	<p>In the sub-Antarctic region, climate change is particularly rapid, while their freshwater ecosystems, such as ponds, host plant species with limited spatial distributions. These particular systems and their plant communities remain however poorly known and the context of their changing habitat calls for deeper insights into these systems. We then performed an extensive survey of 45 ponds over three locations of the Iles Kerguelen during the winter and summer seasons of two years, which included the measurement of 12 abiotic parameters and the assessment of the plant community composition. This sampling design allowed us to test for spatial and temporal variations in aquatic plant communities, as well as to identify the environmental parameters that determine the composition of aquatic plant communities. Overall, our results showed that Iles Kerguelen ponds are shallow freshwater ecosystems harboring species-poor plant communities with high equitability, of which structure did not vary among the sampled locations. Three different habitats were identified among ponds in relation with nutrient supply by marine animals, which ultimately influenced plant community structure and cover. We highlight that these habitats are mostly determined by water depth, nutrients, and temperature (mean and variance). Besides, present plant community composition was more strongly correlated with plant community composition in the previous year than with abiotic conditions. Overall, this study provides new knowledge on the aquatic plant communities and the functioning of Iles Kerguelen freshwater ecosystems, which can serve as a basis for future studies dealing with the impact of climate change in the sub-Antarctic region.</p>

## Introduction

There is now ample evidence that climate change affects a broad range of organisms (see e.g. [Walther et al. 2002](#)), with severe effects for plant species thriving in freshwater habitats ([Lacoul and Freedman 2006](#)). In polar regions, including the sub-Antarctic region, climate change is particularly rapid

([Lebouvier et al. 2011](#); [Leihy et al. 2018](#)), calling for deeper insights into sub-Antarctic ecosystems, characterized by species with restricted spatial distributions ([Frenot et al. 2001](#); [van der Putten et al. 2010](#); [Chau et al. 2021](#)). This seems especially true for freshwater ecosystems harboring the aquatic plant species. Indeed, to our knowledge, their ecology remains poorly known, probably

because of technical difficulties associated with sampling in very harsh climatic conditions and highly remote locations.

Freshwater ecosystems of the sub-Antarctic region include numerous rivers and lakes, but aquatic plants preferentially colonize shallow and lentic systems of small sizes, *i.e.* ponds (Hennion et al. 1994) including elephant seal wallows. Ponds are indeed the only limnetic systems of this region. So far, most works dealing with sub-Antarctic aquatic plants have focused on their morphological (Hennion et al. 1994; Hennion and Walton 1997) and genetic variations (Siljak-Yakovlev et al. 2020; Chau et al. 2021), while no study has considered community assembly mechanisms. Nevertheless, we can identify two main processes, dispersal and environmental filtering, that often play key influences on plant community assembly through space and/or time (Vellend 2010). Yet, the actual influence of these processes in sub-Antarctic ponds has never been tested. Dispersal and environmental filtering in sub-Antarctic ecosystems should be strongly modulated by the specific traits of aquatic plants, and by the harsh environmental conditions encountered by the species. Dispersal in the sub-Antarctic aquatic plant appears limited, as they do not display specific adaptations to zoochory, and seem alternatively prone to hydrochory (Hennion and Walton 1997). Dispersal limitation usually results in spatial differentiation in plant communities. Climatic specificities of the sub-Antarctic region suggest that temporal variations in abiotic parameters may differ from what is usually observed in regions and habitats from lower latitudes (Smith 1985). Indeed, Hennion et al. (1994) reported that alternating periods of evaporation and heavy precipitation (seasonality) resulted in frequent and sometimes drastic fluctuations in the water depth of ponds of the sub-Antarctic Iles Kerguelen. It is thus likely that these seasonal variations of the pond habitat characteristics ultimately result in temporal modifications of the plant community composition.

Seasonal variations of water depth should therefore shape pond habitat *per se* or by modulating other physical and chemical parameters (Lacoul and Freedman 2006). Ponds are small water bodies, and as such, their physical and chemical characteristics would highly differ from sub-Antarctic larger water bodies, such as lakes (see e.g. Camacho 2006; Saunders et al. 2008). Changes in water temperature, which are linked to pond size (Bornette and Puijalon 2011), should be especially critical in the rapidly warming sub-Antarctic region (Lebouvier et al. 2011). Water temperature influences not only plant metabolism (Bornette and Puijalon 2011) but also microbial processes involved in nutrient cycling (MacKay et al. 2009; Biddanda 2017; Velthuis et al. 2017), as well as the concentrations of dissolved gasses (Bornette and Puijalon 2011). Besides, ponds are enriched by nutrients conveyed by marine animals, with these enrichments being temporarily variable depending on animal migrations (Smith and Froneman 2008). Characterizing water depth, water temperature, and nutrient availability within these freshwater ecosystems is thus crucial to improve our understanding of the drivers of the assembly of aquatic plant community through time.

The current lack of knowledge on the sub-Antarctic aquatic biodiversity combined with recent works demonstrating that sub-Antarctic plants are already strongly affected by climate change (Le Roux et al. 2005; Frenot et al. 2006; Le Roux and McGeoch 2008; Bergstrom et al. 2015) call for scrutinizing how variations in abiotic and biotic characteristics of ponds drive plant community assembly. Indeed, there are now ample evidences of varying climate modification across the sub-Antarctic region. In the Iles Kerguelen and Marion Island, temperatures increase while annual precipitations are strongly reduced (Lebouvier et al. 2011; McClelland et al. 2018). In Macquarie Island however, summers and winters become respectively drier and wetter (Bergstrom et al. 2015). Given that under harsh environmental

conditions, the abiotic filter is known to be a strong driver of plant community composition, in particular within sub-Antarctic terrestrial ecosystems (Bazzichetto et al. 2021; Momberg et al. 2021), it was critically important to characterize and monitor the main abiotic parameters that are known to affect the physiological status, and thus survival, of aquatic plants like *Ranunculus* species (Hennion et al. 2012; Labarrere et al. 2019).

In this study, as a part of the survey of the aquatic plant communities conducted on 45 ponds located along the shore of the main island of the Iles Kerguelen over two years, we expected that (i) pond plant communities should vary both through time (season, year) and space (location) in the Iles Kerguelen because of the stochastic impacts of marine animals on nutrient dynamics in ponds, and the low dispersal ability of aquatic plant species, reducing a potential community homogenization among ponds; (ii) water depth, water temperature, and nutrient availability should be major parameters characterizing ponds habitat; (iii) under the harsh climatic conditions of the archipelago, abiotic characteristics of ponds should prevail over biotic ones (past plant community composition), in determining the present plant community composition.

## Materials and methods

### Study area

This study was conducted on the main island of the Kerguelen archipelago (hereafter referred to as ‘Kerguelen’) located in the sub-Antarctic region (South Indian Ocean) (48°30’00” to 50°00’00” S, 68°27’00” to 70°35’00” E). The climate is characterized by cool temperatures (annual mean of 4.6 °C with little variation over the year, from 2.1 °C to 7.7 °C) (Frenot et al. 2001, 2006; Lebouvier and Frenot 2007), and low to abundant precipitations *i.e.* ranging from 500 mm to 3200 mm per year along an East-West gradient (Frenot et al. 1998). However, Kerguelen currently experiences rapid

climate change with increasing mean and variability of temperatures, and strongly reduced precipitations (Lebouvier et al. 2011). Overall, this leads to harsh environmental conditions for species adapted to cold and stable temperatures.

We focused on the shallow freshwater ponds located nearby the eastern shore line, including elephant seal wallows. These ponds are particular by being supplied with water, essentially from rainfall, and with nutrient inputs from marine animal dejections (mostly elephant seals and birds) (Smith and Froneman 2008). These specific habitat conditions are comparable to those found in Spit Bay seal wallows of Heard Island (Bergstrom and Selkirk 2000). A preliminary large field prospection performed during the Austral summer 2017, together with the existing literature (Hennion et al. 1994), indicated that these ponds are the main habitat for aquatic plant species at the Kerguelen.

Overall, the Kerguelen are characterized by a low species richness, hosting 22 native Angiosperms only (van der Putten et al. 2010). Based on the literature (Schotsman 1961; Lourteig 1952, 1964; Hennion and Couderc 1992; Hennion et al. 1994), six perennial plant species were expected to occur in the ponds, although aquatic plant communities of the Kerguelen have never been thoroughly described so far. These six aquatic plant species were: *Limosella australis* R.Br. (Scrophulariaceae), *Callitriche antarctica* Engelm (Plantaginaceae), *Juncus scheuchzerioides* Gaudich. (Juncaceae), and three species of Ranunculaceae: *Ranunculus biternatus* Smith, *R. pseudotrullifolius* Skottsb., and *R. moseleyi* Hook.f. Individuals of these six species are able to horizontally propagate through clonal growth (van Groenendael et al. 1996). Due to water depth fluctuations, we also anticipated that additional non-aquatic plant species (*i.e.* species that usually colonize terrestrial habitat) would colonize ponds from their edges.

### Field survey

Sampling was conducted twice a year (during the summer and the winter) from the Austral summer 2018 to the Austral summer 2020, at three locations of the main island of the Kerguelen archipelago. The locations were distributed along the sea shore at low altitudes, and described a West-East gradient: Molloy, Isthme Bas, and Cap Ratmanoff (Table 1, Figs. S1, S2). Location flatness and proximity to sea shore allows the presence of sea animals. At each location, fifteen ponds were randomly selected to describe a gradient of pond size (Table 1). Size was variable among ponds but also within ponds, due to important fluctuations of water depth (Hennion et al. 1994). GPS coordinates (precision of 1 m) of pond positions were recorded at each location. These positions were then used in GIS (QGis 3.20.3) to calculate the distances between ponds and the sea shore as a proxy for the frequency of visitation by marine animals.

Within each pond and at each sampling date, we randomly positioned three to five 1 m<sup>2</sup>-quadrats to measure a range of biotic and abiotic parameters. The number of quadrats depended on the pond size: five quadrats were realized for ponds whose surface was >5m<sup>2</sup>, while three to four quadrats were used for ponds <5m<sup>2</sup>. At each sampling date, quadrat positions and size allowed to sample both ponds' edges and centers. To characterize the composition of pond plant communities, the abundance (*i.e.* percentage of covered quadrat surface) of the different species, and of bare soil, were

estimated for each quadrat. All these abundances were recorded twice a year, once in the Austral summer (November), and another time during the Austral winter (May), which correspond to the beginning and to the end of the vegetation growth season, respectively. In addition, ten physical and chemical parameters were measured every three months, in November, February, May, and August over the two consecutive years of the study. Within each quadrat, we measured the mean water depth (based on three measurements), pH, specific conductance, and mean dissolved oxygen concentration (calculated from three measurements performed near the surface, in the middle of the water column, and at the bottom of the pond; HQ20, HACH™, Dusseldorf, Germany). At each pond, one 30 mL-water sample, and one 50 mL-sediment sample were also collected for further nutrient analyses in the lab. For these two samples, water and sediments were collected from several points within the pond to account for possible heterogeneity in nutrient distribution.

### Nutrient analyses

After collection, water and sediment samples were stored at 6 °C and brought within 24h to the laboratory. Water samples were further filtered through Whatman GF/F filters (pore size: 0.7µm, Cytiva, Amersham, United Kingdom). All samples (water and sediments) were then stored at -20 °C for several weeks before chemical analyses. N-NH<sub>4</sub><sup>+</sup>, N-NO<sub>3</sub><sup>-</sup> and P-PO<sub>4</sub><sup>3-</sup> concentrations were determined

**Table 1.** Description of the surveyed ponds at the three locations. Means and ranges of pond size were calculated based on measurements replicated on three consecutive years.

	Molloy	Isthme Bas	Cap Ratmanoff
Latitude, longitude	49.36°S - 70.06°E	49.36°S - 70.24°E	49.32°S - 70.53°E
Mean altitude of ponds above sea (±SD, m, N = 15)	11.2 (8.4)	3.4 (2.6)	8.8 (3.6)
Mean pond size (±SD, m <sup>2</sup> , N = 45)	58.9 (±56.9)	140.3 (±344.7)	54.0 (±62.9)
Pond size range (min-max, m <sup>2</sup> , N = 45)	2.4 – 166.5	4.8 – 1,252.2	2.9 – 164.6



based on standard colorimetric methods (Grasshoff et al. 1983) using a sequential analyzer (SmartChem200, AMS Alliance, Frépillon, France).

Nitrogen and organic carbon concentrations in sediments were measured following the “capsule” method (Brodie et al. 2011). Specifically, an amount of five mg ( $\pm 10\%$ ) of homogeneous sediment was acidified with 2M HCl in silver capsules to eliminate carbonates. Liquids were then evaporated on a 65 °C hot plate for 12 hours, before the entire drying out of capsules at 80 °C for a few days. Carbon and nitrogen analyses were then performed using an elementary analyzer (FlashEA 1112 NC Analyzers®, Thermo Fisher Scientific, Waltham, Massachusetts, USA). Following Ni et al. (2016), available organic phosphorus was extracted from 50 mg of dry sediment samples with 5 ml of NaOH (1 M). After extraction during 16 hours on a rotatory shaker at room temperature, the supernatant was collected, and its pH was stabilized at 7 with addition of HCl (4 M). The extracted P that has been converted into orthophosphate was quantified using the molybdate/ascorbic acid blue method (Murphy and Riley 1962), and results were reported in mg of available P (phosphorus available to plant growth) per g of dry sediment.

#### *Water temperature simulation*

Water temperature was recorded every half hour (HOBO Pendant MX2202, ONSET™, Cape Cod, Massachusetts, USA) from September 2020 to October 2021, in the middle of the water column of each pond. We performed linear regression analyses to determine the relationship between water temperature within each pond and air temperature recorded at the meteorological station of the Kerguelen (Météo France 2020-2021 records, Port-aux-Français), after confirming normality of the distribution of model residuals. All relationships between air and water temperatures were significant ( $R^2 \geq 0.55$ ;  $P < 0.05$ ), with the exception of two

ponds. These relationships were then used to infer water temperature occurring during the whole study period (summer 2018-2020) based on Météo France 2018-2020 records.

From these estimated data, we calculated the mean and the variance (square of standard deviation) of daily water temperatures over a period of three months *i.e.* between two dates separating other abiotic parameters measurements.

#### *Data analyses*

Before statistical analyses, abiotic parameters and species abundances recorded from different quadrats per pond were averaged for each sampling date. Species richness, Shannon diversity, and equitability (Pielou index) of plant community were calculated using the *vegan* R package (Oksanen et al. 2016). Pairwise correlations between these indexes were tested using non-parametric Spearman’s rank correlation tests. Species richness and equitability were not correlated while Shannon diversity was strongly correlated with the two other indexes ( $r > 0.75$ , and  $P < 0.05$ ). We therefore removed Shannon diversity from subsequent analyses.

We tested the effects of year, season, and location (Molloy, Isthme Bas, and Cap Ratmanoff) on the two community indexes using general mixed-effect models with pond as random factor (Bolker et al. 2009). Richness index was square-root transformed to satisfy normal distribution of residuals. The statistical significance of the fixed factors and their interactions was determined through type II ANOVA. Calculation of marginal and conditional  $R^2$  associated to the model was performed with the *performance* R package (Nakagawa et al. 2017).

We further used Between-Classes Principal Component Analysis (BCA-PCA; Dolédec and Chessel 1987) as implemented in the *ade4* R package (Dray et al. 2007; Thioulouse et al. 2018) to quantify the amount of variance delivered by time (season, year) and space (location, pond) and explaining plant community composition (*i.e.* relative

frequencies of plant species in each pond at each sampling date). BCA-PCA, belongs to the so-called constrained analysis (ter Braak and Verdonschot 1995) and is a particular case of PCA in which the sample grouping (e.g. in time or space) is accounted for in the analysis. The index characterizing the effect of time (or space) is quantified by between-class variance, which represents the ratio of the amount of variance explained by the sample grouping and the total variance among samples. Between-class variance was tested against simulated values obtained after 9,999 permutations of the rows of the plant species composition tables and allowed to assess the significance of the effects of year, season, location, and pond on plant community composition.

To characterize the habitat of plant species, we performed Principal Component Analysis (PCA) on the pond abiotic parameters using the *FactoMineR* R package (Lê et al. 2008), followed by Hierarchical Clustering on PCA scores (Ward method based on Euclidean distances) to discriminate pond clusters based on abiotic parameters. The mean of each abiotic parameter was then compared between clusters through ANOVA tests based on general linear models, and significant differences between clusters were assessed through TukeyHSD *post-hoc* tests ( $P < 0.05$ ). A similar procedure was applied to determine the relationships between clusters and (i) the plant community indexes, and (ii) the vegetation total cover within the pond. The parameter values were log or arctan transformed when necessary, to satisfy the assumption of the normal distribution of residuals.

To investigate the relationships between plant community composition and abiotic parameters across seasons, we used the STATICO method (Simier et al. 1999; Thioulouse et al. 2004). The method allows the simultaneous analysis of several pairs of tables in one run. In our case, we had four tables *i.e.* two seasons (for each season, we averaged the measurements of two dates) across two years, from November 2018 to

May 2020. This multivariate method combines the potential of (i) co-inertia analysis that allows matching two tables providing a new table (cross-covariance table) that describes the covariance between each environmental variable and each plant species (Dolédec and Chessel 1994; Dray et al. 2003), and that (ii) of partial triadic analysis allowing the simultaneous analysis of several tables in one run with the aim of depicting their similarity (Thioulouse and Chessel 1987), *i.e.* in our case, across seasons and years. In practice, the first step (co-inertia analysis) crossed the two tables (*i.e.* the physical and chemical parameters and the plant community composition) associated to each season of each year. This step ended up with the production of four cross-covariance tables depicting the covariance between each environmental variable and each plant species, at each season of each year. In a second step, the series of cross-covariance tables (one per season and per year) were analyzed with partial triadic analysis, looking for temporal variations in the species-environment relationships. The strengths of these relationships between plant communities and abiotic parameters across seasons were then assessed using the  $R_V$ -coefficient, which is a multidimensional equivalent of the ordinary correlation coefficient between two variables (Robert and Escoufier 1976). We further evaluated the statistical significance of each of the four computed  $R_V$ -coefficients by a random permutation test using 999 replicated matches of two tables (after random permutations of array rows), and we compared the observed  $R_V$ -coefficient and the distribution of values obtained from permutations.

Finally, to assess the relative contributions of biotic (plant community composition of preceding seasons) *vs.* abiotic (physical and chemical parameters of preceding seasons) characteristics of ponds to the variability of the plant community composition observed at a given date, we used the analysis proposed by Townsend et al. (2003) and used by de Castro et al. (2017). This analysis was performed between the

plant community composition recorded in November 2020 (at the end of the survey), and the biotic and abiotic characteristics of ponds from November 2018 to November 2020. Let  $PCPi$  and  $PCCi$  denote respectively the physico-chemical parameter table and the plant community composition table at the  $i$ th sampling date, and consider  $PCC_{N20}$  as the plant community composition table in November 2020. Assuming that the physico-chemical parameters at the  $i$ th sampling date would be a more efficient driver of the plant community composition in November 2020 than the plant community composition, we tested the null hypothesis  $R_V(PCPi, PCC_{N20}) = R_V(PCCi, PCC_{N20})$  against the alternative  $R_V(PCPi, PCC_{N20}) > R_V(PCCi, PCC_{N20})$  and we performed bootstraps on the statistics  $t = R_V(PCPi, PCC_{N20}) - R_V(PCCi, PCC_{N20})$  using 999 replicates. We assessed the statistical significance of the observed difference between pairs of  $R_V$ -coefficient by comparing it to the distribution of the simulated values. We used this approach for the 36 pairs of potential differences between the four physical and chemical parameters and the four plant community composition tables.

All data simulations and statistical analyses were performed using R 4.1.2. (R Core Team 2021).

## Results

### *Description of plant communities within ponds at Kerguelen*

Pond plant communities of the Kerguelen were characterized by a low species richness (S), and a high equitability (E). On average, ponds provide a habitat for five to six plant species, while equitability was on average  $> 0.7$  suggesting that plant species displayed similar relative frequencies. These two indices varied with time but not through space within the studied geographic area (Table 2). Species richness was higher in the second sampling year ( $S_{\text{summer2019}}=5.77\pm 1.27$ ;  $S_{\text{winter2020}}=5.64\pm 1.26$ ) as compared with the first one ( $S_{\text{summer2018}}=5.45\pm 1.33$ ;

$S_{\text{winter2019}}=5.22\pm 1.57$ ), while equitability slightly increased in winter ( $E_{\text{winter2019}}=0.81\pm 0.14$ ;  $E_{\text{winter2020}}=0.79\pm 0.12$ ) compared to summer ( $E_{\text{summer2018}}=0.76\pm 0.15$ ;  $E_{\text{summer2019}}=0.72\pm 0.16$ ).

Analyzing the composition of plant communities showed that relative frequencies of aquatic species varied from 0.00 to 0.30 across all locations and dates of sampling (Fig. 1). Overall, the most abundant aquatic species was *Juncus scheuchzerioides* while the rarest ones were *Limosella australis* and *Ranunculus moseleyi*. *R. moseleyi* was almost absent from the three sampled locations during the two winter periods, suggesting that the species was sensitive to seasonal variations in environmental factors. Non-aquatic species altogether [*i.e.* *Poa annua*, *Acaena magellanica*, *Agrostis magellanica*, and *Montia fontana*] generally dominated pond communities with mean relative frequencies ranging from 0.20 to 0.55 (Fig. 1).

The first three axes of the PCA performed on the mean relative frequencies of plant species, explained 49.3% of total inertia. Permutation tests revealed that the season had no significant effect on plant community composition in ponds (between-class variance = 0.011; *simulated-P* > 0.05), while the year and the location respectively explained only 1.0% (between-class variance = 0.010; *simulated-P*=0.046) and 7.1% (between-class variance = 0.070; *simulated-P*=0.001) of their variations. In contrast, a high proportion of variations in plant community composition (*i.e.* between-class variance= 0.595; *simulated-P*=0.001) was explained by differences among ponds, suggesting that mechanisms driving plant community structure operated at the local scale of the pond.

*Physical and chemical characteristics of ponds*

Kerguelen ponds appeared as shallow freshwater ecosystems (mean water depth < 16cm, although they can easily exceed 30 cm in depth depending on rain supply) with highly variable availability in nutrients (Table 3). pH was very close to neutral on average but its range indicated strong variations between ponds of the same location (Table 3). Water temperature was cool and overall stable among days (mean temperature and temperature variance, Table 3) but variations in pond size and water depth could cause strong within-day variations (up to  $\pm 10$  °C, A.-K. Bittebiere - field observation).

**Table 2.** Variations of plant community indexes in space (location) and time (year, season) assessed with mixed-models and pond as random factor. The significance of the explanatory variables was determined by ANOVA tests. Marginal R<sup>2</sup> indicates the percentage of index variance explained by the fixed effects; Conditional R<sup>2</sup> indicates the percentage of index variance explained by the whole model (including fixed and random effects).

	Marginal R <sup>2</sup>	Conditional R <sup>2</sup>	Year		Season		Location		Year×Season		Year×Location		Season×Location		Year×Season×Location	
			X <sup>2</sup>	P	X <sup>2</sup>	P	(df=1)	(df=2)	X <sup>2</sup>	P	X <sup>2</sup>	P	(df=2)	X <sup>2</sup>	P	X <sup>2</sup>
Richness <sub>‡</sub>	0.07	0.48	6.1	*	1.7	ns	2.8	ns	0.2	ns	2.3	ns	0.5	ns	2.3	ns
Equitability	0.07	0.50	3.3	t	12.8	***	1.2	ns	0.7	ns	2.3	ns	1.0	ns	0.3	ns

Notes:  $t$   $0.1 < P < 0.05$ , \*  $P < 0.05$ ; \*\*\*  $P < 0.001$ ; ns = not significant. †square-root-transformed.

**Table 3.** Mean ( $\pm$ SD) abiotic parameters measured in the ponds of Iles Kerguelen depending on the year, season, and location of sampling. Values in *italic* indicate the maximum and the minimum (*i.e.* the range) recorded for each season per year on each location.

Date	Location	Mean Temp. (°C)	Temp. variance (°C)	Water depth (cm)	Conduct. ( $\mu$ S.cm <sup>-1</sup> )	pH	DO (mg.L <sup>-1</sup> )	N-NH <sub>4</sub> <sup>+</sup> ( $\mu$ g.L <sup>-1</sup> )	N-NO <sub>3</sub> <sup>-</sup> ( $\mu$ g.L <sup>-1</sup> )	P-PO <sub>4</sub> <sup>3-</sup> ( $\mu$ g.L <sup>-1</sup> )	P <sub>bio</sub> (mg.g <sup>-1</sup> )	C/N	N <sub>tot</sub> (g.g <sup>-1</sup> )
Summer 2018	Isthme Bas	4.55	2.72	16.07	240.23	7.00	7.25	233.27	201.14	24.98	0.88	13.84	0.017
		( $\pm$ 1.34)	( $\pm$ 2.10)	( $\pm$ 11.75)	( $\pm$ 85.82)	( $\pm$ 0.81)	( $\pm$ 4.73)	( $\pm$ 298.24)	( $\pm$ 268.35)	( $\pm$ 38.97)	( $\pm$ 0.59)	( $\pm$ 2.35)	( $\pm$ 0.007)
		6.34	7.66-0.57	50.53-	452.00-	8.98-	14.65-	1597.00-	1379.50-	197.85-	2.26-	19.99-	0.032-
		1.82		3.60	142.35	5.88	0.08	76.60	45.50	0.00	0.17	8.95	0.003
	Molloy	4.64	6.03	15.04	155.66	7.04	9.84	566.13	254.30	25.65	0.79	12.63	0.013
		( $\pm$ 1.95)	( $\pm$ 1.48)	( $\pm$ 7.55)	( $\pm$ 51.85)	( $\pm$ 0.56)	( $\pm$ 4.86)	( $\pm$ 1415.07)	( $\pm$ 329.60)	( $\pm$ 54.60)	( $\pm$ 0.56)	( $\pm$ 1.43)	( $\pm$ 0.007)
	6.92-	9.34-3.59	35.11-	336.80-	8.07-	15.90-	7545.00-	1275.50-	221.97-	2.34-	17.32-	0.029-	
	1.89		4.22	102.54	6.10	0.15	59.55	28.00	0.00	0.00	10.06	0.002	
Cap		4.41	4.05	10.66	255.34	6.73	5.77	924.19	236.54	33.95	0.83	11.75	0.021
Ratmanoff		( $\pm$ 1.63)	( $\pm$ 1.08)	( $\pm$ 4.86)	( $\pm$ 77.13)	( $\pm$ 0.74)	( $\pm$ 4.16)	( $\pm$ 1677.30)	( $\pm$ 435.32)	( $\pm$ 50.44)	( $\pm$ 0.58)	( $\pm$ 1.25)	( $\pm$ 0.009)
		6.55-	6.02-2.15	27.50-	482.00-	9.09-	17.95-	7840.00-	2341.00-	199.55-	1.95-	13.87-	0.043-
		2.15		1.47	164.46	5.58	0.14	68.10	29.50	0.95	0.01	8.02	0.006
Winter 2019	Isthme Bas	3.31	3.00	14.10	238.10	6.78	8.57	95.48	103.31	31.38	0.70	16.38	0.015
		( $\pm$ 1.46)	( $\pm$ 2.43)	( $\pm$ 8.83)	( $\pm$ 117.77)	( $\pm$ 1.23)	( $\pm$ 4.39)	( $\pm$ 123.55)	( $\pm$ 39.55)	( $\pm$ 35.80)	( $\pm$ 0.32)	( $\pm$ 2.26)	( $\pm$ 0.006)
		5.17-	9.87-0.52	37.33-	605.20-	10.23-	13.54-	681.50-	198.50-	147.62-	1.24-	21.69-	0.029-
		-0.31		2.33	125.86	3.62	0.15	22.10	35.50	1.25	0.15	12.03	0.003
	Molloy	2.66	6.64	14.76	121.07	6.70	10.11	117.56	583.78	13.74	0.72	14.40	0.010
		( $\pm$ 1.91)	( $\pm$ 2.10)	( $\pm$ 8.00)	( $\pm$ 48.22)	( $\pm$ 0.60)	( $\pm$ 4.33)	( $\pm$ 247.10)	( $\pm$ 1085.69)	( $\pm$ 35.39)	( $\pm$ 0.37)	( $\pm$ 1.36)	( $\pm$ 0.005)
	5.04-	12.03-3.25	29.20-	230.34-	7.70-	16.14-	1401.70-	4793.00-	181.17-	1.45-	17.45-	0.022-	
	-0.30		0.83	66.92	5.28	0.15	8.15	50.50	0.00	0.04	11.49	0.003	
Cap		2.79	4.46	12.48	184.62	6.63	8.44	112.08	267.74	20.90	0.71	14.05	0.014
Ratmanoff		( $\pm$ 1.63)	( $\pm$ 1.49)	( $\pm$ 4.23)	( $\pm$ 53.31)	( $\pm$ 0.38)	( $\pm$ 4.17)	( $\pm$ 111.13)	( $\pm$ 711.41)	( $\pm$ 35.12)	( $\pm$ 0.38)	( $\pm$ 1.76)	( $\pm$ 0.006)
		5.20-	7.76-1.95	22.93-	319.00-	7.55-	15.84-	651.05-	3813.00-	152.66-	1.51-	18.66-	0.025-
		0.33		5.00	116.84	5.70	0.14	29.55	25.00	2.08	0.17	10.89	0.004
Summer 2019	Isthme Bas	5.68	4.51	17.00	197.00	6.85	10.87	71.61	75.38	28.24	0.70	16.11	0.015
		( $\pm$ 2.37)	( $\pm$ 4.02)	( $\pm$ 9.25)	( $\pm$ 29.18)	( $\pm$ 0.70)	( $\pm$ 2.74)	( $\pm$ 61.49)	( $\pm$ 24.59)	( $\pm$ 21.27)	( $\pm$ 0.45)	( $\pm$ 2.13)	( $\pm$ 0.005)

Summer 2019	Isthme Bas	5.68	4.51	17.00	197.00	6.85	10.87	71.61	75.38	28.24	0.70	16.11	0.015
		(±2.37) 9.77- 2.12	(±4.02) 16.82-0.62 2.80	(±9.25) 44.93- 2.80	(±29.18) 275.33- 147.86	(±0.70) 8.47- 5.41	(±2.74) 16.83- 4.40	(±61.49) 324.50- 31.00	(±24.59) 136.50- 13.50	(±21.27) 79.62- 4.30	(±0.45) 1.70- 0.23	(±2.13) 20.92- 12.25	(±0.005) 0.026- 0.004
	Molloy	6.44	9.99	18.63	141.47	7.21	12.99	629.84	72.15	6.97	0.96	15.23	0.010
		(±3.50) 10.99- 2.20	(±4.40) 20.51-3.93 8.25	(±6.57) 32.73- 8.25	(±115.35) 688.00- 73.52	(±0.86) 9.53- 6.00	(±2.76) 19.03- 6.39	(±1195.31) 5630.50- 51.00	(±54.43) 259.50- 21.50	(±6.72) 32.53- 0.00	(±0.60) 2.25- 0.09	(±2.42) 19.92- 10.63	(±0.005) 0.019- 0.002
	Cap	5.88	6.71	13.84	198.35	6.89	11.91	770.34	380.83	18.62	0.65	14.86	0.014
		(±2.87) 9.27- 2.40	(±3.05) 13.22-2.35 4.00	(±5.92) 28.33- 4.00	(±81.01) 411.40- 5.70	(±0.48) 8.23- 5.61	(±1.89) 17.09- 9.03	(±1566.66) 7330.00- 31.50	(±1121.00) 4590.00- 23.00	(±33.20) 145.38- 0.00	(±0.40) 1.69- 0.11	(±1.41) 17.76- 11.19	(±0.006) 0.022- 0.003
Winter 2020	Isthme Bas	5.04	3.72	22.65	212.45	7.11	10.40	126.34	116.59	49.57	0.59	14.29	0.018
		(±1.60) 7.37- 2.22	(±3.33) 13.94-0.51 6.43	(±13.93) 67.07- 6.43	(±43.76) 333.60- 151.18	(±0.41) 8.09- 6.39	(±2.19) 14.88- 4.62	(±46.37) 223.00- 65.50	(±102.82) 425.00- 3.00	(±50.71) 237.60- 5.01	(±0.39) 1.52- 0.01	(±1.83) 18.65- 9.72	(±0.007) 0.041- 0.004
	Molloy	5.41	8.24	17.41	112.13	6.83	10.97	395.76	180.07	7.04	0.59	13.61	0.011
		(±2.36) 8.34- 2.31	(±3.68) 16.99-3.21 4.00	(±7.84) 34.67- 4.00	(±54.82) 332.67- 54.94	(±0.46) 8.10- 6.08	(±2.90) 14.15- 1.70	(±804.68) 3334.50- 37.50	(±324.14) 1575.00- 3.00	(±6.86) 33.61- 0.00	(±0.35) 1.65- 0.07	(±1.48) 17.47- 11.30	(±0.005) 0.027- 0.004
	Cap	5.04	5.54	13.79	192.86	6.80	10.93	299.50	77.70	5.29	0.59	12.48	0.018
		(±1.95) 7.37- 2.48	(±2.54) 10.96-1.92 4.00	(±6.86) 31.33- 4.00	(±53.34) 326.00- 120.98	(±0.64) 7.68- 4.63	(±3.17) 14.38- 3.86	(±908.52) 4836.00- 21.00	(±182.17) 1030.50- 5.00	(±4.21) 21.50- 0.00	(±0.37) 1.48- 0.14	(±2.39) 16.86- 8.05	(±0.008) 0.034- 0.005

Notes: Temp. temperature; Conduct. specific conductance; Pbio: phosphore bioavailable. N = 30.

Locations and time (year, season) affected all these physical and chemical parameters (Tables 3, S1) either alone or in interactions, with no general pattern in the observed responses. For instance, all abiotic parameters varied with the sampling year except  $\text{NH}_4^+$ , and this response additionally depended on the season (mean and variance of water temperature, specific conductance, dissolved oxygen, C/N,  $\text{N}_{\text{tot}}$ ) and/or the location (temperature variance, dissolved oxygen,  $\text{PO}_4^{3-}$ ).

We performed a PCA on all abiotic parameters measured in the ponds. The first-three axes explained 46.7% of total variance (Fig. 2). The first axis described the trophic status of ponds based on water and sediment nutrient concentrations, and dissolved oxygen concentration (Fig. 2a), while the second and third axes were related to physical parameters, temperature variance and water depth on the one hand, mean temperature and pH on the other hand (Fig. 2b). We detected three different pond clusters regardless of time (year, season), and locations (Table S2). Cluster 1 corresponded to ponds with a high variance in water temperature together with high concentrations of dissolved oxygen, low concentrations of phosphorus (bioavailable P in sediments and  $\text{PO}_4^{3-}$ ) and nitrogen ( $\text{N}_{\text{tot}}$  in sediments,  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ ) (Fig. 2c). Cluster 2 was characterized by the highest values of water depth, low temperature variance, and intermediate concentrations of phosphorus

**Table 4.** Relationships between the plant community composition and the physical and chemical parameters recorded in ponds at each sampling date. Parameters from the permutation test in STATICO analysis are given with  $R_v$  quantifying the strength of the relationship (on a 0-1 scale), and simulated-P as the statistical significance of the observed  $R_v$ .

	$R_v$	Simulated-P
summer 2018	0.285	***
winter 2019	0.229	**
summer 2019	0.276	***
winter 2020	0.238	**

Notes: \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

(bioavailable P and  $\text{PO}_4^{3-}$ ) (Fig. 2c). Cluster 3 was related to occasionally extreme values in nutrient concentrations in water and sediments ( $\text{NH}_4^+$ ,  $\text{NO}_3^-$ ,  $\text{PO}_4^{3-}$ , and bioavailable P), high water temperature and low dissolved oxygen.

We detected a significant difference in pond distance to sea shore among pond clusters (ANOVA,  $F_{2/332}=25.4$ ,  $P < 0.001$ ; Fig. 3a). Ponds of clusters 2 and 3 were significantly closer to sea shore than ponds of cluster 1. In addition, the pond cluster affected the total vegetation cover (ANOVA,  $F_{2/164}=13.8$ ,  $P < 0.001$ ; Fig. 3b). Indeed, ponds of cluster 1 had significantly lower vegetation cover than those of cluster 2, while cluster 3 showed intermediate vegetation cover. Regarding plant community structure, species richness did not depend on the pond cluster (ANOVA,  $X_{1/165}=1.7$ ,  $P > 0.05$ ; Fig. 3c), while equitability was respectively the highest and the lowest in ponds of cluster 2 and 1, those of cluster 3 displaying an intermediate equitability (ANOVA,  $F_{2/164}=8.0$ ,  $P < 0.001$ ; Fig. 3d).

**Table 5.** Relationships between present plant community composition *i.e.* recorded during the last campaign of survey (summer 2020), and past plant community compositions (PCC), and past and present physical and chemical parameters (PCP, *i.e.* recorded during summer 2020 and the preceding seasons).  $R_v$ : strength of the relationship; *simulated-P*: statistical significance of the observed  $R_v$ .

	$R_v$	Simulated-P
PCC, winter 2020	0.575	<0.001
PCC, summer 2018	0.568	<0.001
PCC, summer 2019	0.553	<0.001
PCC, winter 2019	0.458	<0.001
PCP, winter 2019	0.227	<0.030
PCP, summer 2019	0.216	<0.040
PCP, winter 2020	0.196	ns
PCP, summer 2020	0.191	ns
PCP, summer 2018	0.179	ns

Notes: summer = November; winter = May.

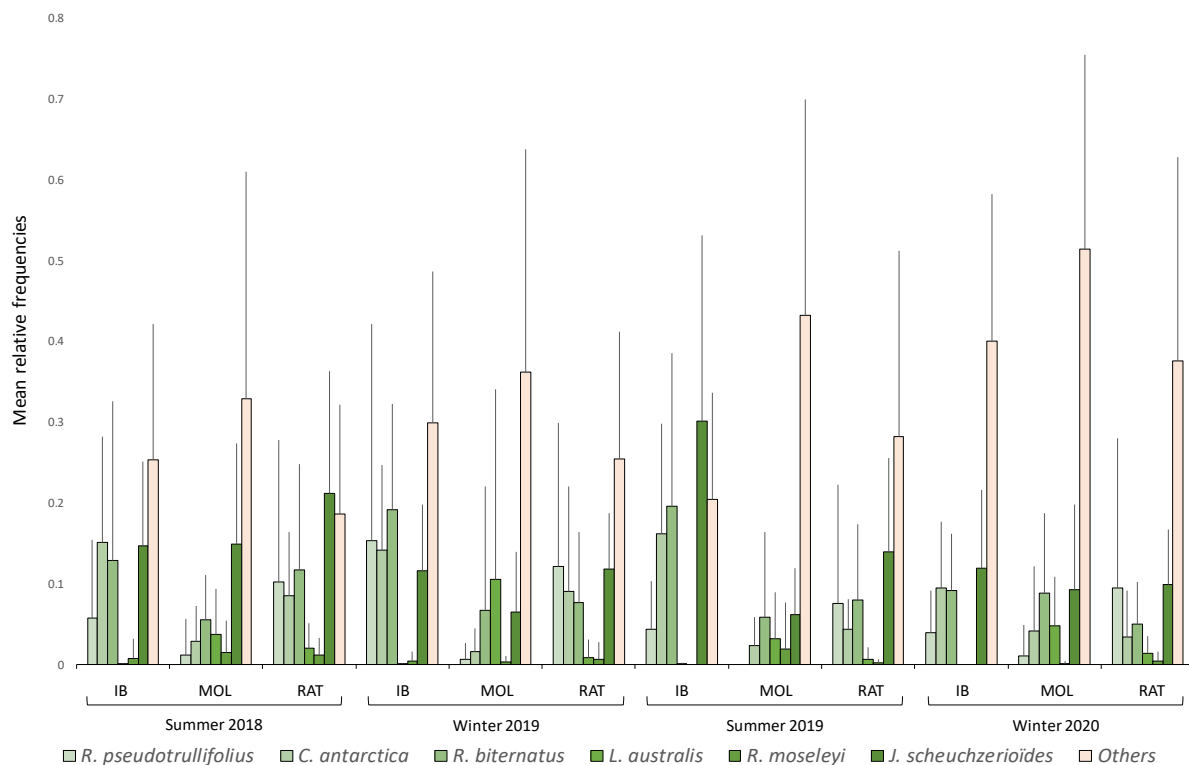


### Abiotic and biotic drivers of plant community composition through time

The composition of the plant community was significantly related to the physical and chemical parameters of ponds with a slightly stronger response in summer compared to winter (Table 4). No strong covariation of relative frequencies was detected among aquatic plant species (Figs. S3a, c, e, g). The plant community composition was similar in summers 2018 and 2019 (Figs. S3a, e), and more seasonally stable during the second sampling year in comparison with the first one (Figs. S3a, c, e, g). In addition, plant community composition was very similar between locations of sampling (Figs. S3a, c, e, g). More importantly, regardless of the sampling season and year, the variance of daily water temperature was a strong driver of the plant community composition. This effect was independent of mean water temperature (Figs. S3b, d, f, h). Ponds with higher water temperature variance among days were preferentially inhabited by *Juncus*

*scheuchzerioides* (summer 2018-2019 and winter 2019; Figs. S3a, e, g) and *R. pseudotrullifolius* (winter 1; Fig. S3c). The plant community composition during summer was also strongly determined by bioavailable P in sediments ( $P_{\text{bio}}$ ) and the specific conductance of pond water (Figs. S3b, f). During winter, the importance of abiotic parameters for plant community composition was more variable across sampling years, but nitrogen availability in water and sediments seemed determinant ( $N_{\text{tot}}$ , and  $\text{NO}_3^-$  or  $\text{NH}_4^+$ ) (Figs. S3d, h). Besides, sampling locations were mostly differentiated by the abiotic parameters especially along the second STATICO axis (Fig. S4) *i.e.* by the specific conductance of water (winter 2019 and summer 2019, Figs. S3d, f), and by the availability in  $\text{NH}_4^+$  (winter 2020, Fig. S3h).

Most tested relationships between the present (summer 2020) and past (summer-winter 2018-2020) physical and chemical parameters and plant community composition, and the present plant community composition (summer 2020;



**Figure 1.** Mean ( $\pm$ SD) composition of pond plant communities depending on the season and year. Varying shades of green represent different aquatic plant species (see accompanying legend), while light orange was used to represent relative frequencies of all non-aquatic species. IB: Isthme Bas, MOL: Molloy, RAT: Cap Ratmanoff.

Table 5) were statistically significant (Table 5) indicating the influence of past physical and chemical parameters (in winter and summer 2019 only), and of all past plant community compositions on present plant community composition. The differences in  $R_v$ -coefficients between plant community composition and physical and chemical parameters were all negative when significant (Table S3), suggesting that the relationships between present and past plant community compositions were overall stronger than the relationships between present plant community composition and present and past physical and chemical parameters. In addition, plant community composition of the two preceding seasons (winter 2020 and summer 2019) similarly influenced present plant community composition (summer 2020, Table S3).

## Discussion

In this study, our first assumption was partially validated, as indices of plant community structure varied through time but not through space. We confirmed that water depth, water temperature, and nutrient availability were the major parameters characterizing sub-Antarctic ponds habitat. Surprisingly, and contrary to our hypothesis, abiotic characteristics of ponds did not prevail on biotic ones in determining the plant community composition.

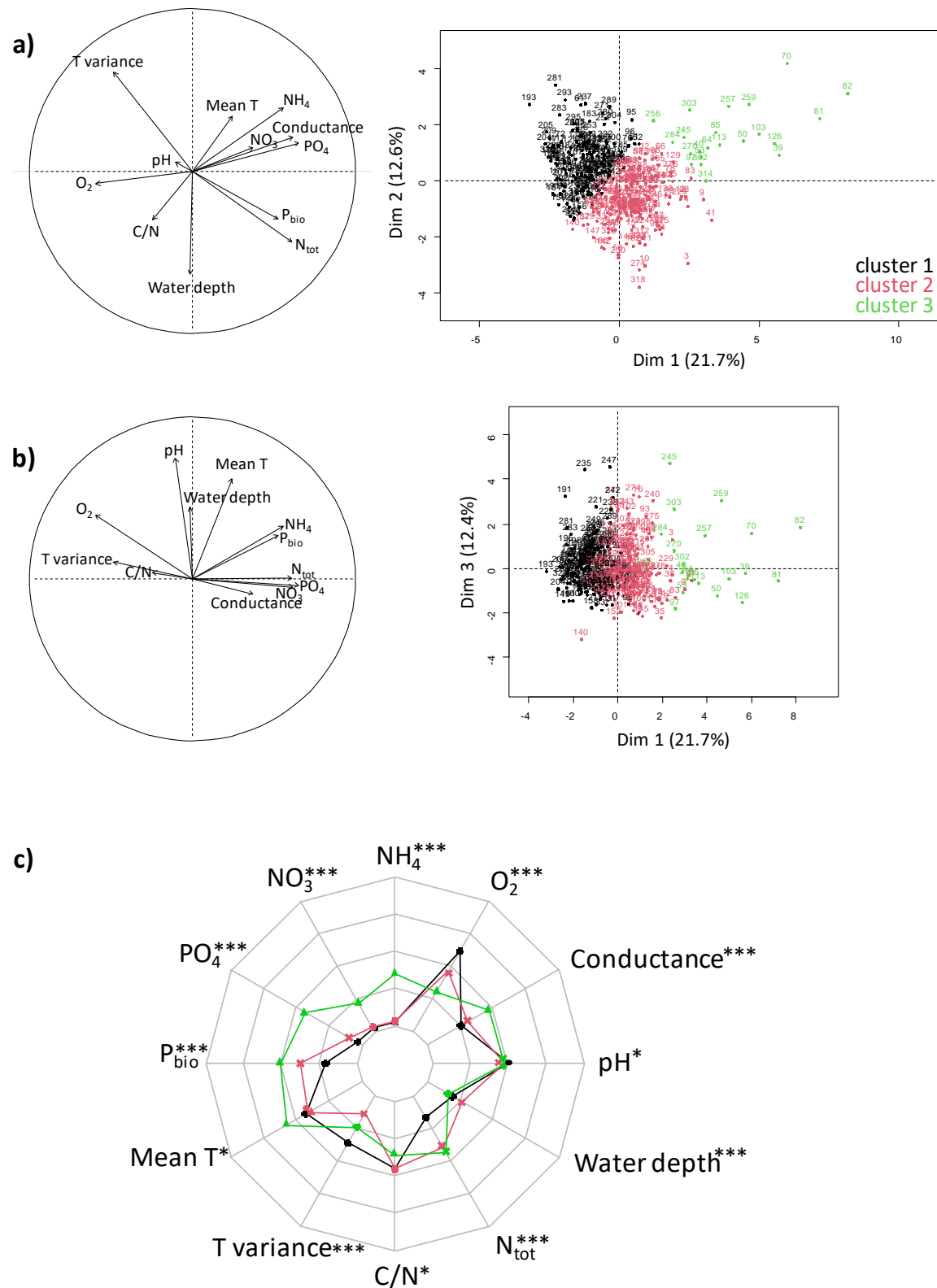
### *Pond habitats and their plant communities through space and time*

The studied ponds consisted in shallow freshwater ecosystems [mean water depth at 15.5 ( $\pm$ 8.7) cm]. They were characterized by intermediate level of specific conductance [186.1 ( $\pm$ 84.2)  $\mu\text{S}\cdot\text{cm}^{-1}$ ] and dissolved oxygen concentration [9.9 ( $\pm$ 4.1)  $\text{mg}\cdot\text{L}^{-1}$ ], which were consistent with rainfall supply. Indeed, [Voisin et al. \(2018\)](#) showed that specific conductance of urban wetlands receiving stormwater runoff ranged from 50 to 200  $\mu\text{S}\cdot\text{cm}^{-1}$ . Nutrient availability in the water was highly

variable, and pH was on average close to neutral (*i.e.* softwater habitat; see [Lacoul and Freedman 2006](#)) although the maximal and minimal values indicate heterogeneity among the ponds, likely reflecting different levels of photosynthetic activity (e.g. [Buapet et al. 2013](#)). At similar latitudes, close values of mean pH were recorded within lakes of the Macquarie and Kerguelen islands ([Tyler 1972](#)), and of South Georgia ([Hansson et al. 1996](#)). However, these ecosystems display higher specific conductance and lower phosphate concentration ([Hansson et al. 1996](#)) than that observed in our studied ponds. Phosphorus appears to be the limiting nutrient as usually observed in freshwaters ([Toivonen and Huttunen 1995](#); [Sarneel et al. 2011](#)). Indeed, mean N:P atomic ratio in water column (using  $\text{N-NH}_4^+$ ,  $\text{N-NO}_3^-$  and  $\text{P-PO}_4^{3-}$  concentrations reported on Table 3) was strongly higher (55:1) than the Redfield N:P ratio of 16:1, suggesting that P was a more limiting nutrient for primary producers than N ([Geider and La Roche 2002](#)). Mean daily temperature of water was about 4.7 °C, and was similar on average among consecutive days, albeit strong within days' variations were recorded. Specifically, water temperature could heat up during sunny days, sometimes reaching around 20 °C (AK. Bittebiere, field observations).

Location and time (year, season) affected all of the considered physical and chemical parameters measured from the ponds, either alone or in interaction, but we could not detect any general pattern in the observed changes. These complex patterns may result from factors such as variations in pond morphometry (pond size, depth) ([Hanson et al. 2007](#); [Nõges 2009](#)) and climatic conditions (air temperatures, rainfall) ([Dodds et al. 2019](#)) interacting through space and time, although this hypothesis remains to be thoroughly tested.

The studied ponds were poorly colonized by plants, with only five to six species being present, which is consistent with former studies performed at high

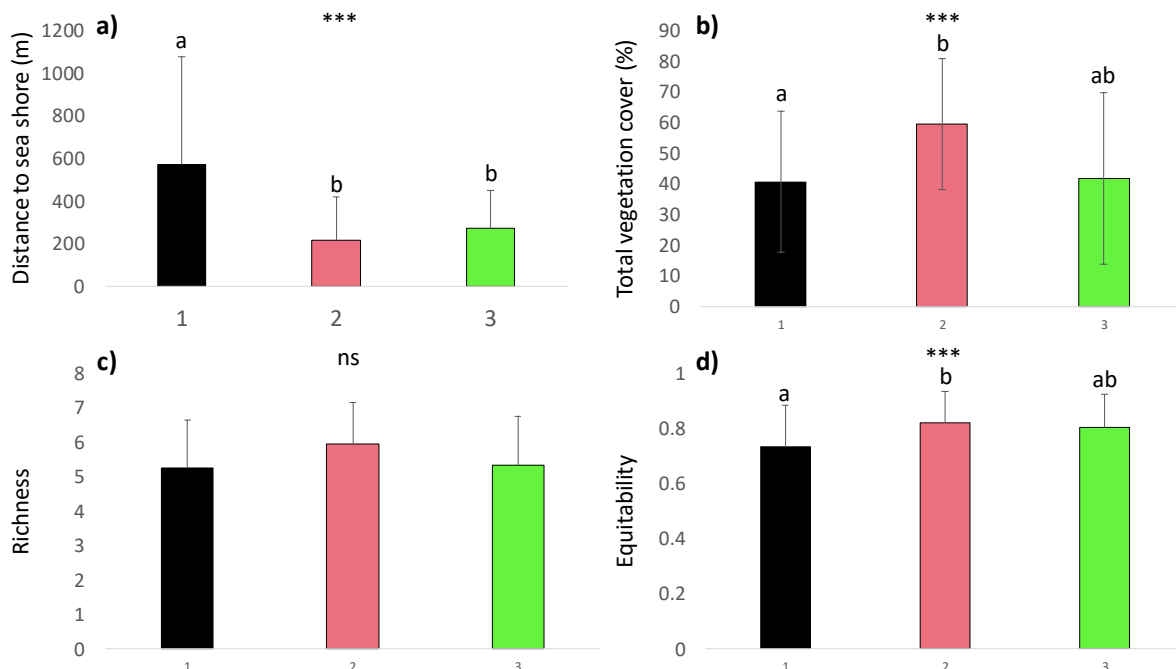


**Figure 2.** Principal component analysis and hierarchical clustering performed on the abiotic parameters of all ponds. Abiotic parameters and pond scores projected along a) axes 1 and 2, and b) axes 1 and 3. c) Mean abiotic parameters characterizing the clusters shown with different colors). Asterisks indicate significant difference of mean abiotic parameters between clusters (ANOVA tests) \*P < 0.05; \*\*\* P < 0.001, different symbols indicate different means (Tukey post-hoc tests). Tvariance – temperature variance, mean T – water temperature, O<sub>2</sub> – dissolved oxygen, P<sub>bio</sub> – bioavailable P. In a and b different numbers refers to different ponds at varying dates of sampling, and within different locations (N = 360 in total).

latitudes on aquatic ecosystems (Lacoul and Freedman 2006; Heino and Toivonen 2008). Field observations also reveal the presence of algae and cyanobacteria in these systems (AK. Bittebiere, field observations). Plant species like *Poa annua* and *Acaena magellanica* colonized ponds from their edges, likely benefiting from more frequent decrease in water depth related to rainfall reduction (Casanova and Brock 2000). These species even became the most frequent, although not dominant (high equitability), probably because they display faster growth rate and higher competitive ability than the rarest aquatic species *Ranuncunculus moseleyi* and *Limosella australis*. Different mechanisms were suggested to explain high equitability of aquatic plant communities in the literature, such as low pressure of vegetative propagules, high water level (Li et al. 2015), or disturbance (e.g. through grazing, reducing the dominance of the most abundant species) (Wood et al. 2012). In the shallow ponds of Kerguelen, as all species are clonal, we can hypothesize that disturbance,

probably by sea animals, is the mechanism preventing species from becoming dominant.

Contrary to our expectations, this composition of pond communities did not vary much at the regional scale, suggesting that aquatic species dispersal was not limited within Kerguelen (Capers et al. 2010). Our observations reveal that most variation of the plant community composition was actually detected among ponds. Mechanisms driving pond community assembly thus operated at local scale, likely involving abiotic and biotic filters (Violle et al. 2012) such as water trophic level (Alahuhta 2015) and species interactions (Sarneck et al. 2011). The rarest species may thus only occur where the ecological conditions match with their biological and ecological requirements. Based on our results, we argue that future studies of pond systems have to be conducted at this spatial scale.



**Figure 3.** Mean ( $\pm$ SD) cluster values (labelled from 1 to 3 along the first axis of the PCA performed on abiotic parameters) for a) distance from sea shore, b) percentage of vegetation cover within the pond, c) plant community richness, d) plant community equitability. Asterisks above the figures indicate the significance of the clustering on the response variable (ANOVA tests), ns  $P > 0.05$ ; \*\*\*  $P < 0.001$ , different letters indicate significant differences in mean response variable among clusters (Tukey post-hoc tests).

### *Different pond habitats*

Three pond clusters, *i.e.* habitats, related expectedly to water nutrients, water depth, and temperature, could be discriminated across ponds. More importantly, not only the mean parameters, but also their variance, determined pond habitats. These differences could be, at least partially, explained by the distance to sea shore, *i.e.* by the frequency of visitation by sea animals such as elephant seals and penguins. Indeed, ponds that were the most distant from the sea shore (cluster 1) displayed the lowest nutrient concentrations. By contrast, ponds close to the sea shore, *i.e.* more easily reachable by sea animals, showed intermediate (cluster 2) to high concentrations of phosphorus (P bioavailable,  $\text{PO}_4^{3-}$ ) and nitrogen ( $\text{N}_{\text{tot}}$ ,  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ ) leading to eutrophication episodes associated with high water temperature, and involving low dissolved oxygen, cluster 3). Differences in nutrient availability between ponds of clusters 2 and 3 may have resulted from stochastic visitation of different sea animals. Indeed, penguins and elephant seals may supply pond water into varying source of nitrogen ( $\text{NH}_4^+$ ,  $\text{NO}_3^-$ , urea, and uric acid) that can be differentially assimilated by plant species (Erskine et al. 1998). In particular, *Callitriche antarctica* strongly benefits from the guano deposition from penguins (Erskine et al. 1998). In addition, seasonal variations in their feeding habits and use of ponds (Cherel et al. 2007) may explain the observed nitrogen dynamics in water and sediments. This interpretation suggests that these ecosystems heavily rely on trophic exchanges with surrounding oceanic waters, as formerly suggested by Smith (2008) and Lebouvier et al. (2011). Similar influence of sea animals that deposit substantial amount of feces, urine, and molted skin or feathers together with carcasses, have been demonstrated in other Antarctic and sub-Antarctic ecosystems such as terrestrial grasslands at Marion Island (Panagis 1985) or larger freshwater ecosystems (lakes) in the Antarctic (Smith 1985). Interestingly, the habitat differentiation that we have highlighted here,

occurred within restricted area (at the location scale) along a few hundred meters.

Ultimately, changes in the nutrient availability caused variations in plant community structure and pond ecosystem functioning. Intermediately fertilized ponds had higher vegetation cover and equitability. In plant communities with low equitability, fertilization usually enhances the dominance of already successful competitors, and accelerates local extinction rates (Wilsey and Polley 2004). However, in our studied ponds, dominance within plant communities was low and the different species were equally rare. It has been shown in the literature that sea animal fertilization could enhance species persistence, by increasing population sizes (Hillebrand et al. 2007) and stimulating higher plant growth. Nevertheless, higher fertilization did not seem to benefit to plant cover in the present survey, probably because of eutrophication phenomenon, involving water turbidity that would have limited light availability.

Finally, our results reemphasize the tight trophic interaction that exists between marine and terrestrial ecosystems at the sub-Antarctic islands (Smith 1985; Convey and Lebouvier 2009). Elephant seals may additionally structure aquatic plant communities through trampling and soil compaction (Tejedo et al. 2009) although this effect was not considered in our study. In the end, this suggests that decrease in sea animal populations, as observed for example in Macquarie Islands (Hindell et al. 2017), could have serious impacts on the plant community dynamics in ponds (Jenkin 1997; Erskine et al. 1998).

### *Physical and chemical parameters of ponds determine plant community composition*

Our result showed how the physical and chemical parameters of ponds could drive the plant community composition. This abiotic control appeared slightly stronger in summer, *i.e.* the growing season, than in winter, and was mostly attributed to the variance in daily

water temperature within ponds, regardless of the sampling season and the year. In Kerguelen, water temperature appears independent from pond area and water depth (Douce et al., in prep.). Ponds with higher variation in water temperature among days were preferentially inhabited by *J. scheuchzerioides* and *R. pseudotrullifolius*, suggesting that these two aquatic species could be more tolerant than the four others to the instability of temperatures resulting from climate changes of Kerguelen, although this assertion remains to be tested. This finding additionally raises the question of the ability of the other species to cope with these changes in the upcoming years (Lebouvier et al. 2011). Besides, aquatic plant species found in the sub-Antarctic region have restricted distribution areas (*R. moseleyi* is even suspected to be endemic of Kerguelen) (Hennion et al. 1994; Chau et al. 2021), and conservation issues are also of outmost concern in the face of climate change. More widely, since aquatic plants play a major role in the functioning of freshwater ecosystems (Jeppesen et al. 1997; Iacarella et al. 2018; Reitseman et al. 2018; Lürig et al. 2020), the resistance of pond ecosystem to the on-going rising of water temperature is highly questionable.

A new finding emanated from our study, which demonstrated that the past abiotic conditions in ponds acted more significantly on the present plant community composition than present abiotic conditions. However, and contrary to our expectations, this abiotic influence did not prevail on the ‘footprint’ associated to past plant community composition on the present one. Indeed, one can have expected that under the harsh abiotic conditions of Kerguelen combined to the high variability in pond abiotic parameters observed through years and seasons, abiotic conditions would be the strongest determinant of plant community composition. The effect of past experience in aquatic plants can be explained by two non-mutually exclusive hypotheses related to their clonal properties (as studied communities were dominated by perennials). First, aquatic plants display both

ramets and connections of which lifespans exceed the year, ensuring the stability of their population sizes (Winkler and Fischer 2002; Stöcklin and Winkler 2004) within ponds. Connections are in particular involved in resources storing (carbohydrates) at the more or less long term, to support further individual growth (Stuefer and Huber 1998, 1999). Second, clonal plants are known to integrate the past experience of their interactions and adjust their present growth accordingly (Turkington et al. 1991; Bittebiere and Mony 2015), ultimately determining their persistence within the present community (Bittebiere and Mony 2015). This memory-like process is based on the availability of resources: ramets share information on resource depletion by neighbors within the clone, depending on the integration distance that mimic the duration of clone memory of the habitat conditions (Louâpre et al. 2012). Therefore, longer term studies are needed to precisely determine the actual duration of the influence exerted by abiotic and biotic parameters on pond plant communities.

## Conclusions

To our knowledge, this study is the first focusing on pond ecosystems at Kerguelen. It provides new insights on the relationships between the dynamics and functioning of pond plant communities and their habitat, which can serve as a basis for future studies dealing with the impact of climate change within the whole sub-Antarctic region. Indeed, other archipelagos like Prince Edward Islands (Chau et al., 2021), and Heard and MacDonald Islands (Bergstrom and Selkirk 2000) harbor the same aquatic species and pond habitats.

In particular, we have demonstrated the importance of past abiotic and biotic parameters on pond plant communities, highlighting the need for long-term studies dedicated to these threatened ecosystems, especially in a context of climatic warming. Our study additionally showed that water temperature variability is critical for plant

community and subsequently for the whole pond ecosystem. This result motivates for conducting new studies on the mechanisms underlying the responses of aquatic plants to temperature by investigating how thermal stress may affect plant growth (Riis et al. 2012) and physiological strategies (Arbona et al. 2013).

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### Author contributions statement

AKB, FMB, LS, DR, and CS conceived and designed research. AKB and PD collected the data. FV performed the chemical analyses of the samples. AKB, PED, and SD analysed data. All authors contributed to the writing and approved the manuscript.

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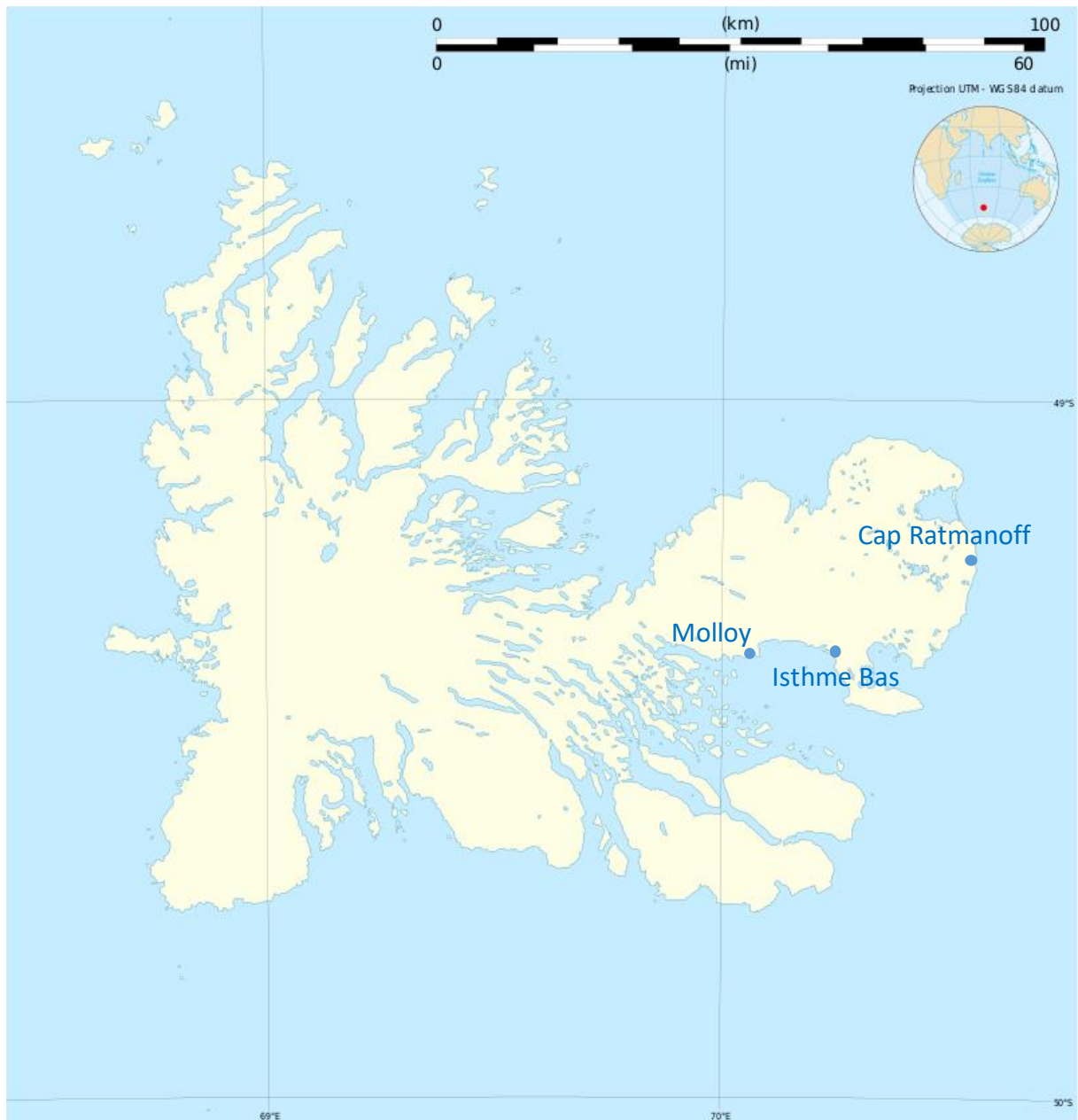
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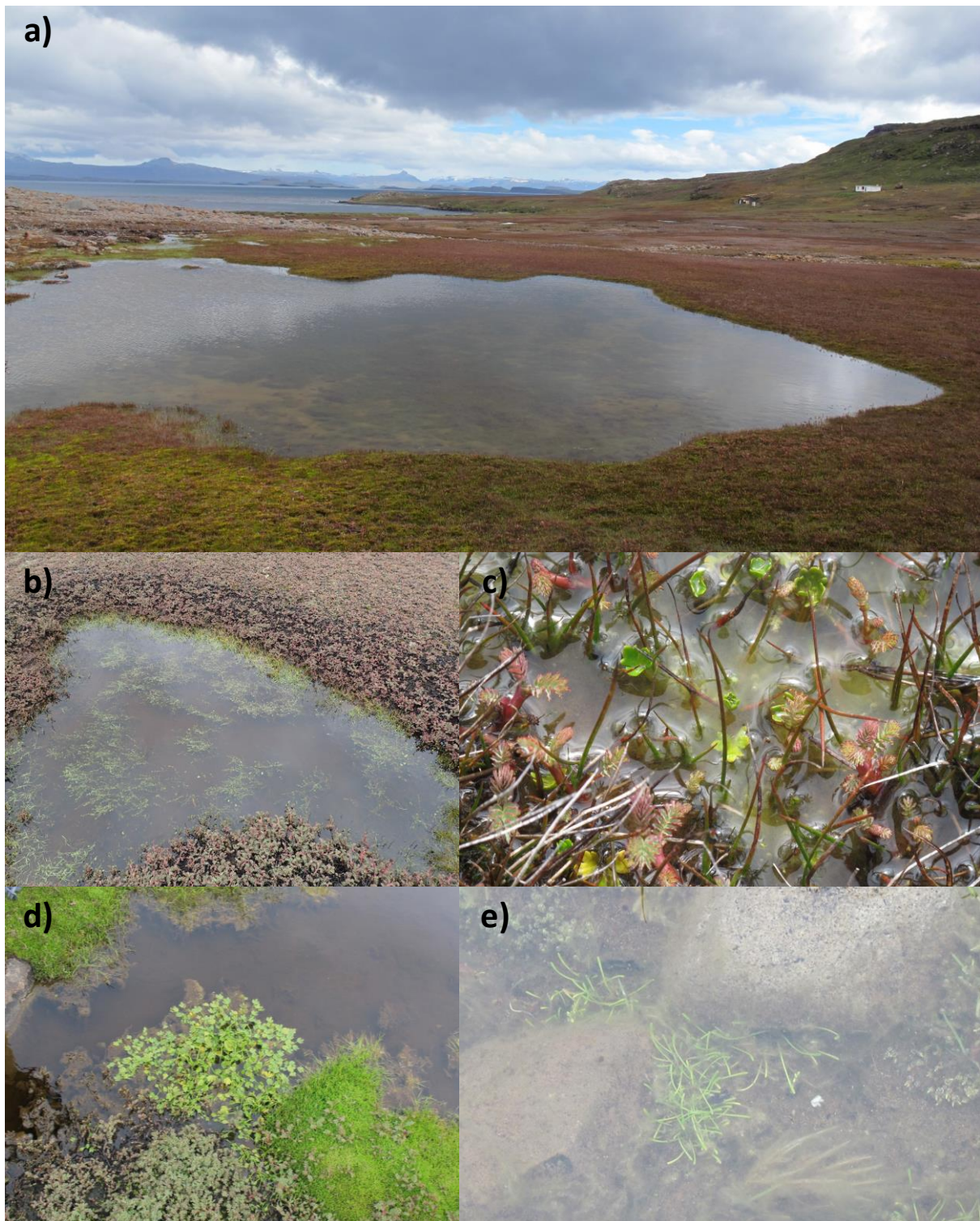
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## Supplementary information



**Figure S1.** Distribution of the sampling locations within the Kerguelen archipelago.



**Figure S2.** Description of the studied systems. a) Studied pond of Molloy including patches of *Ranunculus moseleyi*, b) pond with floating canopy of *Callitriche antarctica*, c) mixture of *Juncus scheuchzerioides*, *Ranunculus biternatus*, and *Acaena magellanica*, d) floating leaves of *Ranunculus pseudotrullifolius*, e) submerged plants of *Limosella australis*.

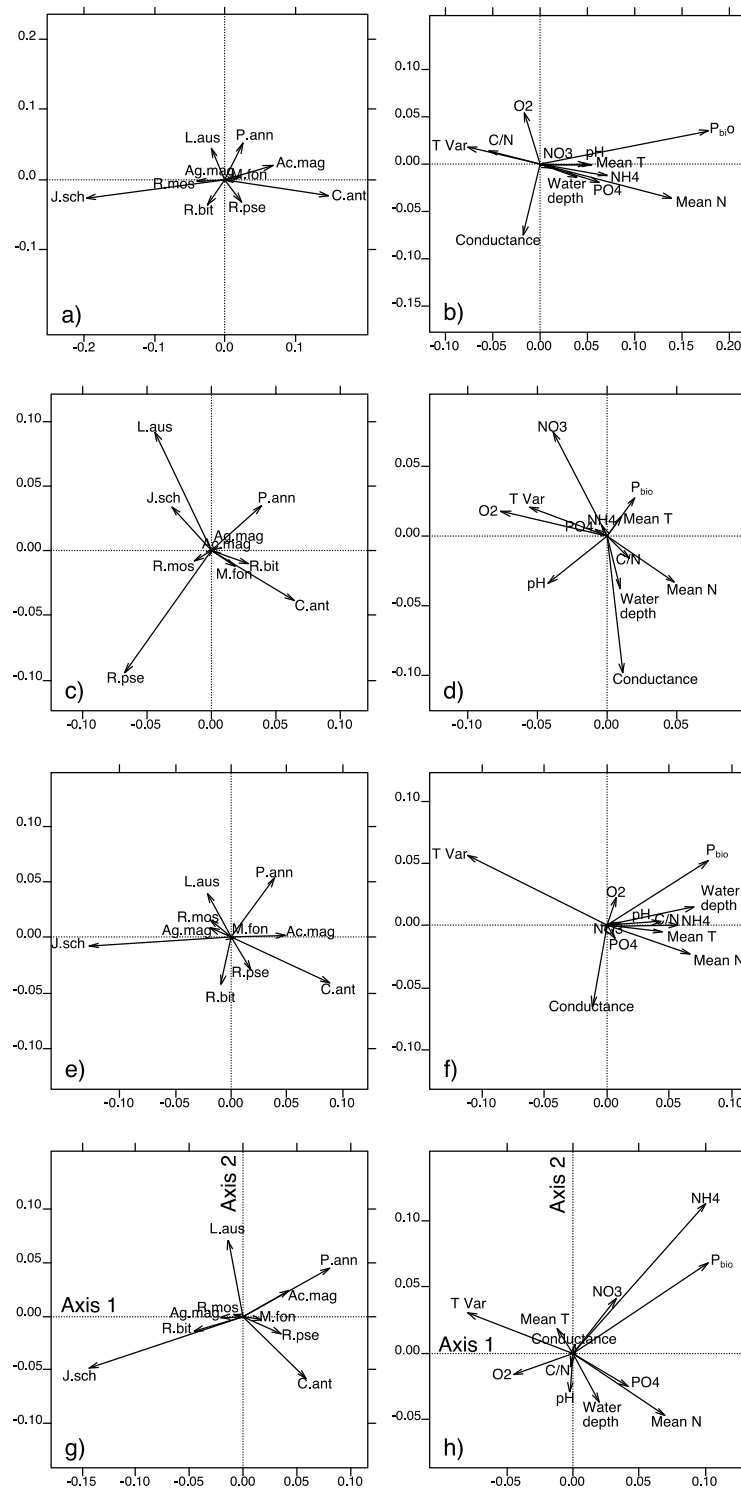
**Table S1.** Abiotic parameters of ponds through space (location) and time (year, season). The effects of year, season, and location on abiotic parameters were assessed through mixed-model procedures with the pond as random factor, and the significance of the explanatory variables was determined through ANOVA tests.

	Year		Season		Location		Year*Season		Year*Location		Season*Location		Year*Season*Location	
	(df=1)	P	(df=1)	P	(df=2)	P	(df=1)	P	(df=2)	P	(df=2)	P	(df=2)	P
	X <sup>2</sup>		X <sup>2</sup>		X <sup>2</sup>		X <sup>2</sup>		X <sup>2</sup>		X <sup>2</sup>		X <sup>2</sup>	
Mean temperature (°C)↓	44.3	***	30.3	***	3.9	ns	25.8	***	3.2	ns	2.6	ns	2.6	ns
Temperature variance (°C)↓	56.1	***	2.3	ns	30.3	***	12.9	***	8.8	*	0.3	ns	1.7	ns
Water depth (cm)	32.8	***	1.1	ns	4.2	ns	1.6	ns	3.1	ns	3.2	ns	13.6	**
Specific conductance (mS.cm <sup>-1</sup> )	10.6	**	9.3	**	48.0	***	4.4	*	1.7	ns	7.5	*	3.5	ns
pH	4.6	*	5.3	*	1.9	ns	1.2	ns	0.2	ns	6.3	*	3.5	ns
Dissolved oxygen (mg.L <sup>-1</sup> )	68.8	***	0.1	ns	8.5	*	12.8	***	7.3	*	4.2	ns	1.2	ns
NH <sub>4</sub> <sup>+</sup> (µg.L <sup>-1</sup> )	0.2	ns	14.0	***	5.8	t	1.7	ns	1.0	ns	7.2	*	0.1	ns
NO <sub>3</sub> <sup>-</sup> (µg.L <sup>-1</sup> )	4.8	*	0.1	ns	4.6	t	1.5	ns	4.3	ns	6.7	*	2.9	ns
PO <sub>4</sub> <sup>3-</sup> (µg.L <sup>-1</sup> )	3.9	*	0.5	ns	6.8	*	1.3	ns	13.5	**	12.9	**	0.6	ns
P <sub>bio</sub> (mg.g <sup>-1</sup> )	5.5	**	16.1	***	0.4	ns	0.6	ns	4.0	ns	1.9	ns	5.3	t
C/N	9.7	**	0.5	ns	31.1	***	119.8	***	3.8	ns	0.8	ns	2.0	ns
N <sub>tot</sub> (g.g <sup>-1</sup> )	4.2	*	1.7	ns	11.2	**	49.4	***	2.8	ns	1.1	ns	9.2	**

Notes: t 0.1 < P < 0.05; \* P < 0.05; \*\* P < 0.01; \*\*\* P < 0.001; ns = not significant. ↓arctan-transformed

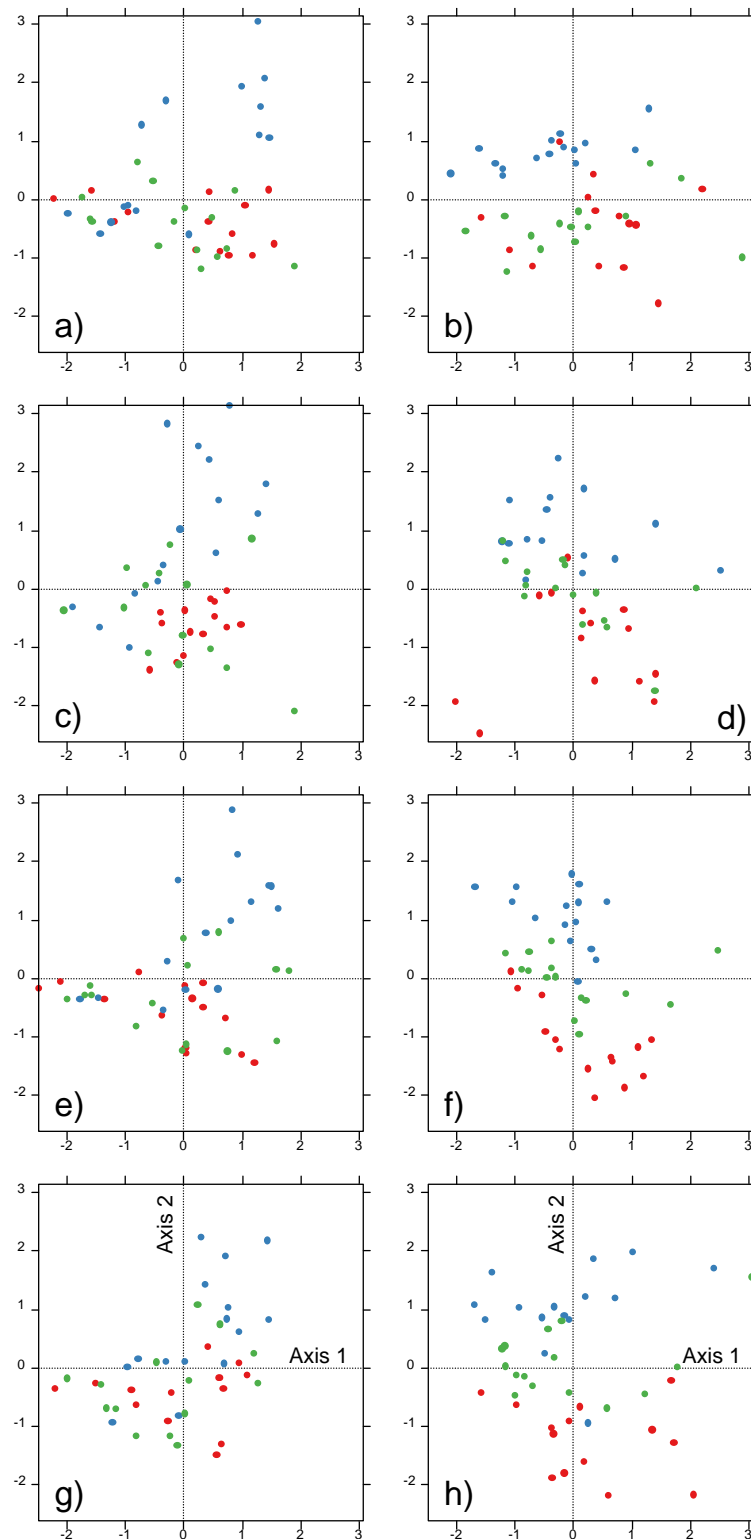
**Table S2.** Number of pond occurrences per cluster detected through the Ward analysis (performed from the PCA of pond abiotic parameters). One occurrence corresponds to one date of abiotic parameters measurements. IB Isthme Bas, MOL Molloy, RAT Cap Ratmanoff.

	Cluster1	Cluster2	Cluster3	Total
IB2	7	0	0	7
IB3	7	1	0	8
IB4	0	5	2	7
IB5	0	8	0	8
IB6	0	8	0	8
IB7	0	8	0	8
IB8	2	6	0	8
IB9	0	8	0	8
IB10	5	3	0	8
IB11	5	2	0	7
IB12	0	8	0	8
IB13	0	8	0	8
IB14	2	6	0	8
IB15	1	2	3	6
MOL1	4	2	1	7
MOL2	6	2	0	8
MOL3	3	5	0	8
MOL4	3	5	0	8
MOL5	2	3	2	7
MOL6	6	1	1	8
MOL7	6	2	0	8
MOL8	6	0	0	6
MOL9	8	0	0	8
MOL10	7	0	0	7
MOL11	8	0	0	8
MOL12	8	0	0	8
MOL13	8	0	0	8
MOL14	1	5	2	8
MOL15	4	3	0	7
RAT1	5	3	0	8
RAT2	1	3	2	6
RAT3	0	4	3	7
RAT4	0	5	3	8
RAT5	3	3	1	7
RAT6	0	7	1	8
RAT7	2	6	0	8
RAT8	0	8	0	8
RAT9	3	4	0	7
RAT10	8	0	0	8
RAT11	7	1	0	8
RAT12	8	0	0	8
RAT13	0	8	0	8
RAT14	2	6	0	8
RAT15	5	1	1	7



**Figure S3.** Results of a STATICO analysis showing the loadings of plant species (left) and the corresponding loadings of physical and chemical parameters (right) along the first-two STATICO axes with a) and b) for summer 2018, c) and d) for winter 2019, e) and f) for summer 2019, and g) and h) for winter 2020. The length and orientation of the arrows indicates the strength of correlations between axes 1 and 2, and either species abundances (left) or physical and chemical parameters (right). T Var – temperature variance, Mean T – water temperature, O<sub>2</sub> – dissolved oxygen, P<sub>bio</sub> – bioavailable P; L.aus - *Limosella australis*, C.ant - *Callitriche antarctica*, J.sch - *Juncus scheuchzerioides*, R.bit - *Ranunculus biternatus*, R.pse - *R. pseudotrullifolius*, R.mos - *R. moseleyi*, P.ann - *Poa annua*, Ac.mag - *Acaena magellanica*, Ag.mag - *Agrostis magellanica*, M.fon - *Montia fontana*.





**Figure S4.** Results of a STATICO analysis showing the scores of ponds from plant communities (left), and the corresponding scores of ponds from physico-chemical parameters (right) along the first two axes with a) and b) for summer 2018, b) and c) for winter 2019, d) and e) for summer 2019, and g) and h) for winter 2020. Colors stand for ponds belonging to a given location with Molloy in blue, Cap Ratmanoff in green, and Isthme Bas in red.

**Table S3.** Differences in the strengths of the relationships ( $R_v$ -coefficients) between the plant community composition of summer 2020 and the different plant community composition and the physico-chemical parameters of previous seasons. P: statistical significance of the observed  $R_v$  differences.

	observed $R_v$ differences	Simulated P
PCP <sub>N18</sub> -PCC <sub>M20</sub>	-0.396	0.001
PCP <sub>N18</sub> -PCC <sub>N18</sub>	-0.389	0.001
PCP <sub>N20</sub> -PCC <sub>M20</sub>	-0.383	0.001
PCP <sub>M20</sub> -PCC <sub>M20</sub>	-0.379	0.001
PCP <sub>N20</sub> -PCC <sub>N18</sub>	-0.377	0.001
PCP <sub>N18</sub> -PCC <sub>N19</sub>	-0.374	0.001
PCP <sub>M20</sub> -PCC <sub>N18</sub>	-0.372	0.001
PCP <sub>N20</sub> -PCC <sub>N19</sub>	-0.362	0.001
PCP <sub>N19</sub> -PCC <sub>M20</sub>	-0.359	0.001
PCP <sub>M20</sub> -PCC <sub>N19</sub>	-0.357	0.001
PCP <sub>N19</sub> -PCC <sub>N18</sub>	-0.353	0.001
PCP <sub>M19</sub> -PCC <sub>N18</sub>	-0.342	0.001
PCP <sub>N19</sub> -PCC <sub>N19</sub>	-0.337	0.001
PCP <sub>M19</sub> -PCC <sub>N19</sub>	-0.327	0.001
PCP <sub>N18</sub> -PCC <sub>M19</sub>	-0.279	0.017
PCP <sub>N20</sub> -PCC <sub>M19</sub>	-0.267	0.008
PCP <sub>M20</sub> -PCC <sub>M19</sub>	-0.262	0.022
PCP <sub>N19</sub> -PCC <sub>M19</sub>	-0.243	ns
PCP <sub>M19</sub> -PCC <sub>M19</sub>	-0.232	ns
PCC <sub>M20</sub> -PCC <sub>M19</sub>	0.116	0.001
PCC <sub>N18</sub> -PCC <sub>M19</sub>	0.110	0.001
PCC <sub>N19</sub> -PCC <sub>M19</sub>	0.095	0.001
PCC <sub>M20</sub> -PCC <sub>N19</sub>	0.022	ns
PCP <sub>M20</sub> -PCP <sub>N18</sub>	0.017	ns
PCC <sub>N18</sub> -PCC <sub>N19</sub>	0.015	0.008
PCP <sub>N20</sub> -PCP <sub>N18</sub>	0.012	ns
PCC <sub>M20</sub> -PCC <sub>N18</sub>	0.006	ns
PCP <sub>N19</sub> -PCP <sub>M19</sub>	0.000	ns
PCP <sub>M19</sub> -PCC <sub>M20</sub>	-0.000	ns
PCP <sub>N20</sub> -PCP <sub>M20</sub>	-0.005	ns
PCP <sub>M20</sub> -PCP <sub>N19</sub>	-0.020	ns
PCP <sub>N20</sub> -PCP <sub>N19</sub>	-0.024	ns
PCP <sub>M20</sub> -PCP <sub>M19</sub>	-0.030	ns
PCP <sub>N20</sub> -PCP <sub>M19</sub>	-0.035	ns
PCP <sub>N18</sub> -PCP <sub>N19</sub>	-0.037	ns
PCP <sub>N18</sub> -PCP <sub>M19</sub>	-0.047	ns

Notes: PCC plant community composition table; PCP physico-chemical parameters table; N November - summer; M May - winter; 18 2018, 19 2019, 20 2020. For example: PCP<sub>N18</sub> refers to the table of physico-chemical parameters measured within ponds in November 2018.

## b. Approche en conditions contrôlées

Les systèmes de type mésocosme permettent de faire varier précisément les conditions thermiques et les assemblages d'espèces (*i.e.* interactions plantes-plantes), tout en s'affranchissant des effets confondants des multiples autres paramètres rencontrés *in situ*. Ils apportent ainsi des réponses convaincantes en écologie, mais ne peuvent pas reproduire parfaitement la complexité des facteurs abiotiques, avec leurs variations et leurs interactions.

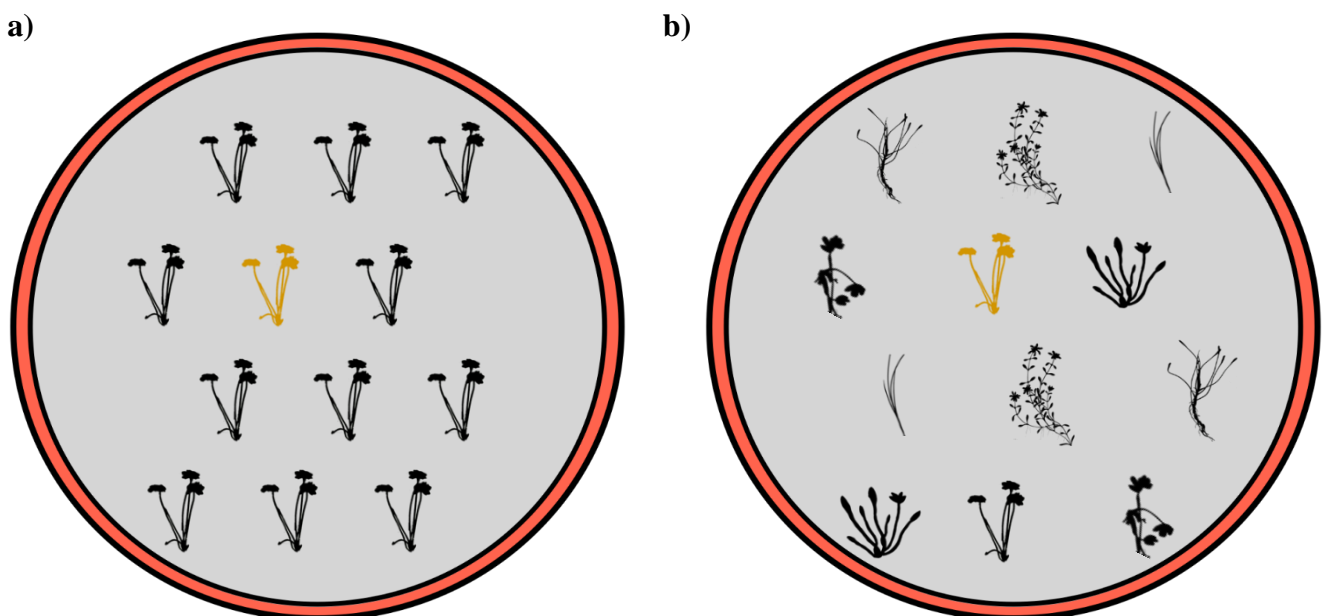
Deux expérimentations ont été réalisées en conditions contrôlées, en chambres thermorégulées. La première expérimentation, menée sur la plateforme technique et scientifique des Iles Kerguelen « BIOMAR », se place à l'échelle spécifique et vise à identifier les mécanismes sous-jacents aux réponses observées *in situ*, par l'étude de l'effet conjoint d'un gradient de température et des interactions plantes-plantes, chez trois espèces de macrophytes de la région subantarctique (**article V**). La deuxième expérimentation, menée au sein de la plateforme « Indoor » du LEHNA (Villeurbanne), s'inscrit dans une dynamique Eco-Evo à l'échelle de l'écosystème et vise à tester comment la réponse fonctionnelle d'une espèce de macrophyte à la combinaison des interactions plante-plante × températures peut affecter la décomposition de la litière et les processus écosystémiques associés, et impacter par rétroaction les traits fonctionnels et la performance (*i.e.* biomasse et multiplication clonale) des individus de cette même espèce (**article VI**).

### i. Expérimentation au BIOMAR : réponses fonctionnelles de trois espèces de macrophytes à des températures extrêmes dans un contexte d'interactions plantes-plantes

Cette expérimentation vise à déterminer la réponse fonctionnelle de trois espèces de macrophytes (*C. antarctica*, *R. moseleyi*, *R. pseudotrullifolius*) à un gradient de températures et différentes modalités d'interactions plantes-plantes. *R. biternatus*, *L. australis* et *J. scheuchzerioides* ont également été utilisées comme espèces compétitrices. Les cultures de cette expérimentation ont été établies à partir de modules adultes (*i.e.* unités composées de tiges, feuilles, racines et un entrenœud de connexion) récoltés sur divers sites de la Grande Terre (Iles Kerguelen) afin de maximiser leur variabilité génétique. Trois types de cultures en pots ont été réalisées pour chacune des trois espèces : un module seul (témoin sans compétition) et un module cible cultivés avec un voisinage de conspécifiques (monoculture – compétition

intraspécifique) ou constitué des cinq autres espèces de macrophytes rencontrées *in situ* (compétition interspécifique). Ces assemblages ont été cultivés sous trois températures [température témoin  $T = 13^{\circ}\text{C}$ ,  $T-5^{\circ}\text{C}$ ,  $T+5^{\circ}\text{C}$ ]. La température témoin à  $13^{\circ}\text{C}$  correspond à la température moyenne de l'eau des mares observée en journée et en période de végétation *in situ*. Ainsi, les températures à  $-5^{\circ}\text{C}$  et  $+5^{\circ}\text{C}$  correspondraient respectivement à des limites basses et hautes des températures optimales de croissance. Le témoin sans compétition visait à déterminer la gamme de tolérance thermique pour chacune des espèces étudiées. Les deux autres modalités d'interactions ont permis de tester si les effets des variations de températures sur les traits fonctionnels des trois espèces de macrophytes, et donc la résistance à un potentiel stress thermique froid ou chaud, dépendaient du voisinage environnant. Au total, neuf modalités de cultures ont été testées par espèces, répliquées dix fois chacune. Un génotype a été assigné par réplicat, afin de prendre en compte l'effet de différents génotypes sur la réponse et de mesurer la plasticité comme la norme de réaction du génotype.

La modalité témoin consistait à cultiver un unique module au centre du pot. Pour les modalités d'interactions inter- et intraspécifiques, un patron de plantation en quinconce hexagonal (Birch et al., 2007) de 12 modules espacés de 2 cm a été choisi (Figure 11). La position centrale a été assignée au module cible sur lequel nous avons mesuré ultérieurement les réponses des traits, et les 11 autres positions étaient occupées soit par des modules conspécifiques (modalité d'interactions intraspécifiques), soit par des modules appartenant aux six espèces de l'étude (modalité d'interactions interspécifiques).



**Figure 11.** Patron de plantation hexagonal pour les modalités d'interactions intraspécifiques (a) et interspécifiques (b). Les modules cibles sont indiqués en orange.

Les modules voisins ont été transplantés onze jours avant les modules cibles afin qu'ils soient établis au moment où les cibles ont été elles-mêmes transplantées. Pendant ces onze jours, et jusqu'à deux jours après la transplantation des modules cibles, les cultures ont été gardées à 13°C pour permettre aux plants de récupérer du stress de la transplantation, avant de les répartir dans les chambres thermorégulées.



**Figure 12.** Illustration de l'expérimentation en conditions contrôlées au sein du BIOMAR.

Un mélange stérile de 20% de sable et 80% de terreau commercial (N: 250g/m<sup>3</sup>, P<sub>2</sub>O<sub>5</sub>: 120 g/m<sup>3</sup>, K<sub>2</sub>O: 80 g/m<sup>3</sup>) a été utilisé et les pots ont été placés au sein de bacs pour maintenir les plants partiellement immergés et ainsi recréer les conditions hydriques rencontrées *in situ* (+ 1cm au-dessus de la surface du substrat, niveau d'eau ajusté toutes les semaines) (Figure 12). Pendant les premières semaines, les eaux de cultures ont été renouvelées toutes les deux semaines pour limiter la concentration en nutriments issus du lessivage du terreau commercial. Les pots ont été randomisés une fois par semaine. Un régime de lumière cyclique de 12h jour/ 12h nuit a été adopté, avec une luminosité suffisante pour la bonne croissance des individus.

Après 73 jours de cultures, les modules cibles se sont multipliés par croissance clonale et ont formé chacun un clone qui a été récolté. Des traits fonctionnels et de performance à

l'échelle du module et du clone ont été mesurés pour l'ensemble des cibles et reliés aux modalités de température × interactions plantes-plantes :

1. A l'échelle du clone : le nombre de modules et la biomasse sèche totale ont été mesurés pour caractériser la performance du clone.
2. A l'échelle du module : un module mature et nouvellement produit a été choisi au hasard pour mesurer plusieurs traits morphologiques, connus pour caractériser les stratégies de croissance des modules. De plus, ils sont connus pour réagir plastiquement à la température et à la compétition (Hutchings et al., 1997 ; Cornelissen et al., 2003 ; Butterfield & Callaway, 2013 ; Bittebiere & Mony, 2015 ; Wang et al., 2016 ; Gray & Brady, 2016 ; Loughnan & Gilbert, 2017 ; Bittebiere et al., 2019 ; Colom & Baucom, 2020 ; Dostálek et al., 2020). Différentes catégories de traits ont été étudiées : (i) les traits aériens avec la hauteur, la surface spécifique foliaire (SLA) et la teneur en matière sèche foliaire (LDMC) ; (ii) les traits clonaux avec la longueur d'un entrenœud et la masse spécifique de l'entrenœud (rapport entre la masse sèche et la longueur de l'entrenœud) ; et les traits racinaires avec la longueur maximale des racines et la masse spécifique des racines (rapport entre la masse sèche et la longueur de la racine). Une feuille mature du même module a été choisie au hasard pour évaluer la SLA et le LDMC selon Cornelissen et al. (2003). Nous avons également mesuré la performance du module résultant de sa croissance par sa biomasse sèche totale.

Les résultats issus de cette étude sont présentés dans le chapitre 2, dans l'**article V**.

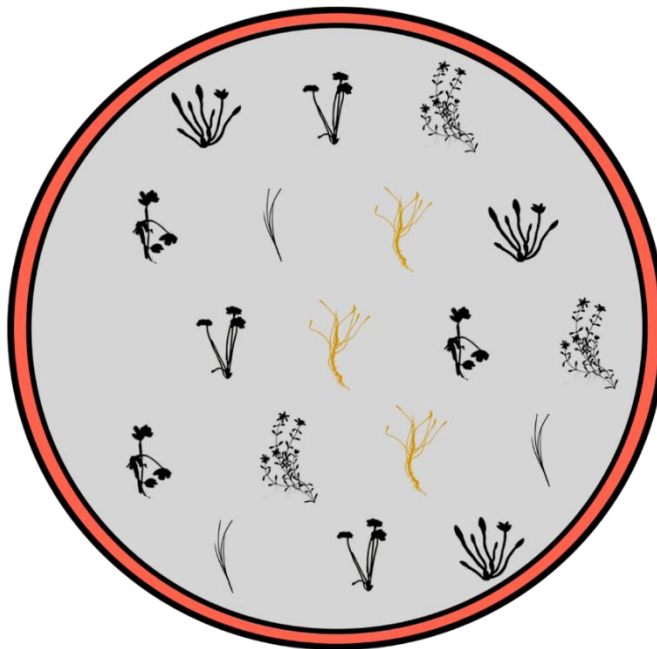
ii. [Expérimentation au LEHNA : réponses fonctionnelles de \*L. australis\* à la hausse des températures dans un contexte d'interactions biotiques. Conséquences sur le fonctionnement de l'écosystème](#)

Cette expérimentation s'est déroulée en deux phases. La première phase a eu pour objectif de déterminer les effets de la température et des interactions plantes-plantes sur les réponses fonctionnelles de l'espèce de macrophyte *L. australis*. La deuxième phase a visé à déterminer l'effet de ces réponses fonctionnelles sur le fonctionnement de l'écosystème mare, en particulier, sur le processus de dégradation de la litière. Puis par effet de rétroaction, elle a visé à montrer comment ces différences au niveau du processus de dégradation de la litière a pu affecter les traits fonctionnels et la performance d'une plante cultivée dans ce système. Aussi, cette expérimentation s'intègre parfaitement dans les dynamiques Eco-Evo pour la

compréhension des réponses des communautés et du fonctionnement des écosystèmes face aux changements climatiques rapides.

### *Phase 1*

Pour la première phase de l'expérimentation, trois modalités d'interactions plantes-plantes ont été choisies : un témoin sans interaction, et deux traitements impliquant des interactions intra- et interspécifiques. Afin de tester les effets d'un réchauffement, ces assemblages ont été cultivés à trois températures [température témoin  $T = 13^{\circ}\text{C}$ ,  $T+5^{\circ}\text{C}$ ,  $T+10^{\circ}\text{C}$ ]. La température témoin à  $13^{\circ}\text{C}$  correspond à la température moyenne observée en journée en période de végétation. Ainsi, les températures à  $+5^{\circ}\text{C}$  et  $+10^{\circ}\text{C}$  simulent respectivement une élévation modérée et sévère des températures. En effet, des températures dépassant les  $30^{\circ}\text{C}$  sont fréquemment enregistrées au sein des mares peu profondes, montrant que des épisodes climatiques extrêmes sont de plus en plus fréquents. Au total, neuf modalités ont été testées, répliquées dix fois chacune. Comme pour l'expérimentation au « BIOMAR », un génotype a été assigné par réplicat, pour prendre en compte uniquement la part de variabilité des traits générée par la plasticité (contrôle de l'effet « génotype »).

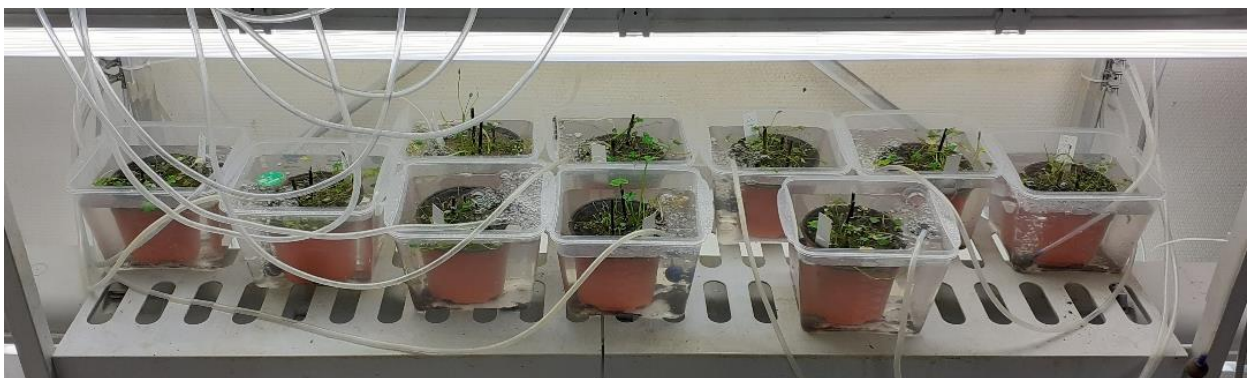


**Figure 13.** Patron de plantation hexagonal pour la modalité de compétition interspécifique. Les modules cibles de *L. australis* sont indiqués en orange. Trois modules ont été initialement plantés par espèce présente.

Pour les modalités de traitement avec interactions, un patron de plantation hexagonal de 18 modules a été choisi. Trois modules de *L. australis* appartenant au même clone ont été positionnés au centre de ce patron (Figure 13). En fonction du traitement d'interactions, les 15 modules voisins appartenaient soit également à l'espèce *Limosella australis* (interactions intraspécifiques), soit aux cinq autres espèces de macrophytes (à raison de trois individus par espèces) rencontrées dans les mares *in situ*, avec leurs positions randomisées sur le patron de plantation (interactions interspécifiques).

Les modules voisins ont été transplantés quinze jours avant les modules cibles de *L. australis*. Pendant cette période, tout module sénescant a été remplacé. Ce délai a permis aux modules voisins d'être bien établis lors de la transplantation des modules cibles. Pendant ces quinze jours, et jusqu'à deux jours après la transplantation des modules cibles, les cultures ont été gardées à 13°C pour permettre aux modules de récupérer du stress de la transplantation.

Un mélange de 50% de sable et 50% de terreau commercial (N: 250g/m<sup>3</sup>, P<sub>2</sub>O<sub>5</sub>: 120 g/m<sup>3</sup>, K<sub>2</sub>O: 80 g/m<sup>3</sup>) a été utilisé et chaque pot a été placé dans des bacs individuels pour maintenir les plants partiellement immergés (+ 2cm au-dessus de la surface du substrat, niveau d'eau ajusté toutes les semaines) (Figure 14). Pendant les premières semaines, les eaux de cultures ont été renouvelées toutes les semaines pour diminuer la concentration en nutriments apportés par le terreau commercial. Les pots ont été randomisés une fois par semaine. Un régime cyclique de 12h jour/ 12h nuit a été adopté.



**Figure 14.** Première phase de l'expérimentation, au cours de laquelle les réponses fonctionnelles des individus de *L. australis* à la température et au type d'interactions plantes-plantes ont été testées.

Après 13 semaines, les trois modules de *L. australis* initialement transplantés se sont multipliés par voie végétative (clonale), et ont donc formé des clones. Ces trois clones ont été



collectés. Des traits (détaillés ci-après) ont été mesurés sur l'un d'eux pour évaluer la réponse fonctionnelle de *L. australis* aux effets combinés de la température et des interactions plantes-plantes, à l'échelle du module et du clone (dynamique Eco vers Evo) : quatre traits foliaires (SLA, LDMC, teneur en carbone et ratio C : N), la hauteur du module, ainsi qu'un trait de performance à l'échelle du module (masse sèche) et deux traits de performance à l'échelle du clone (nombre de modules et masse sèche du clone).

## **Phase 2**

La deuxième phase de cette expérimentation consistait à tester comment les variations de traits fonctionnels en réponse aux interactions plantes-plantes × température pouvaient affecter la qualité des litières, et par conséquent leurs taux de décomposition en lien avec la température testée. Ces variations du processus de décomposition étaient supposées impacter les traits fonctionnels des individus par rétroaction.

Dans un premier temps, la biomasse sèche aérienne (*i.e.* les feuilles, les tiges et les connexions clonales) des clones cibles de *L. australis* qui restaient de la première expérience, a été utilisée pour créer des sachets de litière (après passage à l'étuve à 65 °C pendant 48 h). Nous avons supposé que la qualité de cette litière différait entre les neuf traitements testés dans la première phase. Toute la biomasse sèche aérienne restante provenant de tous les modules d'un même traitement, a été regroupée et mélangée de façon homogène, avant d'être répartie dans des sachets. Ainsi, tous les sachets de litière provenant d'un même traitement avaient la même qualité de litière et pouvaient être considérés comme des répliqués. Les litières consistaient en 5 mg +/- 10 % de biomasse sèche aérienne, placées dans des sacs en nylon (6 cm × 4 cm) à mailles fines pour se focaliser sur la décomposition microbienne. Pour déterminer les effets de la température sur la décomposition de la litière, cinq répliqués de litières de même qualité ont été placés sous trois températures (13 °C, 18 °C, 23 °C) dans des pots en verre de 250 mL (9,5 cm de diamètre, 11 cm de hauteur) (Figure 15). Le plan expérimental comprenait 135 mésocosmes au total *i.e.* 9 qualités de litière × 3 températures × 5 répliqués.

Au sein de ces mésocosmes, des conditions semblables à celles rencontrées dans les mares *in situ* ont été recrées. Pour cela, les pots ont été remplis de 150 mL d'eau stérilisée ultra pure (pour éviter la contamination microbienne et l'ajout de nutriments exogènes) et de 100 mL de substrat sédimentaire. Ce substrat était composé de 2/3 de sable stérilisé et 1/3 de sédiments

prélevés directement dans les mares des Iles Kerguelen, afin d'assurer un apport en micro-organismes décomposeurs identiques à ceux trouvés *in situ*.

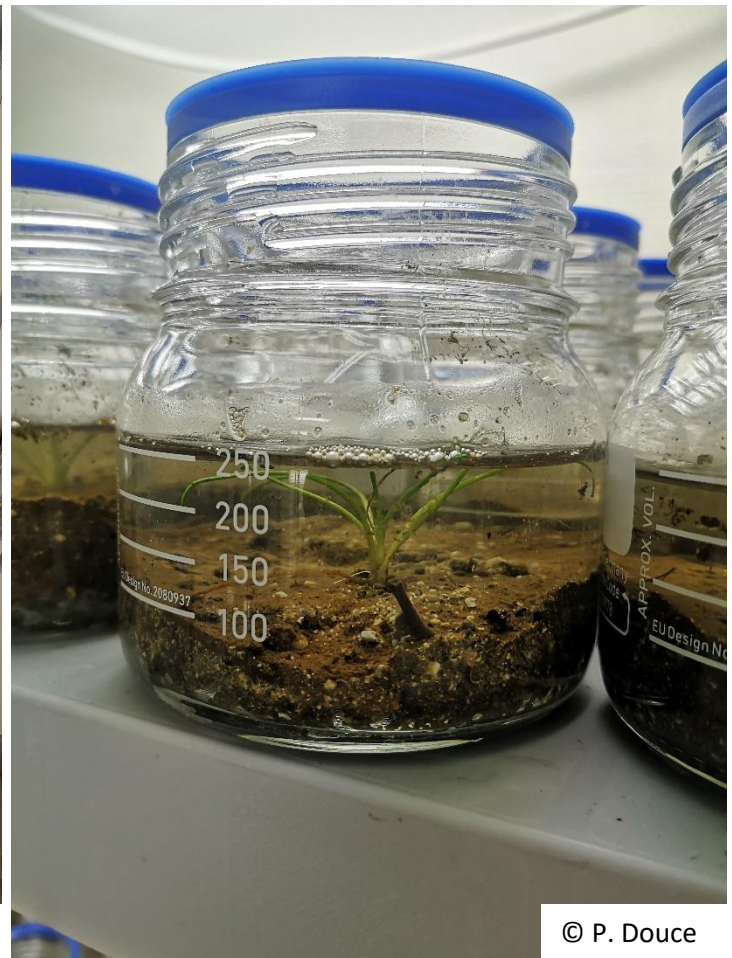
De plus, dans chaque mésocosme, une semaine avant l'introduction des litières, un module de *L. australis* a été transplanté afin d'évaluer les effets croisés de la décomposition de la litière et de la température sur sa croissance et ses traits (Figure 15). Un génotype a été attribué pour chacun des cinq réplicats pour s'affranchir de l'effet « génotype » et ne mesurer que la plasticité phénotypique. Pour cela, 27 modules provenant du même clone ont été standardisés par leur hauteur, et ont été répartis entre les 27 traitements testés. Les conditions de luminosité ont été réglées à un régime de 12 h jour/12 h nuit.

Cette deuxième phase a été arrêtée lorsque tous les sachets de litières avaient perdu au moins 50 % de leur masse initiale, soit après 56 jours. Les litières restantes dans les sachets ont été nettoyées et lyophilisées pendant deux jours avant d'être pesées pour estimer le taux de décomposition qui a été relié à la qualité de la litière (dynamique Evo vers Eco) et à la température de décomposition. Les clones issus de la propagation végétative des modules initialement transplantés, ont également été récoltés et nettoyés. Les mêmes mesures de traits à l'échelle du clone et du module que celles évoquées dans la première phase de l'expérience ont été réalisées pour évaluer l'effet du processus de décomposition sur la croissance et les performances des plantes (dynamique Eco vers Evo).

Les résultats issus de cette étude sont présentés dans le chapitre 3, dans l'**article VI**.



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**Figure 15.** Influence des variations de traits fonctionnels en réponse aux interactions plantes-plantes  $\times$  température sur la qualité des litières, et par conséquent sur leurs taux de décomposition en lien avec la température testée. L'impact par rétroaction de ces variations du processus de décomposition sur les traits fonctionnels des individus, a également été testé. Sur les photos, chaque pot représente un mésocosme avec un sachet de litière mis à décomposer en présence d'un module de *L. australis* qui s'est multiplié par clonalité au cours de l'expérimentation. Un substrat semblable à celui rencontré dans les mares *in situ* a été recréé à l'aide d'un mélange de sable stérilisé et de sédiments prélevés directement dans les mares.

### 3. L'approche fonctionnelle comme méthode d'étude

L'approche fonctionnelle a pour objectif de décrire les organismes par leurs traits fonctionnels, plutôt qu'au travers de leur appartenance taxonomique (Lavorel et al., 1997). Cette approche permet de relier ces caractéristiques fonctionnelles à des patrons de réponses face aux conditions environnementales, de préciser les mécanismes sous-jacents à ces réponses (Cornwell & Ackerly, 2009 ; Bernard-Verdier et al., 2012 ; Herben & Goldberg, 2014 ; Kraft et al., 2015a ; Cadotte & Tucker, 2017), et même de déterminer les effets de ces réponses fonctionnelles sur les écosystèmes (Lavorel & Garnier, 2002 ; Naeem & Wright, 2003 ; Diaz et al., 2007). Par ailleurs, elle autorise la prise en compte d'une variabilité intraspécifique (Jung et al., 2010 ; Albert et al., 2011 ; Violle et al., 2012) et admet que certains traits peuvent présenter une grande part de variabilité liée aux variations intraspécifiques (Messier et al., 2010 ; Albert et al., 2010a).

Il est souvent difficile de relier les patrons observés aux processus d'assemblages des communautés, surtout dans les études *in situ*. Pour cela, plusieurs auteurs ont suggéré d'explorer les causes de la variabilité des traits fonctionnels à travers la partition de variance des traits fonctionnels. En effet, cette méthode est adéquate pour déterminer l'échelle écologique (temps, espace, phylogénie) qui joue le plus grand rôle dans les mécanismes d'assemblage des communautés (Messier et al., 2010 ; Luo et al., 2016 ; Henn et al., 2018 ; Liu et al., 2018). La variation d'un trait peut ainsi (i) être majoritairement temporelle en raison des changements environnementaux par exemple (Grassi et al., 2005 ; Muraoka et al., 2010 ; Fullana-Pericas et al., 2017), ou être décrite (ii) à une échelle spatiale en raison de la diversité des conditions environnementales (Reich & Oleksyn, 2004 ; Zadworny et al., 2016), (iii) ou à l'échelle phylogénétique *i.e.* à l'échelle interspécifique ou intraspécifique (Swenson et al., 2006 ; McGill, 2008). Pourtant, il est surprenant que beaucoup d'études testent la variation des traits sur une seule de ces échelles écologiques, alors que leur combinaison permettrait d'obtenir une vision plus complète des processus sous-jacents à l'assemblage des communautés (mais voir Messier et al., 2010 ; Luo et al., 2016 ; Fyllas et al., 2020 ; Liu & Ng, 2020). En effet, le risque est de sous-estimer ou de surestimer l'importance d'une échelle écologique pour les mécanismes d'assemblage. L'approche fonctionnelle permet également la prise en compte de l'importance des variations intraspécifiques des traits fonctionnels dans les réponses spécifiques aux conditions environnementales (Jung et al., 2010 ; Violle et al., 2012), de même que leur impact sur la performance des individus (Geber & Griffen, 2003) et donc sur le devenir d'une

communauté au sein de conditions changeantes ([Ghalambor et al., 2007](#)). Cette approche méthodologique fait l'objet de l'article suivant (**article II**) qui vise à déterminer le rôle de plusieurs traits dans les réponses des individus aux filtres biotiques et/ou abiotiques de leur habitat et les conséquences sur leurs performances.

## How does trait variance partitioning help us to understand plant community assembly?

### The example of pond communities at the Kerguelen Islands

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Article Informations	Abstract
<p><i>Article history:</i></p> <p>Submitted in <i>Journal of Vegetation Science</i></p> <hr/> <p><i>Keywords:</i></p> <p>Functional traits</p> <p>Plant performance</p> <p>Variance partitioning</p> <p>Intraspecific trait variability</p> <p>Macrophyte</p>	<p>In the current context of biodiversity erosion, functional approaches have emerged to study community assembly mechanisms and to better predict the fate of plant species. Assessing patterns of trait variation should be a powerful tool to determine community assembly mechanisms. Yet, studies on trait variation and their consequences on individual performance are usually incomplete as they focus on a single ecological scale or filter, and do not include relationships between traits, resulting in a fragmented view of plant community assembly. We focused on the macrophyte communities living in particular freshwater ecosystems <i>i.e.</i> the ponds of the Iles Kerguelen, in the sub-Antarctic region. We measured different categories of traits (aerial, root, and clonal) on all occurring species to study trait variations across years, sites and taxonomic scale (between species and within species), and in response to multiple habitat abiotic and biotic variables. The consequences of these traits variations and the effects of their correlations for plant individual performance were also explored. Our results first highlighted a filter operating on the overall distribution of trait values within the region, whereas we observed a high amount of intraspecific trait variation allowing individuals to resist to filters. Second, traits responses to biotic and/or abiotic factors were trait-dependent, and this combination of simultaneous trait responses should allow the plant as a whole to face several simultaneous constraints. Lastly, almost all traits have either direct or indirect effects on individual performance. As a conclusion, partitioning trait variance is a relevant approach to detect at which scale operate the most decisive processes in plant community assembly without scale dependency issues, and then orient further researches. Furthermore, we plead to consider multi-traits approach, and several biotic and abiotic variables in future studies to better understand the effects of environmental changes on plant communities.</p>

### Introduction

In the current context of biodiversity erosion, it is crucial to improve our understanding of the mechanisms underlying plant community

dynamics for getting reliable predictions of the fate of plant species. Two decades ago, functional approaches have emerged and have allowed to rebuild community ecology and to

produce general principles on assembly mechanisms (Calow, 1987; McGill et al., 2006). By considering the concept of ecological function, where species are no longer described by their taxonomic identities alone but by their biological attributes through the measurements of functional traits (Albert, Thuiller, Yoccoz, Douzet, et al., 2010), functional approaches have been fruitfully developed for addressing a range of key pending ecological questions. Functional traits correspond to any morphological, physiological, and phenological characteristics that impact individual performance, either directly or indirectly, through individual growth, reproduction or survival (Violle et al., 2007). More recent studies evidenced that large trait variations can also occur in the field at inter- but also intraspecific levels (Albert, Thuiller, Yoccoz, Soudant, et al., 2010; Messier et al., 2010; Taudiere & Violle, 2016). These variations would be the consequences of a range of biological processes operating at different spatial and temporal scales, and ultimately leading to species coexistence.

So far, organismal trait variation has usually been observed through the lens of space, time, or taxonomy independently, and this has resulted in a fragmented view of community assembly (but see Fyllas et al., 2020; Liu & Ng, 2020; Messier et al., 2010 for variance partitioning across spatial and taxonomic scales). Temporal trait variation is, for example, reported as part of plant seasonal strategies allowing them to permanently adjust trait performance to deal with external stresses. Adjustment of physiological (photosynthetic capacity *e.g.* Grassi et al., 2005; Muraoka et al., 2010) or morphological traits (leaf thickness *e.g.* Fullana-Pericas et al., 2017) is thus frequently reported in plant species. Spatial scales, owing to the diversity of environmental conditions they encompass, also shape overall trait variations, which can arise from species specific responses to various environmental filtering processes. Consistently, both aboveground (Reich et al., 2004) and belowground (Zadworny et al., 2016) traits have been found to spatially vary

depending on environmental temperatures (Reich et al., 2004). By subsequently decomposing trait variations through taxonomy (McGill, 2008; Swenson et al., 2006) so that inter- vs. intraspecific trait variations can be considered, it is possible to determine whether species identity is a critical factor in the filtering processes or whether individuals are rather filtered out depending on their trait values. Overall, studies providing information on the scale which carries the most important trait variations are of particular interest, as the results should be promising to understand many community patterns and processes (McGill, 2008; Taudiere & Violle, 2016; Violle et al., 2007, 2012), and thus to assess the scale dependency issue in community ecology (*e.g.*, Cavender-Bares et al., 2009; Swenson et al., 2006).

Over the last ten years, studies reported the major role of intraspecific trait variability (ITV) in ecological processes, and showed that ITV can account for up to 30% to 40% of trait variance within a plant community (Albert, Thuiller, Yoccoz, Soudant, et al., 2010; Jung et al., 2010). ITV would allow a better resistance to filters (Jung et al., 2010; Violle et al., 2012), in particular by adaptation (genetic variability) and/or phenotypic plasticity (Albert et al., 2011; Byars et al., 2007; Ghaleb et al., 2007). Most morphological traits in plants are key for coping with different environmental filters (see *e.g.* Lavorel & Garnier, 2002). Responses to both biotic and abiotic filters have indeed been extensively evidenced in traits involved in growth or resource acquisition (in particular Specific Leaf Area SLA, Leaf Dry Matter Content LDMC, height, and root traits) (Bittebiere & Mony, 2015; Butterfield & Callaway, 2013; Colom & Baucom, 2020; Cornelissen et al., 2003; Dostálek et al., 2020; Lavorel & Garnier, 2002), as well as in clonal traits (internode length, specific connection mass) (Bittebiere & Mony, 2015; Huber & Stuefer, 1997; Hutchings et al., 1997; Pilon & Santamaria, 2002; Rusch et al., 2011). It remains however unclear how traits will respond to simultaneously varying biotic and

abiotic conditions, as their effects are usually studied separately (see *e.g.* Dudley & Schmitt, 1996; Greulich & Bornette, 1999; Riis et al., 2012; Suding et al., 2008). In some cases, this knowledge gap may lead to misinterpretation of patterns of traits variations, especially for studies conducted *in situ* (Cadotte & Tucker, 2017; Kraft et al., 2015). We thus argue that partitioning intraspecific trait variations should help determining the role of traits in species biotic and abiotic resistance to environmental filters (Le Bagousse-Pinguet et al., 2017; R. Liu et al., 2018). Traits should simultaneously respond to both biotic and abiotic conditions, but with varying strengths depending on the trait under consideration.

Variations in traits ultimately influence individual performance (*i.e.* production of vegetative biomass, and reproduction rates) (Geber & Griffen, 2003) and thus the species fate in the plant community (Ghalambor et al., 2007). However, direction and intensity of the influence of the trait on organismal performance will depend on the measured trait. For instance, in plant individuals, clonal traits mainly drive spatial positioning and resource storage (Klimešová et al., 2021), while aerial (*e.g.* height, SLA) and root traits (*e.g.* specific root length) determine efficiency of resources acquisition (Garnier et al., 2004). We thus expect aerial and root traits to have stronger importance on the intensity and direction of individual performance in comparison with clonal traits. Nevertheless, it is also very important to bear in mind that several traits co-vary and/or are subjected to tradeoffs, within plant individuals to coordinate different biological functions (Maire et al., 2013; Valladares et al., 2007; Violle et al., 2007). Yet, literature studies usually neglect these trait relationships that can result in indirect influence on individual performance. The identification of the direct and indirect influence of traits on organismal performance likely imposes hierarchies among plant traits, and this can be revealed through Structural Equation Modelling (Ackerly et al., 2000;

Dwyer & Laughlin, 2017; Saiz et al., 2018; Vile et al., 2006).

Recently, a growing number of theories and concepts in ecology have been tested in the sub-Antarctic region, as they represent valuable sentinel ecosystems and open air laboratories (Bergstrom & Chown, 1999). In these regions, climate change, in particular warming, is especially rapid (Walther et al., 2002), with strong impacts on aquatic ecosystems, including ponds (Douce et al., *in prep*). Moreover, their plant communities (macrophytes) are remarkably poor, resulting in simplified interaction networks. In this study, we used macrophyte communities as system models, and measured different categories of traits (aerial, root, clonal, and of performances) on all pond-occurring species at the French sub-Antarctic Iles Kerguelen. Trait variations were studied across spatial, temporal and taxonomic scales, and covered multiple habitat abiotic and biotic conditions. Consequences for plant individual performance were also explored. The following hypotheses were specifically tested:

- (i) Partitioning of trait variance among spatial, temporal, and taxonomic scales would allow to detect the mechanisms involved in plant community assembly. We expect a high amount of intraspecific trait variability.
- (ii) Traits are expected to simultaneously respond to both biotic and abiotic conditions, but the direction and intensity of responses should be trait-dependent.
- (iii) Traits related to resource acquisition (aerial, and root traits) would affect individual performance directly, with stronger influence than clonal traits. However, relationships between traits may modulate these influences.



## Materials and methods

### Study model

The study was carried out in the field, at the French sub-Antarctic Iles Kerguelen (South Indian Ocean) (48°30–50°S, 68°27–70°35E). The climate of this archipelago is characterized by cold temperatures (annual mean of 4.6 °C with few variations - Frenot et al., 2006; Lebouvier et al. 2011), and abundant precipitations (range from 500 mm to 3200 mm along an East-West gradient - Frenot et al., 1998 and Meteo France). Many plant communities from polar regions are paucispecific, resulting in simplified plant-plant interactions, and subjected to highly reduced anthropogenically-induced environmental pressure. As such, they constitute a relevant model to infer mechanisms of community assembly, especially within constrained abiotic environments (Bergstrom & Chown, 1999).

The study was conducted in ponds from three sites located along the shore of the main island of the archipelago (Supporting information 1): Cap Molloy, Isthme Bas, and Cap Ratmanoff. These three sites are less than 40 km apart, and display similar climates. Conversely, overall abiotic conditions of the ponds are more variable locally as compared with variation levels among sites (Douce et al., submitted). For each site, 15 ponds of varying area were selected to overcome bias related to system size, which influences water temperatures (Bornette & Puijalon, 2011). All investigated ponds but one (180800 m<sup>2</sup>) have relatively small size (average area = 181.57 ± 382.39 m<sup>2</sup>) (Douce et al., in prep). They are shallow freshwater systems, enriched by nutrient inputs from marine fauna like seabirds and seals owing to their littoral proximity (Smith, 2008). Mean water depth was relatively similar among ponds (average of the 45 ponds: 15.52 ± 8.72 cm, Douce et al., in prep).

Macrophyte communities are mainly composed by six native species: *Limosella australis* R.Br. (Scrophulariaceae), *Callitriche antarctica* Engelm

(Plantaginaceae), *Juncus scheuchzerioides* Gaudich. (Juncaceae), together with three Ranunculaceae species: *Ranunculus biternatus* Smith, *R. pseudotrullifolius* Skottsb., and *R. moseleyi* Hook.f. All of these species are perennials displaying a clonal network structure, *i.e.* plants are composed of related ramets (shoots with leaves and roots) that are connected through plagiotropic stems. *C. antarctica*, *L. australis*, *R. pseudotrullifolius*, and *R. moseleyi* are hydrophytes, while *R. biternatus* and *J. scheuchzerioides* are helophytes. Only *C. antarctica* harbors a floating canopy, while the five other species display a rosette architecture and are rooted in pond sediments.

### Field sampling

The study was conducted in 2017, 2018, 2019 and 2020, and the sampling of plant ramets was conducted each year, in the three sites, in November. In each pond, we randomly positioned three to five 1m × 1m quadrats depending on the pond area. In each quadrat, we collected one ramet (with its leaves and roots, and one connection internode) of each of the six above-mentioned species when present, to measure plant traits. In addition, we recorded species abundances within each quadrat.

Pond abiotic conditions were monitored every three months over a year, starting from November 2019, and ending in November 2020. For each sampling date and pond, water samples were collected manually for nutrients and phytoplankton concentration analyses. Sediment samples were also collected for subsequent nutrients analyses. In each pond, the three samples were collected at three distinct points of the pond, and were further mixed together to consider nutrient spatial heterogeneity. One composite water sample (30 mL) and one composite sediment sample (50 mL) were obtained per pond. As abiotic variables are likely to vary within ponds, we randomly positioned three (pond area < 5 m<sup>2</sup>) to five (pond area > 5 m<sup>2</sup>) quadrats (1 m<sup>2</sup>) and measured: water mean depth (based on three measurements), pH,

electric conductivity (EC) and mean dissolved oxygen (DO – average of three depths in the water column) in each quadrat. These measurements were performed using a multiparameter HQ40D HACH sensor ( $C \pm 0.1 \text{ mS.cm}^{-1}$ ,  $\text{DO} \pm 0.01 \text{ mg.L}^{-1}$ ). Water temperature of the whole pond was also recorded every half hour using loggers (Hobo MX2202) positioned in the middle of the water column (From September 2020 onwards). Water temperatures were then simulated from November 2019 to August 2020 using their relationship with air temperatures recorded by Meteo France (2020 records, Port-aux-Français) [see Douce et al., in prep]. Each pond area (length  $\times$  width) was measured in November 2019.

#### *Trait measurements*

Seven functional traits were measured on ramets sampled from the ponds; for each specimen, leaves, roots, and one connection internode was collected. The selected traits characterize ramet growth strategies (Table 1), and are known to be responsive to a range of biotic and abiotic variables (Table 1). Three main categories of traits were investigated: aerial, clonal and root traits (see Table 1 for details).

Specific Leaf Area (SLA) and Leaf Dry Matter Content (LDMC) were measured following Cornelissen et al. (2003) on one healthy and mature leaf randomly per ramet. Internode length was measured on one of the internodes attached to the ramet. Internode mass was calculated as the ratio between internode dry mass and length ( $\text{g.cm}^{-1}$ ). Root mass was calculated as the ratio between root dry mass and maximum root length ( $\text{g.cm}^{-1}$ ). We also estimated performance of ramets resulting from their growth strategy, by measuring their total biomass (*i.e.* dry masses of leaves, stems, roots and one connection internode). Measurements of dry masses were performed after drying plant parts for 48 hours in an oven at 65 °C. All plants were cleaned in water before measurements.

#### *Nutrients and phytoplankton quantity assay*

For the measurements of water nutrient and phytoplankton concentrations (as depicted by the amount of chlorophyll a per mL of water), water samples were filtered through GF/F filters (0.7 $\mu\text{m}$ , Whatman) to remove coarse and fine particles and phytoplanktonic organisms within 24 hours of sampling. All samples (filtered water and sediments, and filters) were stored at -20 °C for several weeks before chemical analyses in metropolitan France.

Chlorophyll a pigments were quantified from GF/F Whatman filters using the Unesco method (Vohra, 1966) with a spectrophotometer, and allowed the quantification of phytoplankton per volume of water in each pond. N-NH<sub>4</sub><sup>+</sup>, N-NO<sub>3</sub><sup>-</sup> and P-PO<sub>4</sub><sup>3-</sup> concentrations of the water samples were determined using colorimetric methods with a sequential analyzer (SmartChem200, AMSAlliance) (Grasshoff et al., 1999). In sediment samples, organic carbon to nitrogen ratio (C:N) was measured using the “capsule method” (Brodie et al., 2011). An aliquot of 5 mg  $\pm$  10 % of homogeneous sediment sample was acidified into 100  $\mu\text{L}$  of 2M HCl in silver capsules to eliminate carbonates. Capsules liquids were evaporated on a 65°C hot plate for 12 hours, before capsules were oven-dried at 80 °C for two days. Organic carbon and nitrogen total contents were then measured with an elementary analyzer (FlashEA 1112 NC Analyzers®, Thermo Fisher Scientific, Waltham, Massachusetts, USA). The bioavailable P concentration in sediments was determined following the protocol of (Ni et al., 2016). Available P was extracted from 50 mg of dry sediment samples with 5 ml of NaOH (1 M). Then, the supernatant was collected, its pH was stabilized with HCl (3.5 M), and the extracted P that has been converted into orthophosphate was quantified using the molybdate/ascorbic acid blue method (Murphy & Riley, 1962); results were reported in mg of available P per g of dry sediment.

#### *Data analysis*

We tested for correlations between all pairs of traits using Spearman rank correlations to detect possible co-variations among traits. We did not detect significant strong correlations between any pair of traits (Spearman's  $\rho < 0.7$ , [Dormann et al., 2013](#)).

**Table 1.** The plant functional traits measured and their associated responses to abiotic and biotic conditions.

Traits	Description	Calculation	Abiotic variables with evidenced trait shifts	Biotic interactions with evidenced trait shifts
<i>Aerial traits</i>				
Specific Leaf Area (SLA)	Proxy of plant photosynthetic capacity and resource acquisition	Ratio of area and dry mass of leaf ( $\text{mm}^2 \cdot \text{mg}^{-1}$ )	temperature [a, ab, b, c, d], nutrients [a, e, ab], moisture [f, g], light [ac]	Competition for light [h, i], above-ground competition [j, g], facilitation [i]
Leaf Dry Matter Content (LDMC)	Proxy of physical resistance of leaves and resources storage	Ratio of dry and fresh masses of leaf ( $\text{mg} \cdot \text{g}^{-1}$ )	Temperature [b, c], moisture [k, g], soil nutrients [e, k], water nutrients [l]	Competition [m, g]
Height	Allow optimal light exposure	Shortest distance between the upper limit of the main photosynthetic tissues and the ground level (cm)	Temperature [a, n], water availability [o, p, g], water depth [q], soil nutrients [a, r]	Aerial competition [m, i], belowground competition [i, g], facilitation [i]
<i>Clonal traits</i>				
Internode length	Plant ability to exploit local environment and to disperse at short distance	Distance between two successive ramets (cm)	Soil nutrients [t, u, v, s], light [ac, w]	Spatial competition [m, x, s]
Specific internode mass	Proxy of resources allocation for clonal multiplication and storage	Ratio of dry mass and length of connection ( $\text{mg} \cdot \text{cm}^{-1}$ )	Soil nutrients [s, t]	Competition [m]
<i>Root traits</i>				
Maximum root length	Acquisition of nutrients	Length of the longest root (cm)	Temperature [a, ad, n], soil nutrients [a, e]	Competition [y]
Specific root mass	Proxy of resources storage	Ratio of dry mass and length of root ( $\text{mg} \cdot \text{cm}^{-1}$ )	Temperature [a, q], nutrients [a, e], Moisture [a, n]	

a= (Cornelissen et al., 2003) ; ab= (Gong & Gao, 2019) ; ac= (Santamaría, 2002) ; ad= (Freschet et al., 2017) ; b= (Meng et al., 2015) ; c= (Dostálek et al., 2020) ; d= (Poorter et al., 2009) ; e= (Lavorel & Garnier, 2002) ; f= (Jung et al., 2010) ; g= (Loughnan & Gilbert, 2017) ; h= (Violle et al., 2009) ; i= (Butterfield & Callaway, 2013) ; j= (Rooney & Kalff, 2000) ; k= (Wehn et al., 2017) ; l= (Fu et al., 2018) ; m= (Bittebiere & Mony, 2015) ; n= (Gray & Brady, 2016) ; o= (Moles et al., 2009) ; p= (Tao et al., 2016) ; q= (Wang et al., 2016) ; r= (Martinez-Almoyna et al., 2020) ; s= (Hutchings et al., 1997) ; t= (Rusch et al., 2011) ; u= (Louâpre et al., 2012) ; v= (Slade & Hutchings, 1987b) ; w= (Slade & Hutchings, 1987a) ; x= (Bittebiere et al., 2019) ; y= (Colom & Baucom, 2020).

Thus, each trait was indicative for a part of global strategy of growth.

#### *Abiotic and biotic characterization of ponds*

First, to characterize the abiotic conditions within ponds, the mean of daily (day and night) water temperatures was calculated from November 2019 to November 2020 for each pond (Douce et al., in prep). Abiotic variables that have been measured at quadrat scales have been averaged at pond scale. Depending on the analysis, we performed several reductions of abiotic variables. Water nutrients dimensions (N-NH<sub>4</sub><sup>+</sup>, N-NO<sub>3</sub><sup>-</sup>, P-PO<sub>4</sub><sup>3-</sup>) were reduced to the first axis of a Principal Component Analysis (PCA), in which data were centered and standardized by standard deviation (Supporting information 2), hereafter named 'PCAwater'. PCA Axis 1 (42.06%) was negatively related to the concentration of N-NH<sub>4</sub><sup>+</sup> and N-NO<sub>3</sub><sup>-</sup>. Similar reduction of dimensions was done for sediment nutrients (C:N ratio, bioavailable phosphorus) (Supporting information 3), hereafter named 'PCAsediments'. PCA Axis 1 (58.59%) was negatively related to the C:N ratio and positively related to the bioavailable P concentration.

Second, to characterize the biotic conditions within ponds, we calculated two non-correlated indices: the macrophyte species richness, and the Pielou evenness. Biotic dimensions describing species abundance in each pond were reduced to the first-three axes of a Factorial Correspondence Analysis (FCA) (Supporting information 4). The first axis (33.81%) was respectively positively and negatively driven by the abundances of *R. moseleyi* and *C. antarctica*. The second axis (24.99%) was positively correlated with the abundance of *R. pseudotrullifolius* and negatively with *J. scheuchzerioides*. The third axis (16.99%) was related to the abundances of *L. australis* (positively) and *R. biternatus* (negatively). In parallel, to assess the functional characteristics of pond communities, we calculated the overall functional dispersion (then referred as FDis) with seven traits

(height, SLA, LDMC, internode length, specific internode mass, maximum root length and specific root mass), using the *fdisp* function of package FD (Laliberté & Legendre, 2010).

#### *Variance partitioning across nested scales*

We used traits measurements from 2017 to 2020 to partition trait variances across four nested scales. A variance component analysis was performed using the *Parvart* procedure (package Cati), for each of the seven studied traits, across temporal, spatial, and taxonomic (including inter- and intraspecific variations) scales introduced in this order in the model: time (year), space (site), species, and within-species. For example, the part of variation of the species scale represents the variance of the species means around the mean of their site. To that aim, the mean value of each species is calculated, then the variance of these species means are calculated around the site mean to which they belong. Thus, the intra-site variation is the sum of the species and within-species variations, that is the trait means variation between species in each site, and between individuals in each species in each site. Trait data were previously normalized (log or square-root transformations). The significance of the variance components was assessed by building 95% confidence intervals (CI) through a bootstrapping procedure. We randomly selected 100 individuals out of the 1430 of our dataset with replacement (Messier et al., 2010), and calculated the trait variance partitioning between the four nested scales. We repeated this procedure 500 times to ultimately calculate a 95% CI for each variance component. To get rid of the imperfect nesting of species within sites, we ran alternative partitioning models by deleting species scale (Supporting information 5).

*Trait responses to biotic and abiotic filters*

We aimed to determine which traits and categories of traits were involved in their biotic and/or abiotic resistance. On the one hand, we considered univariate responses and tested for the effects of abiotic and biotic variables measured or calculated at pond scale, on trait values measured in November 2020 and averaged at pond scale, on all ramets of all species. In the full models, we included as explanatory variables: species identity (categorical variable assessing the species to which ramets belong to), macrophyte species richness, Pielou evenness, community FDis, the first three axes of the FCA performed on macrophyte species abundances (Supporting information 4), and the phytoplankton concentration for biotic variables; water depth, pH, electric conductivity, dissolved oxygen, mean temperature, pond area, and the first axis of the two PCA performed on water nutrients and sediment nutrients (Supporting information 2 and 3) for abiotic variables. Trait data were previously normalized (log or square-root transformations) when needed, and standardized. We applied a stepwise model reduction based on the AIC criteria (MuMIn package, [Bartoń, 2013](#)) on the full model to select the most parsimonious model and we performed an ANOVA test (type II).

On the other hand, similar procedure was applied to test for the effects of the above-listed abiotic and biotic variables on traits grouped into three categories (multivariate responses): aerial (height, SLA, and LDMC), clonal (internode length, and specific internode mass), and root traits (maximum root length, and specific root mass). Trait data were previously normalized (log or square-root transformations) when needed and standardized. We selected variables by a backward elimination on the full model (deleting the non-significant effects), and then performed a MANOVA test (type II, Pillai statistic) based on the reduced model.

*Traits and abiotic variable effects on species performance*

Ramet total biomass (*i.e.* performance) and trait values recorded in November 2020 were averaged per species at the pond level ( $n=97$ ), and standardized separately for each species to get rid of variance due to species identity. We tested for the direct and indirect effects of the seven traits on individual performance using a Structural Equation Modeling (SEM) procedure ([Grace et al., 2010](#)). All possible relationships between traits were included based on the literature (Supporting information 6). We performed a path analysis with the lavaan package ([Rosseel, 2012](#)), and reduced the full model by variable selection based on AIC values.

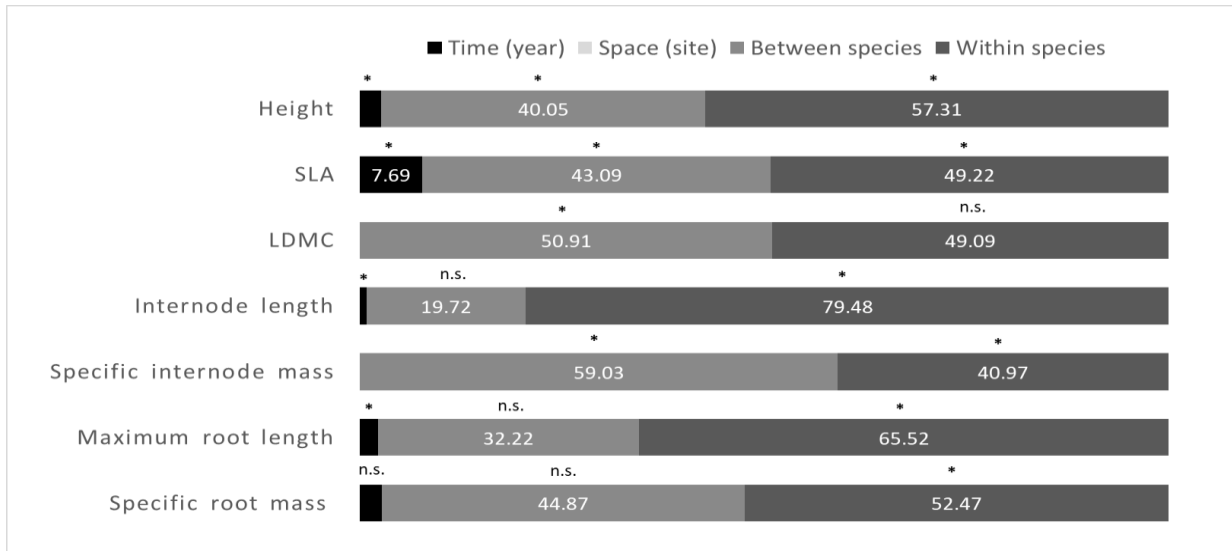
All statistical analyses were carried out with R 4.0.3.

**Results***Traits mostly varied within macrophyte species*

All studied traits exhibited larger variations within sites than among sites. Time (year) and space (site) had few influence (both additive effects explaining less than 8% of variance in all traits), even when they were significant. Conversely, taxonomy explained most of the variance within sites (Fig. 1). Most traits (with the exception of internode mass and LDMC) exhibited higher trait variance at the intraspecific scale as compared with the interspecific one. The intraspecific variance of the trait was even maximal in the internode length (79.48%) and the maximum root length (65.52%).

*Variations of most traits were affected by both abiotic and biotic variables*

Within ponds, growth strategies relied on aerial, clonal, and root categories of traits. Aerial traits as a whole responded to water nutrients only, while clonal and root traits were impacted by several biotic and abiotic variables (Table 2). Clonal traits responded to



**Figure 1.** Partitioning of individual traits variance across four nested scales through Partvar procedure, using data collected from 2017 to 2020. All data were normalized (log-transformation), except for specific root mass values which have been square-root transformed. The significance of the variance components (\*  $p < 0.05$ ; n.s.  $p > 0.05$ ) was assessed by bootstrapping.  $N = 1430$ .

species abundance, water depth, electric conductivity and nutrients, while root traits were impacted by species abundance, phytoplankton concentration, and water temperature.

Four traits responded to either pond abiotic (height, SLA and internode length, respectively 3.15%, 14.31% and 5.03% of explained variance) or biotic (specific internode mass, 10.28% of explained variance) variables only (Table 2). Nevertheless, variations in the three other traits *i.e.* LDMC, maximum root length, and specific root mass were influenced as expected, by both biotic and abiotic variables (Table 2). Our results showed that the responses of these three traits to the different tested variables were trait dependent, with a higher cumulative influence of biotic variables (Table 2). LDMC and maximum root length were rather predicted by species abundances (5.90% and 4.37% of explained variance respectively), whereas specific root mass was mostly predicted by phytoplankton concentration (10.49%). To a lesser extent, water physico-chemistry (*i.e.* temperature, pH, and nutrients) influenced both root traits, while LDMC was impacted by sediment nutrients.

#### *Plant traits directly and indirectly affected individual performance*

Among all tested traits, LDMC did not affect individual biomass, while we identified multiple direct or indirect effects of all other traits (Fig. 2). Traits related to resource acquisition (aerial, and root traits) did not have a stronger influence on individual performance than clonal traits. On the one hand, traits directly influencing individual biomass (*i.e.* height, and all clonal and root traits), also supported the biomass, with height (0.38\*\*\*) and specific internode mass (0.43\*\*\*) displaying the strongest effects. These direct effects on individual performances were additionally modulated *i.e.* amplified or decreased, by their correlations (Fig. 2). For example, internode length and specific root mass were correlated to height, indirectly supporting their total positive effect on individual performance, while specific internode mass indirectly and positively impacted individual performance *via* its correlation with internode length and specific root mass. On the other hand, SLA did not have any direct effects on individual performances, yet influencing it negatively through its relationship with specific internode mass (-0.20\*).

**Table 2. Traits responses to abiotic and biotic variables of pond habitat.** Traits were considered by category (all, MANOVA tests) or one by one (ANOVA tests). MANOVA and ANOVA tests were both performed based on the most probable models (see Materials and Methods for details), using data recorded in 2020. Bolded predictors had a significant effect on trait values. Water and sediment nutrient dimensions were each reduced to the first axis of a PCA analysis (Appendix 2 and 3), referred as ‘water nutrients’ and ‘sediment nutrients’. To take the influence of species abundance within ponds into account, we also added the first-three axes of a FCA performed on species abundance (Appendix 4). Among the tested variables, functional diversity, Pielou evenness, dissolved oxygen, and pond area did not have effects on any trait responses

Trait	Explanatory variables of selected model					
	<i>n</i>	Predictor	F	d.f.	Model coefficient	Part of explained variance (%)
<i>Aerial</i>						
All	99	<b>Species identity</b>	9.31***	5		
		<b>Water nutrients</b>	9.88***	1		
Height	101	Functional diversity	3.49.	1	0.12	1.55
		<b>pH</b>	8.77**	1	-0.20	3.15
		Species richness	3.30.	5	-0.13	1.46
		<b>Species identity</b>	23.62***	1		52.24
		Water depth	3.06.	1	0.12	1.35
		Residuals			91	
SLA	102	<i>J. sce, R.ps</i> abundance	3.50.	1	-0.14	1.97
		<b>Electric conductivity</b>	8.66**	1	0.27	4.86
		<b>Water temperature</b>	4.56*	1	0.18	2.57
		Phytoplankton concentration	2.38 <sup>n.s.</sup>	1	-0.13	1.34
		<b>Water nutrients</b>	12.24***	1	-0.32	6.88
		<b>Species identity</b>	11.54***	5		32.40
		Residuals			89	
LDMC	100	<i>L. aus, R. bit</i> abundance	9.87**	1	-0.23	5.90
		Functional diversity	2.65 <sup>n.s.</sup>	1	0.11	1.58
		<b>Sediment nutrients</b>	7.62**	1	-0.22	4.55
		<b>Species identity</b>	11.22***	5		33.56
		Residuals			91	
<i>Clonal</i>						
All	97	<b>Species identity</b>	8.48***	5		
		<b>Water depth</b>	6.86**	1		
		<b>Electric conductivity</b>	3.41*	1		
		<i>C. ant, R. mos</i> abundance	3.52*	1		
		<b>Water nutrients</b>	3.34*	1		
Internode length	98	pH	2.33 <sup>n.s.</sup>	1	-0.11	1.78
		Species richness	3.71.	1	-0.15	2.83
		<b>Species identity</b>	5.79***	5		22.20
		<b>Water depth</b>	6.22*	1	0.19	5.03
		Residuals			89	



Specific internode mass	102	<b><i>C. ant</i>, <i>R. mos</i> abundance</b>	5.60*	1	-0.17	2.71
		Water conductivity	2.89.	1	-0.12	1.39
		<b>Phytoplankton concentration</b>	7.33**	1	-0.18	7.57
		<b>Species identity</b>	18.37***	5		44.37
		Residuals		91		43.96
<b>Root</b>						
All	101	<b>Species identity</b>	11.98***	5		
		<b>Phytoplankton concentration</b>	5.56**	1		
		<b>Water temperature</b>	3.24*	1		
		<b><i>C. ant</i>, <i>R. mos</i> abundance</b>	3.68*	1		
		<b><i>L. aus</i>, <i>R. bit</i> abundance</b>	8.01***	1		
Maximum root length	102	<b><i>C. ant</i>, <i>R. mos</i> abundance</b>	9.21**	1	0.24	4.37
		<b><i>L. aus</i>, <i>R. bit</i> abundance</b>	3.61.	1	-0.14	1.71
		<b>Water temperature</b>	7.70**	1	-0.21	3.66
		<b>Species identity</b>	19.10***	5		45.39
		Water depth	2.42	1	0.11	1.18
Residuals		92		43.69		
Specific root mass	101	<b>pH</b>	4.11*	1	-0.15	1.92
		<b>Phytoplankton concentration</b>	22.42***	1	-0.41	10.49
		Pielou evenness	3.77.	1	-0.13	1.76
		<b>Water nutrients</b>	7.26**	1	-0.24	3.40
		<b>Species identity</b>	17.03***	5		39.85
Residuals		91		42.58		

Notes: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ ; ‘.’  $0.05 < p < 0.1$ ; ‘n.s.’ not significant ( $p > 0.1$ ). ‘n’ number of points to calculate relationship. To normalize data: log transformation on all traits, except for height and maximum root length that have been square-root transformed. ‘*C. ant*’ *Callitriche antarctica*, ‘*L. aus*’ *Limosella australis*, ‘*R. bit*’ *Ranunculus biternatus*, ‘*R. mos*’ *Ranunculus moseleyi*.

Finally, when considering total trait effects on plant performance (Fig. 2b), only SLA had a negative impact, while all other traits displayed overall positive effects.

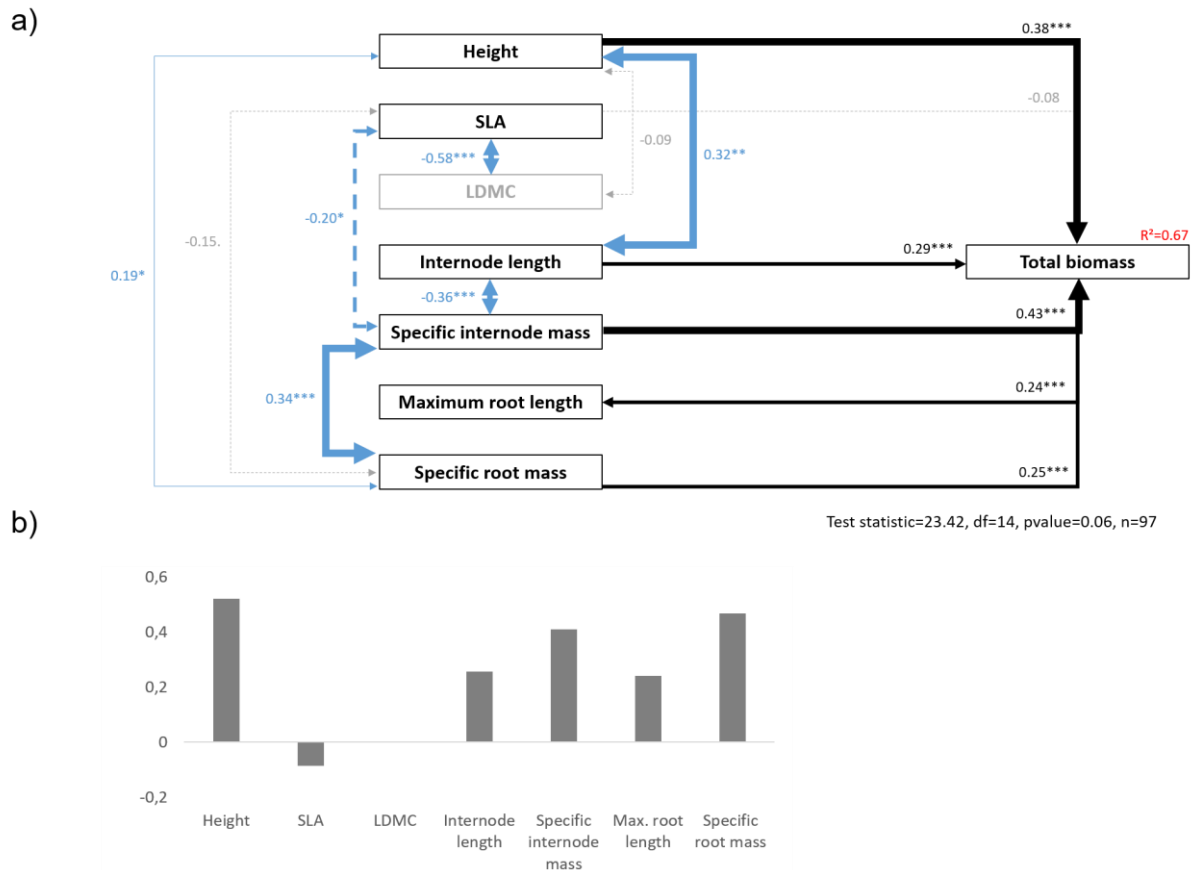
## Discussion

### *Taxonomy explains most of trait variations*

Linking patterns to processes in community ecology is often challenging, especially in field-based studies. Several authors have suggested to use trait variations to infer community assembly mechanisms (McGill, 2008; Taudiere & Violle, 2016; Violle et al., 2007, 2012). To tease apart the multiple factors that drive community assembly in aquatic systems, we partitioned the variance of several traits among three distinct, yet interacting, scales, *i.e.* space, time, and taxonomy. Importantly, studies

simultaneously taking different scales into account remain rare (but see *e.g.* Henn et al., 2018; R. Liu et al., 2018; Luo et al., 2016), and to our knowledge, none of them have so far considered an interannual effect over several years.

In the present study, variance partitioning among tested scales is uniform among traits, indicating that the processes determining these different trait values are similar. Community assembly mechanisms operating through time (year) and space (regional scale) are responsible for a low percentage of total trait variance, in line with the observations formerly reported by Fu et al. (2013). These authors also partitioned trait variance, but across spatial scales only, and they found that large spatial scale (*i.e.* regional scale including different lakes) does not account much for the root/shoot ratio, and leaf number variations in the macrophyte



**Figure 2.** a) Structural equation model representing the direct and indirect effects of trait values on individual performances, with all species included. We used the trait measurements of November 2020 for this analysis. Trait values were standardized separately for each species to get rid of variance due to species identity. The initial model is presented in Appendix 6 and was reduced with lavaan package through variable selection based on AIC criteria. All variables were calculated at pond level. Single dark headed arrows indicate direct effects. Double headed blue arrows indicate correlation between two model variables. Standardized path coefficients are given in blue for correlations and in black for direct effects with their p-values: \*\*\* $p < 0.001$ ; \*\* $p < 0.01$ ; \* $0.05 < p < 0.1$ ; no asterisk  $p \geq 0.1$  not significant. The widths of the lines are proportional to the strength of relationships (values of path coefficients). Solid and dashed lines respectively indicated positive or negative direct effects. Grey paths and grey variables indicated paths and variables that did not have any significant direct or indirect effects on species performance.  $R^2$  values were the variance proportion of response variables explained by their explanatory variables. b) Absolute direct and indirect effects of trait values on individual performance.

species *Potamogeton maackianus*. In our work, trait distributions are fairly conserved among sites and suggests a filter operating on the overall distribution of trait values within the region. Then, we showed that intra-site variations (inter and intraspecific scales) were overwhelmingly dominant in comparison with inter-site variations, for all traits. In other words, the trait means were variable among species in each site, and among individuals in each species. Thus, a mechanism participated

in spreading trait values around the optimum values within sites. This observed pattern can arise from several non-exclusive hypotheses. First, adaptation to habitat heterogeneity within sites can lead to different optimal trait values depending on the micro-site considered. Second, biotic interactions can disperse trait values to limit the similarity between individuals, thus reducing competition. As highlighted by [Messier et al. \(2010\)](#), both niche and neutral theory can play

a role in community assembly, since a filter select individuals based on their trait values rather than their species identity, finally constraining trait values at regional scale.

Interestingly, taxonomy accounted for the most of all trait variations, with in particular intraspecific trait variations being higher (56.29% on average) than interspecific variations in most traits. However, the relative importance of interspecific *versus* intraspecific trait variability was trait-dependent which is consistent with previous studies showing that the relative amount of interspecific *versus* intraspecific trait variability differ among studies and traits (see [Albert, Thuiller, Yoccoz, Douzet, et al., 2010](#); [Fajardo & McIntire, 2010](#); [Roche et al., 2004](#)). We found LDMC and specific internode mass to vary more between species than within species. This indicates that traits related to resources conservation are highly conserved among species, allowing different species to specialize and co-occur along habitat gradients (different conditions among ponds). However, growth and resources acquisition traits (height, SLA, internode length, maximum root length) varied more within species than between species, in line with [Siefert et al. \(2015\)](#) who found that “whole-plant traits” (*i.e.* plant height, and architecture) were more variable within population than between species in a global-scale meta-analysis. This high amount of intraspecific trait variability allows populations to resist to filters, and the environmental heterogeneity at very fine scale (within-pond habitat variations) can lead to high variation in phenotypic trait values. Another non-exclusive hypothesis is that, in case of macrophytes, architectural traits can display multiple trait values since individuals are much less constrained by gravitational force than terrestrial species ([Fu et al., 2013](#)).

We confirmed that partitioning trait variance is a relevant approach to detect at which scale operate the most decisive processes in plant community assembly without scale dependency issues ([McGill,](#)

[2008](#)). Moreover, we underlined the strong importance of ITV in shaping community assembly ([Jiang et al., 2016](#); [Violle et al., 2012](#)), and we then argue that not only species mean and community-aggregated trait values ([Schamp et al., 2007](#); [Stubbs & Bastow Wilson, 2004](#)) but also trait distributions have to be analyzed when studying community dynamics and structure ([de la Riva et al., 2016](#); [Henn et al., 2018](#)). Including ITV in community ecology can improve the detection of processes underlying species coexistence at local scale ([Doudová & Douda, 2020](#); [Fu et al., 2014](#); [Violle et al., 2009](#)).

#### *Intraspecific trait variation in response to both biotic and abiotic variables*

Trait based approaches are widely used in the literature to investigate individual responses to abiotic and biotic filters separately ([Violle et al., 2007](#)), although individuals usually cope with both types of filters within plant communities. As a consequence, our vision of ITV in a context of multiple constraints remains partial. In our study, we propose to fill this literature gap by simultaneously testing trait responses to different abiotic and biotic variables.

Contrary to our expectations, in pond living individuals, all traits did not respond to both abiotic and biotic variables. Height, SLA, and internode length on the one hand, and specific internode mass on the other hand, were respectively influenced by abiotic or biotic variables only, although these traits are known to usually respond to these two types of variables ([Bittebiere & Mony, 2015](#); [Loughnan & Gilbert, 2017](#); [Rusch et al., 2011](#); [Santamaría, 2002](#)). However, all other traits variations (*i.e.* LDMC, maximum root length, and specific root mass) were due to both biotic and abiotic variables, as predicted. These different patterns of trait responses indicate that, in a context of multiple constraints, individual plant does not respond as a whole, but instead, each trait has a singular role. This finding challenges the validity of conclusions that assume responses at a whole-plant level ([De Kroon et al., 2005](#)),

and suggests that survival within multi-constrained habitat, relies on low phenotypic integration (Murren, 2002) allowing the expression of multivariate phenotypes. Overall, our study thus underlines the relevance of multi-traits approaches integrating both biotic and abiotic variables, as also stated by Chalmandrier et al. (2022), to efficiently capture plant response strategies, and ultimately identify mechanisms of species coexistence at local scale. Besides, our observations suggest that patterns of trait variations measured *in situ* should be carefully interpreted as they may not reflect responses to one type of filter only, either biotic or abiotic (Duarte et al., 1986; Kõrs et al., s. d.; Su et al., 2019).

In the ponds of the Iles Kerguelen, each trait category was involved in the response to specific habitat variables. First, traits related to nutrient acquisition and light acquisition as SLA did respond to water nutrients. More precisely, SLA decreased when water nutrients increased, suggesting that macrophyte species may be plastic to either maximize the capture of light when higher nutrient concentrations stimulate phytoplankton growth reducing light penetration in water (Rabalais, 2002), or maximize the capture of nutrients (Lavorel & Garnier, 2002). Root length, also involved in nutrient acquisition, was positively impacted by species abundances. Although it could be explained by a lower nutrient availability, resulting in longer roots to a higher nutrients acquisition, competition for nutrient acquisition would also favor root traits divergence and force plants to optimize resource uptake (Ferguson et al., 2016; Manschadi et al., 2006). This result indicates that root trait variations can be useful in detecting responses to biotic competition, although they are poorly considered in field studies due to the difficulty of sampling (Colom & Baucom, 2020). Secondly, traits related to resources conservation, as LDMC, specific internode, and root masses were negatively impacted by competition. Indeed, resource storage decreased within connection internodes and roots in response to species

abundance and/or phytoplankton biomass, perhaps reflecting an escape strategy towards less competitive micro-sites for nutrients or because of a lack of available resources. To a lesser extent, LDMC also responded to sediment nutrients, which is consistent with the literature (Fu, 2020; Garnier et al., 2001). Previous studies suggested indeed that an increase in nutrient availability may induce leaf trait variability towards a low conservation of nutrients, as a decrease in LDMC for instance (Poorter & Garnier, 2007). Lastly, internodes elongated with water depth, probably as part of harsh conditions avoidance strategy (Bittebiere & Mony, 2015; Callaghan et al., 1992; Louâpre et al., 2012).

As a result, while many previous studies focused on the effects of one or few variables on species, we argue to consider several biotic and abiotic variables in future studies to better understand the effects of environmental changes on plant communities (Cavieres et al., 2014; Crain et al., 2004; Klanderud et al., 2015; Mitchell et al., 2017; Morris et al., 2020; Wood et al., 2012).

#### *Effects of trait values and their relationships on macrophyte performance*

The SEM approach allowed us to highlight that all traits, except LDMC, had either direct or indirect effects on individual performance. This observation is especially important as most published studies neglect the relationships between traits when dealing with their influence on individual performance (Engbersen et al., 2022; Pywell et al., 2003), in particular in aquatic ecosystems (Fu et al., 2014; Ma et al., 2022). Our study thus supports the current view in functional ecology underlying the relevance of multi-traits approaches taking trait relationships into account (Albert, Thuiller, Yoccoz, Douzet, et al., 2010; Bittebiere et al., 2019; Blonder et al., 2014; Gustafsson & Norkko, 2019).

As traits are interrelated, adjustments in trait values must be coordinated to produce

a properly functioning organism, also meaning that patterns of trait correlations can greatly change across environments (Murren, 2002). To maintain optimal fitness, it is expected that plant individual should present high correlations among functionally related traits (high integration within functional unit), and lower correlations among functionally different traits (among functional units), conferring flexibility yet coordination to individuals (Nicotra et al., 1997). This is consistent with our results where the highest correlations were found among traits related to resource storage (specific internode mass, specific root mass), or traits related to resource acquisition/conservation strategies (SLA, LDMC).

Comparing the respective effects of traits on individual performance, we observe that clonal traits act more intensely and more directly on performance than expected, suggesting their crucial importance for individual survival. These traits allow to forage for suitable micro-habitats (Suzuki & Stuefer, 1999) and store resources (Dong et al., 2010), which is essential to maintain within constrained habitats. Pooling direct and indirect effects, growth and storage traits (*i.e.* height, specific internode mass, and specific root mass) have stronger positive effects than architectural traits (root and internode length), which is consistent with the results presented in Wildová et al. (2007). Individual growth and storage traits are directly related to individual size, subsequently affecting individual biomass, whereas architectural traits are more related to colonization ability and allocations between organs, thus affecting more indirectly the individual performance (Wildová et al., 2007). Besides, traits related to resource storage have here stronger effects (amplified by the correlation between specific internode mass and specific root mass) than traits related to resource acquisition (SLA), probably implying a priority in investing in resource conservation within constrained habitats like ponds of the sub-Antarctic region.

Finally, abiotic variables can have cascading effects on individual performance through their influence on trait variations. Indeed, changes in abiotic values from season to season and from year to year, within constrained habitats like polar ponds, would greatly impact plant trait values. For example, an increase in water temperature reduces root length, indirectly and negatively affecting individual performance. Thus, although rising water temperatures can stimulate macrophyte performance within the optimum thermal range (Dar et al., 2014), it may present a negative impact within sub-Antarctic ponds, suggesting that this optimal thermal range can be overpassed (Frenot et al., 2006). Similarly, variations of water depth affect plant performance, through its effects on internode length. As water temperatures keep warming up and precipitations keep decreasing (Walther et al., 2002), one can predict that the consequences for the macrophyte community structure and its productivity will be severe.

## Conclusion

Partitioning the variance among multiple ecological scales allows to get a less fragmented picture of all possible underlying variables that can drive community assembly and avoid misinterpretations of traits variations in field studies. Moreover, while many studies focused on mean trait values, we aim to consider the strong role of ITV in species coexistence and their responses to filters. To go further, we plead to consider other trait metrics in future studies to better describe trait distributions and assess the processes underlying plant community assembly. As for example, skewness and kurtosis (Enquist et al., 2015; Gross et al., 2017) are a complement to the mean and the variance and reflect respectively trait distribution asymmetry and the evenness of functional diversity. As such, they could be indicative of competition (Gross et al., 2009; Schamp et al., 2007) or rapid environmental change (Enquist et al., 2015; Le Bagousse-Pinguet et al., 2017). Consequently, these metrics would be very useful to predict for

responses to changing environment or their effects on ecosystem functioning (Gross et al., 2017).

### Conflict of interest

The authors declare that there is no conflict of interest.

### Data availability statement

The data that support the findings of this study are openly available in figshare at <https://doi.org/10.6084/m9.figshare.2162160.0.v1>

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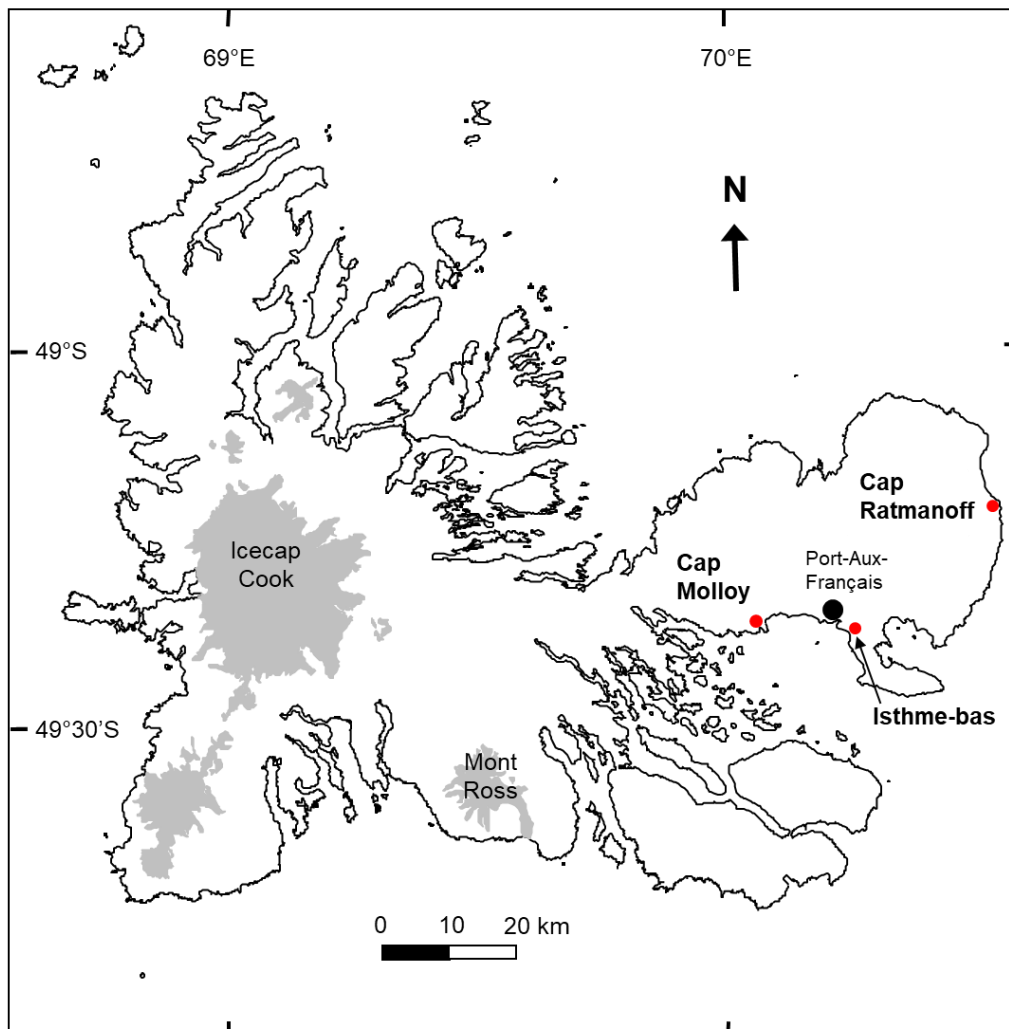
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## Supporting Information



**Supporting Information 1.** Locations (red points) of the three sampled sites on the French sub-Antarctic Iles Kerguelen ( $48^{\circ}30'–50^{\circ}S, 68^{\circ}27'–70^{\circ}35'E$ ). Black point: technical and scientific station.

**Supporting Information 2.** Eigenvector scores for the first axis of a Principal Component Analysis (PCA) performed on water nutrient parameters measured at the pond level. The two highest eigenvector scores are indicated in bold. Variance accounted for by the axis is indicated into brackets. PCA Axis 1 was negatively related to the concentration of N-NH<sub>4</sub><sup>+</sup> and N-NO<sub>3</sub><sup>-</sup> in the water column.

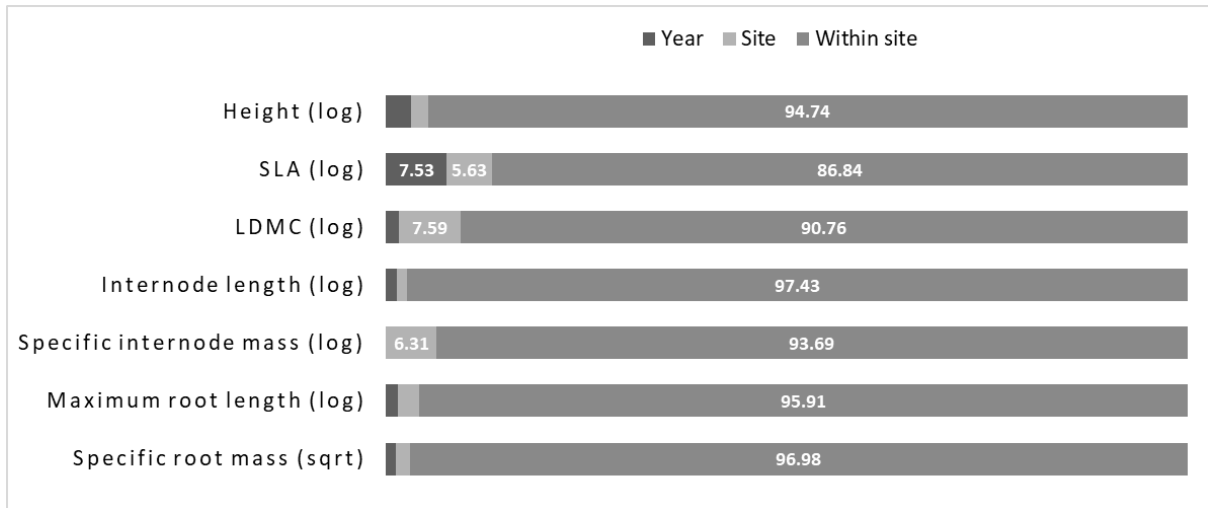
Abiotic variables	PCA 1 (42.06%)
N-NH <sub>4</sub> <sup>+</sup>	<b>-0.79</b>
N-NO <sub>3</sub> <sup>-</sup>	<b>-0.79</b>
P-PO <sub>4</sub> <sup>3-</sup>	-0.006

**Supporting Information 3.** Eigenvector scores for the first axis of a Principal Component Analysis (PCA) performed on abiotic parameters measured at the pond level. Variance accounted for by the axis is indicated into brackets. PCA Axis 1 (58.59%) was negatively related to the C:N ratio and positively related to the amount of bioavailable P in sediments.

Abiotic variables	PCA 1 (58.59%)
C :N	-0.76
Bioavailable P	0.76

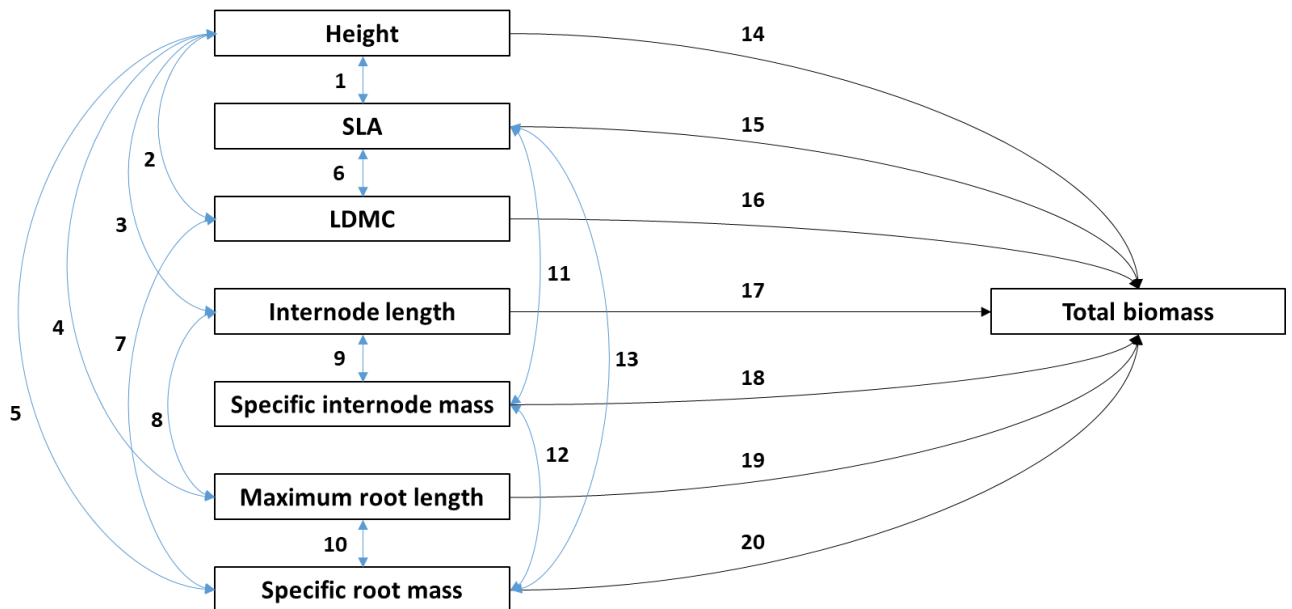
**Supporting Information 4.** Eigenvector scores for the first axis of a Factorial Correspondence Analysis (FCA) performed on water nutrients parameters measured at the pond level. The two highest eigenvector scores for each FCA axis are indicated in bold. Variance accounted for by the axes is indicated into brackets. FCA Axis 1 (33.81%) was positively related to the abundance of *R. moseleyi* and negatively related to the abundance of *C. antarctica*. FCA Axis 2 (24.99%) was positively related to the abundance of *R. pseudotrullifolius* and negatively related to the abundance of *L. australis*. FCA Axis 3 (16.99%) was positively related to the abundance of *L. australis* and negatively related to the abundance of *R. biternatus*.

Abiotic variables	FCA 1 (33.81%)	FCA 2 (24.99%)	FCA 3 (16.99%)
<i>C. antarctica</i>	<b>-0.97</b>	0.08	0.38
<i>J. scheuchzerioides</i>	0.43	-0.43	-0.03
<i>L. australis</i>	0.04	<b>-0.99</b>	<b>1.73</b>
<i>R. biternatus</i>	-0.23	0.03	<b>-0.73</b>
<i>R. moseleyi</i>	<b>1.49</b>	0.99	0.56
<i>R. pseudotrullifolius</i>	-0.03	<b>1.72</b>	-0.10



**Supporting Information 5.** Variance partitioning of individual traits across three nested scales: year, site and within site. Data were normalized (log or square-root transformation). See Materials and Methods section for more details in variance partitioning. These results were complementary to Fig. 1. We ran alternative partitioning model by deleting species level and provided evidences that we obtained similar results when working with imperfect nesting of species within sites.

**Supporting Information 6.** Theoretical structural equation model representing the direct and indirect effects of trait values measured in ponds, on individuals' performance (total biomass). This model was reduced with lavaan package through variable selection based on AIC criteria, and results are presented in Fig. 2. Single dark headed arrows indicate direct effects. Double headed blue arrows indicate correlation between two model variables. All trait values were averaged at pond level. Numbers indicate literature references supporting each tested relations and correlations.



Notes. 1: (Díaz et al., 2016), 2:(Garnier et al., 2001), 3: (Wildová et al., 2007), 5 and 6 : (Wright et al., 2004), 7: (Garnier et al., 2016), 8: (Šmilauerová & Šmilauer, 2007), 9 and 10: (Cornelissen et al., 2003), 11: (Kleyer et al., 2019), 12 and 13: (Fort et al., 2013), 14: (Heinrichs et al., 2010), 15: (Poorter & de Jong, 1999), 16: (Pontes et al., 2007), 17: (Weijschedé et al., 2008), 19: (Lynch, 1995), 4, 18 and 20: added to the test.

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## CHAPITRE 1 : Réponses fonctionnelles des communautés de macrophytes face aux conditions abiotiques des mares

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## Préface

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La détermination des mécanismes sous-jacents à la coexistence des espèces au sein des communautés végétales est essentielle pour prédire leur devenir dans le contexte actuel de changement climatique et de perte de biodiversité (Chapin, 2003). A échelle locale, les plantes interagissent de façon permanente avec leurs voisins immédiats (compétition, facilitation), ce qui façonne également la composition spécifique et fonctionnelle de la communauté (Tilman, 1982 ; Connell, 1983 ; Goldberg & Barton, 1992). Les mécanismes sous-jacents impliqués dans les interactions plantes-plantes et la coexistence des espèces peuvent varier au sein des habitats soumis à des contraintes abiotiques, notamment au sein des systèmes d'eau douce qui comptent parmi les habitats les plus contraints. Pourtant, cette hypothèse n'a été que très peu testée jusqu'à présent, en particulier concernant les interactions facilitatrices (Silknetter et al., 2020).

Le fort filtrage de l'habitat dans les écosystèmes aquatiques influence la composition fonctionnelle et la diversité des communautés de macrophytes, qui jouent toutes deux un rôle important dans les interactions plantes-plantes. En effet, celles-ci dépendent à la fois des traits fonctionnels des individus qui déterminent leur succès compétitif (Gaudet & Keddy, 1988 ; Grace & Tilman, 1990), mais aussi de la différence des valeurs de traits fonctionnels entre concurrents voisins (Kraft et al., 2015b ; Cadotte & Tucker, 2017). Les traits aériens (p. ex., hauteur ou SLA) et racinaires seraient impliqués dans la compétition pour les ressources (Lau et al., 2014 ; Kunstler et al., 2016), en particulier pour la lumière qui est un facteur limitant dans les systèmes aquatiques. Les traits clonaux quant à eux seraient des traits de tolérance aux contraintes abiotiques, permettant de coloniser des micro-habitats présentant des conditions environnementales plus appropriées. Aussi, des valeurs de traits peu différentes entre individus (traduisant des mécanismes de hiérarchie compétitive) devraient fortement impacter les interactions plantes-plantes, à l'inverse des fortes différences de valeurs de traits entre individus (traduisant des mécanismes de « limiting similarity », Kraft et al., 2014). De plus, les variables abiotiques des habitats conditionnent la nature des interactions plantes-plantes. L'hypothèse du Stress Gradient Hypothesis (SGH) prévoit ainsi une intensification des interactions facilitatrices en milieux contraints et des interactions plutôt compétitives dans des milieux moins contraints et/ou plus productifs (Bertness & Callaway, 1994).

Par ailleurs, les espèces au sein d'une communauté ne sont pas distribuées aléatoirement. Leur arrangement spatial (patron spatial) résulterait de processus stochastiques (Hubbell, 2011) et/ou déterministes en lien avec l'hétérogénéité des habitats, les phénomènes de dispersion et d'interactions plantes-plantes (Herben & Hara, 2003). Les relevés de co-occurrences des espèces à fine échelle permettent de déterminer deux types de patrons spatiaux : les agrégations et les ségrégations. Les interactions positives (facilitation) entre espèces amèneraient à des patrons d'agrégations à travers une modification des micro-conditions abiotiques (Eccles et al., 1999 ; Malkinson et al., 2003 ; Kikvidze et al., 2005 ; Raventós et al., 2010). A l'inverse, des interactions négatives (compétition pour les ressources) amèneraient les espèces à se distancier pour limiter la concurrence, créant ainsi des patrons de ségrégation (Seabloom et al., 2005 ; Pottier et al., 2007 ; Schöb et al., 2008). Cependant, ces relations entre patrons spatiaux et interactions plantes-plantes ont été majoritairement étudiées au sein de systèmes arides, et jamais à notre connaissance en milieux aquatiques d'eau douce, qui présentent pourtant des limitations de ressources différentes liées à la hauteur d'eau et la disponibilité en lumière par exemple.

Toutes modifications des variables abiotiques de l'habitat aquatique peuvent entraîner des conséquences sur la biomasse des communautés, notamment la température de l'eau et la luminosité, soit directement *via* leurs effets sur la physiologie (Wrona et al., 2006 ; MacKay et al., 2009 ; Dhir, 2015 ; Hossain et al., 2017 ; Velthuis et al., 2018 ; Zhang et al., 2020a), soit indirectement *via* leurs impacts sur les traits fonctionnels des individus (James et al., 2005 ; Mouchet et al., 2010 ; Dar et al., 2014 ; Kim & Nishihiro, 2020) et les interactions plantes-plantes (Bertness & Callaway, 1994). De plus, les variables environnementales sont interdépendantes (p. ex. relation entre hauteur d'eau et luminosité, entre température et aire du système ; Bornette & Puijalon, 2011) et la prise en compte de leurs covariations est nécessaire pour une meilleure compréhension des mécanismes sous-jacents aux réponses des communautés dans des contextes d'environnements changeants. Pourtant, peu d'études prennent en compte la modulation des variables biotiques par les variables abiotiques, et donc les effets directs et indirects des variables abiotiques sur la biomasse des communautés.

Ce premier chapitre qui repose sur l'**article III** et qui met en jeu des relevés *in situ*, cherche à répondre aux questions suivantes :

- Peut-on inférer la nature des interactions plantes-plantes par la structuration spatiale des communautés de macrophytes ? Nous avons supposé que :
  - Ségrégations et agrégations des espèces reflèteraient respectivement des interactions de compétition et de facilitation.
  
- Comment les conditions abiotiques du milieu et les caractéristiques fonctionnelles du voisinage affectent le sens et l'intensité des interactions plantes-plantes ? En particulier, nous avons émis les hypothèses suivantes :
  - Les traits aériens et racinaires devraient jouer un rôle important dans la compétition pour la lumière, tandis que les traits clonaux seraient des traits de tolérance aux contraintes abiotiques. Par conséquent, les valeurs moyennes des traits aériens et racinaires des individus voisins devraient être davantage impliqués dans les interactions plantes-plantes que les traits clonaux. De même, la diversité fonctionnelle du voisinage jouerait également un rôle dans les interactions plantes-plantes pour limiter la similarité entre les individus.
  
- Comment les variables biotiques et abiotiques se modulent entre elles et quelles sont les conséquences sur la performance des communautés à l'échelle des mares ? Les hypothèses étaient les suivantes :
  - La biomasse des communautés de macrophytes serait affectée par les variables abiotiques du milieu (notamment la luminosité et la température de l'eau), soit par un effet direct, soit indirectement à travers la modulation des variables biotiques caractérisant la structure des communautés (richesse spécifique, diversité fonctionnelle et patrons spatiaux).

**Functional characteristics rather than co-occurrences determine the outcome of interactions between neighbouring plants in sub-Antarctic ponds: consequences for macrophyte community biomass.**

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Article Informations	Abstract
<p><i>Article history:</i> Accepted in <i>Freshwater Biology</i></p> <hr/> <p><i>Keywords:</i> Functional traits Community performance Abiotic filters Species coexistence Local spatial arrangement</p>	<ol style="list-style-type: none"> <li>1. Understanding of the mechanisms underlying species coexistence within plant communities is crucial to predict their fate given the current context of biodiversity loss. Freshwater ecosystems are among the most abiotically constrained habitats because they harbor clonal macrophyte communities. Strong habitat filtering in these ecosystems influences the functional composition and diversity of macrophyte communities, determining the outcome of interactions between neighbours and ultimately affecting local spatial arrangement between neighbours (LSA). This influence may be modulated by environmental conditions in abiotically constrained habitats, such as freshwater ecosystems.</li> <li>2. We focused on macrophyte communities living in ponds in the Iles Kerguelen, in the sub-Antarctic. These freshwater ecosystems are especially abiotically constrained (cold climate), and their plant communities are remarkably species-poor, simplifying the study of interactions between neighbours. We measured several abiotic variables in the ponds, species LSA and interspecific interactions (using the Log Response Ratio metric), and the functional composition of the community using aerial, root and clonal traits. We also determined the biomass of the whole macrophyte community.</li> <li>3. Our results showed that LSA does not effectively assess interactions between neighbours at very small scales, neither at the community (one species <i>versus</i> all neighbouring species) nor the species level (between pairs of species). Secondly, aerial (leaf and stem) and root traits related to resource acquisition played a more important role in interactions between neighbours than clonal traits (<i>i.e.</i> internode length and specific internode mass related to space acquisition and resource storage, respectively).</li> <li>4. Depending on the target species, (i) interactions responded positively or negatively to mean trait and functional diversity of the community,</li> </ol>

and (ii) different traits of neighbours (aerial or root traits) triggered an interaction response. Lastly, abiotic variables, in particular water temperature and light intensity, influenced macrophyte community biomass and plant community structure (*i.e.* species richness, functional diversity and LSA), either directly or through the modulation of other abiotic variables.

5. Our results lead to the two following conclusions: (i) interactions between neighbours do not reflect their local spatial arrangements but are strongly associated with abiotic variables and neighbourhood functional traits (depending on species), (ii) joint integration of biotic and abiotic variables in multivariate analyses enables better inference of biodiversity responses to environment, and the subsequent consequences for ecosystem function, especially in the context of climate change.

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## Introduction

Determining the mechanisms underlying species coexistence within plant communities is crucial to predict their fate in the current context of climate change and biodiversity loss (Chapin, 2003). Both abiotic and biotic drivers are known to structure local assemblages within communities (Cadotte & Tucker, 2017; Kraft, Adler, et al., 2015). Indeed, species that do not possess the functional traits allowing them to resist particular abiotic conditions are filtered out, leading to similar phenotypes among co-occurring species. Moreover, at finer scales, plants permanently interact with their immediate neighbours (*e.g.* competition, facilitation), also ultimately shaping specific and functional composition of the community (Connell, 1983; Goldberg & Barton, 1992; Tilman, 1982). Abiotically constrained habitats exacerbate the importance of interactions between neighbours (Choler, Michalet, & Callaway, 2001), with facilitative interactions being more pronounced under stressful and/or resource-limited conditions (Williams, Zeldin, Semski, Hipp, & Larkin, 2021; Zhang, Wang, & Qi, 2017). Freshwater ecosystems are among the most abiotically constrained, often harboring particular plant communities. They host macrophyte (*i.e.* aquatic plant) communities, dominated by clonal plants (Klimeš, Klimešová, Hendriks, & van Groenendael,

1997; Santamaría, 2002) that interact in both horizontal (for space) and vertical (for resources) directions (Gioria & Osborne, 2014). Altogether, the underlying mechanisms involved in interactions between neighbours and that support species coexistence may vary within a particular freshwater ecosystem, including within abiotically constrained habitats, although this has been poorly tested, especially regarding facilitative interactions (Silknetter et al., 2020).

Strong habitat filtering in aquatic ecosystems (Santamaría, 2002) affects the functional composition and diversity of macrophyte communities (Bornette & Puijalon, 2011; Fu et al., 2014; Zhang, Liu, Luo, Dong, & Yu, 2019), which may in turn play significant roles in interactions between neighbours (Suzuki, Rivero, Shulaev, Blumwald, & Mittler, 2014). The outcome of interactions between neighbours is not only driven by individual functional traits (Gaudet & Keddy, 1988), but may also be determined by the difference between the functional trait values of neighbouring competitors, as predicted by recent theories of species coexistence (Cadotte & Tucker, 2017; Kraft, Godoy, & Levine, 2015). The traits of neighbours are expected to have different effects on the outcome of interactions, in particular when trait values differ from those of the focal plant (Kraft, Crutsinger,

Forrestel, & Emery, 2014), and according to their role in competitive strategies (tolerance vs. competing traits) (Novoplansky, 2009). On the one hand, coexistence is often assumed to arise from high different functional trait values, which alleviate competitive interactions (limiting similarity). On the other hand, small differences in functional traits arising from competitive hierarchies may reduce differences in competitive ability, thereby promoting coexistence of species with similar trait values (Kraft, Crutsinger, Forrestel, & Emery, 2014). In abiotically constrained habitats, high functional convergence between species is expected due to environmental filtering (Cornwell, Schwilk, & Ackerly, 2006; Grime, 2006), suggesting reduced importance of mechanisms involved in traits differentiation. Moreover, clonal traits influencing space acquisition could act as tolerance traits to abiotic constraints as they provide opportunities to find more suitable environmental conditions, while aerial (*e.g.* height or Specific Leaf Area) and root traits should be crucial for resource competition (Kunstler et al., 2016; Lau, Shaw, Reich, & Tiffin, 2014). Thus, aerial and root traits (vertical traits) should be more strongly involved in interactions between neighbours than clonal (horizontal) traits.

Within plant communities, individuals are not randomly distributed. Their spatial distribution can result either from stochastic events (Hubbell, 2011), or from environmental heterogeneity, dispersal, and interactions between neighbours (Herben & Hara, 2003). Therefore, the observed local spatial arrangement between neighbours (hereafter referred as to LSA), would be the outcome of environmental filtering and of their interactions as commonly demonstrated (Blanchet, Cazelles, & Gravel, 2020). Besides, inter-specific interactions between plants are known to depend on abiotic characteristics (Martin & Coetzee, 2014; Shields & Moore, 2016), with a shift from competition to facilitation in harsh conditions (Bertness & Callaway, 1994, stress gradient hypothesis). Facilitation allows for a better

recruitment and survival by improving abiotic conditions at local scales, which is expected to reflect spatial aggregation between plants (Bertness & Callaway, 1994; Kikvidze et al., 2005; Tirado & I. Pugnaire, 2005). Conversely, studies have shown that competition for resources leads better competitors to displace other species, commonly reflecting segregated LSA (Pottier, Marrs, & Bédécarrats, 2007; C. Schöb, Kammer, Kikvidze, Choler, & Veit, 2008; Seabloom, Bjørnstad, Bolker, & Reichman, 2005). As a consequence, spatial aggregation and segregation may indicate facilitation and competition respectively in constrained habitats (Eccles, Esler, & Cowling, 1999; Kikvidze et al., 2005; Malkinson, Kadmon, & Cohen, 2003; Raventós, Wiegand, & Luis, 2010). This assertion has never been tested within aquatic habitats where resource distribution differs strongly from other constrained habitats (for instance arid systems), due to the major effect of water depth on light availability.

Studies on joint effects of biotic and abiotic filters on macrophyte communities remain limited (Shields & Moore, 2016, but see: Anderson & Kalff, 1988; Chambers & Prepas, 1990; Gopal & Goel, 1993; McCreary, 1991), and this highly fragmented knowledge necessarily leads to inconsistencies in the reported effect of abiotic variables on the outcome of interactions between neighbours. In particular, this literature gap does not enable the respective roles of abiotic and biotic variables or their interactions to be determined for the taxonomic and functional composition of the aquatic plant community, and subsequently for its biomass. The biomass of the aquatic plant community can indeed be affected by abiotic variables either directly through their effects on plant physiology [*e.g.* aquatic system morphology, water or sediment chemistry (*i.e.* nutrient cycling) (Dhir, 2015; Hossain et al., 2017; MacKay et al., 2009; Velthuis et al., 2018; Wrona et al., 2006; Zhang et al., 2020)] or indirectly through species selection caused by environmental filtering (Kraft, Godoy, &

Levine, 2015) combined with interactions between neighbours (stress gradient hypothesis, Bertness 1994), and functional traits (Dar, Pandit, & Ganai, 2014; James, Fisher, Russell, Collings, & Moss, 2005; Kim & Nishihiro, 2020; Mouchet, Villéger, Mason, & Mouillot, 2010). In ponds, water temperature, dissolved nutrients, and light intensity are expected to be the main abiotic variables acting directly on plant community biomass and indirectly through the modulation of plant community structure.

In this study, we focused on macrophyte communities living in the ponds of the Iles Kerguelen, located in the sub-Antarctic region. These ponds are particularly useful for testing questions about interactions between neighbours in the context of abiotically constrained habitat, as the climate is very cold, yet warming (Lebouvier et al., 2011), and the remarkably low plant richness provides simplified natural communities (Frenot, Gloaguen, Massé, & Lebouvier, 2001; Van der Putten, Macel, & Visser, 2010). To that aim, within each pond, we measured several abiotic variables, plant species LSA, interactions between neighbours, and the functional composition of the community. We additionally assessed the biomass of the whole macrophyte community in each pond. Through this field sampling approach, we tested the following hypotheses: (i) interactions between neighbours can be inferred by LSA because spatial segregation should reflect negative effects of the neighbour's cover on target species biomass, thus indicating competition; (ii) vertical functional traits (*i.e.* aerial and root traits) influence interactions between neighbours, while horizontal traits (*i.e.* clonal traits) are less significant, so functional characteristics of neighbours influence their interactions; (iii) abiotic variables (water temperature, dissolved nutrients, and light intensity) should influence plant community biomass, either directly or through the modulation of plant community structure (*i.e.* species richness, functional diversity, and LSA).

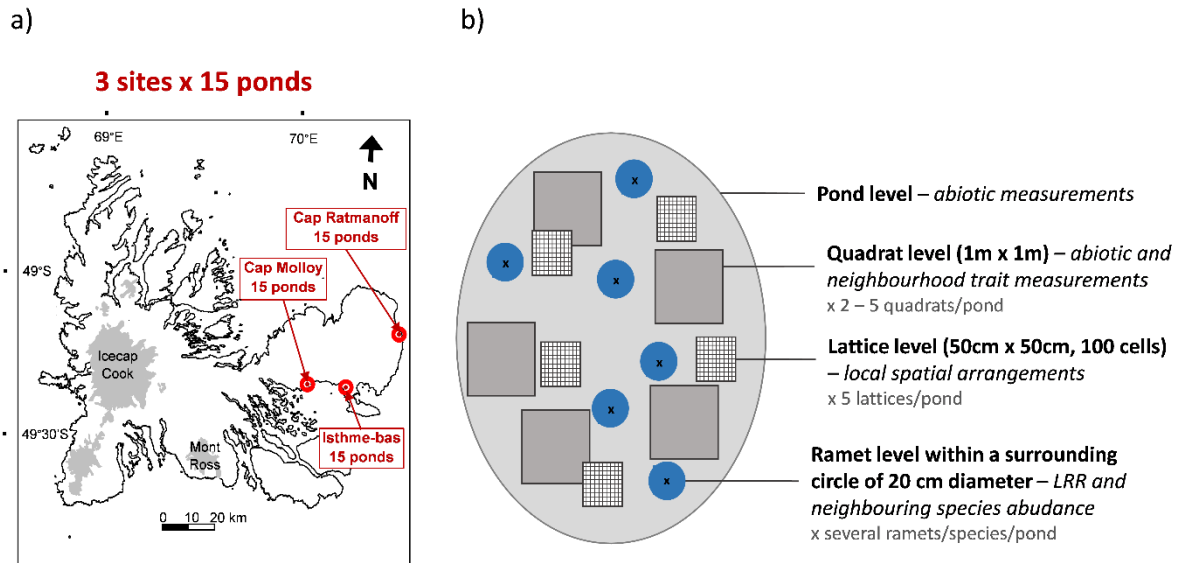
## Materials and methods

### *Study model*

The study was carried out *in situ*, at the Iles Kerguelen in the French sub-Antarctic (South Indian Ocean) (48°30–50°S, 68°27–70°35E). The climate of this archipelago is characterized by cold temperatures (annual mean of 4.6°C with few variations - Frenot et al., 2006; Lebouvier et al., 2011), and abundant precipitations (range from 500 mm to 3200 mm along an East-West gradient - Frenot, Gloaguen, Cannavacciuolo, & Bellido, 1998, and Meteo France). Although remarkably well adapted to cold temperatures, native macrophyte communities are characterized by very low species richness (zero to four co-occurring species per pond) (Frenot et al., 2006). They thus constitute ideal simplified models to infer mechanisms of plant community assembly, especially within constrained abiotic environments (Bergstrom & Chown, 1999).

The study was conducted in ponds at three sites located along the shore of the main island of the archipelago (Fig. 1a): Cap Molloy, Isthme Bas and Cap Ratmanoff. These three sites are less than 40 km apart, and display similar climates. Conversely, abiotic conditions are more variable within ponds than between sites. The ponds investigated have relatively small sizes (average area =  $181.57 \pm 382.39$  m<sup>2</sup> except for one pond 180800 m<sup>2</sup>, Table S1). They are shallow freshwater systems, enriched by nutrient inputs from marine fauna like seabirds and seals owing to their proximity to the ocean littoral (Smith, 2008). At each site, 15 ponds of varying area were selected to represent the variation in pond size, which influences water temperatures (Bornette & Puijalon, 2011). In contrast, mean water depth did not differ among ponds ( $19.03 \pm 9.12$  cm).





**Figure 1.** a) Locations (red points) of the three sampled sites and their associated ponds on the French sub-Antarctic Iles Kerguelen (48°30–50°S, 68°27–70°35E). b) Sampling design within each pond: abiotic variables, neighbours' traits to assess neighbourhood functional characteristics, species co-occurrences to calculate local spatial arrangements between neighbours, targets biomass to calculate LRR and finally the neighbouring species abundance (%).

Macrophyte communities colonizing ponds are composed of six native species that can all co-occur locally: *Limosella australis* R.Br. (Scrophulariaceae), *Callitriche antarctica* Engelm (Plantaginaceae), *Juncus scheuchzerioides* Gaudich. (Juncaceae), together with three Ranunculaceae species: *Ranunculus biternatus* Smith, *R. pseudotrullifolius* Skottsb., and *R. moseleyi* Hook.f. These species are only found in the sub-Antarctic region, and *R. moseleyi* may even be endemic to Iles Kerguelen. All species are perennial, displaying a clonal network structure (*i.e.* plants are composed of related ramets (shoots with leaves and roots) that are connected through plagiotropic stems). *Callitriche antarctica*, *L. australis*, *R. pseudotrullifolius* and *R. moseleyi* are hydrophytes, while *R. biternatus* and *J. scheuchzerioides* are helophytes. Only *C. antarctica* develops a floating canopy, while the five other species possess a rosette growth form rooted in pond sediments. *Ranunculus pseudotrullifolius*, *R. moseleyi*, and *L. australis* are mostly submerged (Hennion et al. 1994; Chau et al. 2021). However, *R. pseudotrullifolius* may also produce floating leaves (Figure S1). *Ranunculus biternatus*

and *J. scheuchzerioides* can also be entirely submerged, depending on variations in pond water level (Figure S1). Most ramets of these species were therefore submerged within ponds (ramet height =  $6.02 \pm 3$  cm, water depth =  $19.03 \pm 9$  cm).

#### Abiotic and biotic characterization of ponds

We characterized abiotic conditions every three months over a year, starting from February 2020 and ending in March 2021 (Fig. 1b). At each sampling date and pond, water and sediment samples were collected from three zones and mixed to obtain one composite water sample (30 mL) and one composite sediment sample (50 mL) taking into account potential spatial heterogeneity within each pond. As other abiotic conditions may also vary spatially in the pond, we randomly positioned three (pond area < 5 m<sup>2</sup>) to five (pond area > 5 m<sup>2</sup>) quadrats (1 m<sup>2</sup>). In these quadrats, three abiotic variables were measured: water depth (calculated as the average of three measurements within the quadrats), electric conductivity (EC), and concentration of dissolved oxygen (DO) (calculated as the average of three measurements performed below water

surface, in the middle of the water column, and at the pond bottom) using a multiparameter HQ40D HACH sensor ( $EC \pm 0.1 \text{ mS.cm}^{-1}$ ,  $DO \pm 0.01 \text{ mg.L}^{-1}$ ). In addition, light intensity and water temperature were continuously recorded in each pond, every half hour since September 2020, using loggers (Hobo MX2202) positioned in the middle of the water column. Based on this dataset, water temperatures and light intensity fluctuations were then simulated for the period of February 2020 to August 2020 (winter season) which was not monitored. Water temperatures were simulated using their relationship with air temperatures recorded by Météo France (2020 records, Port-aux-Français), and winter luminosity from its relationship with summer luminosity (Table S2). Finally, pond area (length  $\times$  width) and proximity to the closest pond were also measured in March 2021.

For the measurements of water nutrient and chlorophyll-a concentrations, water samples were filtered through GF/F filters ( $0.7 \mu\text{m}$  pore size, Whatman GF/C) to eliminate coarse and fine particles within the 24 hours after field sampling. All samples (filtered water and sediments) and GF/F filters were then stored at  $-20^\circ\text{C}$  for several weeks before analyses. Chlorophyll a pigments collected on GF/F Whatman filters were quantified using the Unesco method (Vohra, 1966) with a spectrophotometer. This measure was used to estimate the quantity of phytoplankton per volume of water for each pond.  $\text{N-NH}_4^+$ ,  $\text{N-NO}_3^-$  and  $\text{P-PO}_4^{3-}$  concentrations of water samples were determined using standard colorimetric methods (Grasshoff, Ehrhardt, Kremling, & Anderson, 1999) with a sequential analyzer (SmartChem200, AMSAlliance).

In sediment samples, organic carbon to nitrogen ratio (C:N) was measured using the “capsule method” (Brodie et al., 2011). For each sample, five  $\text{mg} \pm 10\%$  of dry sediment previously lyophilized and homogenized were weighted in a silver capsule and acidified with  $\text{HCl}$  ( $2 \text{ mol.L}^{-1}$ ) to eliminate carbonates. Capsule liquids were

evaporated on a  $65^\circ\text{C}$  hot plate for 12 hours, before capsules were oven-dried at  $80^\circ\text{C}$  for 48 hours. Organic carbon and nitrogen total content were then measured with an elementary analyzer (FlashEA; Thermo Fisher Scientific, Waltham MA, USA). The bioavailable P concentration in sediments was determined following the protocol of Ni et al. (2016). Bioavailable P was extracted with  $\text{NaOH}$  (1 M). Then the supernatant was collected, its pH was stabilized with  $\text{HCl}$  (3.5 M), and its concentration was quantified using the molybdate/ascorbic acid blue method.

#### *Local spatial arrangements of macrophyte species*

In December 2020, within each of the 45 ponds, spatial distribution of all plant species was recorded using five square lattices of  $50 \times 50 \text{ cm}^2$ , randomly positioned on vegetation. The lattice was divided into  $5 \times 5 \text{ cm}^2$  cells (100 cells in total) and the presence/absence of each macrophyte species within each cell was recorded (Fig. 1b). Non-floating species (*i.e.* all species except *C. antarctica*) were considered as present when a ramet was rooted in the target cell, whereas *C. antarctica* was considered as present when a ramet was observed at the cell vertical. The cell size was selected as it corresponds to the scale at which plants are likely to interact (Purves & Law, 2002).

We calculated the species by species co-occurrence matrix in each lattice. In this matrix, the intersection between species *i* and *j* indicates the number of times both species co-occur in a cell of the lattice. We used the matrix to characterize local spatial arrangements between neighbours at two scales: (i) for all pairs of species (species scale), (ii) and for one species *versus* all neighbouring species (community scale). LSA corresponded to the difference between the observed number of co-occurrences within a quadrat and the expected number of co-occurrences at the pond level based on species cover (number of cells where species is present/total number of cells in the pond,

considering all pond lattices simultaneously). Thus, negative values of LSA indicate local spatial segregation while positive values indicate local spatial aggregation. For the species scale, the observed number of co-occurrences was the total number of cells where a pair of species  $i$  and  $j$  co-occurred, and for the community scale, the total number of cells where species  $i$  co-occurred with any other species. Besides, for the species scale, the expected number of co-occurrences  $N_{exp}$  between species  $i$  and  $j$  were calculated by pooling the five lattices of each pond as follows:

$$N_{exp} = \frac{\text{coverspecies}_i \in \text{thepond} \times \text{coverspecies}_j \in \text{thepond}}{\text{totalnumberofcells} \in \text{thepond}}$$

where the cover of a given species is the number of cells in which the species occurred divided by the total number of cells in the pond. For the community scale, the expected number of co-occurrences was the sum of the expected number of pairwise co-occurrences between species  $i$  and all the other species present in the pond.

#### *Assessing neighbours' interactions within ponds*

In March 2021 (*i.e.* at the end of the growing season), for each macrophyte species in each pond, we collected mature ramets with and without interspecific plant interactions (*i.e.* presence of other individuals in their neighbourhood) (Fig. 1b). Ramet neighbourhood was characterized within a surrounding circle of 20 cm diameter (Purves & Law, 2002). We considered 10% of vegetation cover in the neighbourhood as a threshold for the occurrence of interactions between neighbours (*i.e.* target ramet with interactions had neighbourhood cover > 10% while ramet without interactions (control ramet) had neighbourhood cover < 10%). Nevertheless, we further checked that this threshold value of 10% had no influence on our results (threshold value of 35%, see Table S3). For all target ramets, neighbouring species abundances were also recorded

(within 5% precision), along with bare soil to take into account the overall interaction intensity.

For each ramet collected, we measured total biomass, *i.e.* including the leaves, stems, roots, and one internode of clonal connection. When present, fruits were also included in ramet biomass although their biomass was negligible (only 9% of collected ramets had fruits) compared to vegetative growth, in line with previous works conducted on macrophyte species (Barrat-Segretain, 1996; Barrett, Eckert, & Husband, 1993). Measurements of biomass were performed after oven-drying ramets for 48 hours at 65°C. Ramet biomass was used as a proxy of its performance. The effect of neighbouring species on species  $i$  ramet in pond  $j$  on site  $k$  was used as a proxy of interactions between neighbours and was estimated using the Log Response Ratio (hereafter referred as to biomass LRR) (Hedges, Gurevitch, & Curtis, 1999) as follows:

$$\text{Biomass LRR}_{i,j,k} = \log \left( \frac{\text{Biomass of ramet of species}_i \in \text{pond}_j \text{ on site}_k}{\text{Average biomass of control ramets of species}_i \text{ on site}_k} \right)$$

#### *Neighbourhood functional characteristics*

To assess the functional characteristics of plant neighbourhood, we collected one ramet (with its leaves and roots, and one connection internode) of each of the six above-mentioned species when present, within each quadrat of each pond ( $n = 3$  to 5 quadrats per pond). Collection occurred in November 2020, and three categories of traits were measured on the ramets: (i) above-ground competition traits: aerial traits including height, Specific Leaf Area (SLA) and Leaf Dry Matter Content (LDMC) to characterize the plant photosynthetic efficiency and tissue conservation; (ii) below-ground competition traits: root traits including maximum root length and specific root mass to characterize nutrient uptake; (iii) competition for horizontal space traits: clonal traits including internode length to characterize the avoidance response, and specific internode

mass to characterize ramet investment into resource storage.

To measure SLA and LDMC following [Cornelissen et al. \(2003\)](#), one healthy mature leaf was randomly selected per ramet. Internode length was measured on one of the internodes attached to the ramet. Specific internode mass was calculated as the ratio between internode dry mass and length ( $\text{g}\cdot\text{cm}^{-1}$ ). Specific root mass was calculated as the ratio between root dry mass and maximum root length ( $\text{g}\cdot\text{cm}^{-1}$ ). Measurements of dry masses were performed after oven-drying plant parts for 48 hours at  $65^\circ\text{C}$ . All plants were cleaned before measurements were taken.

We tested for correlations between all pairs of traits using Spearman rank correlations to detect possible co-variations among traits. We did not detect significant correlations between any pair of traits (Spearman's  $\rho < 0.7$ , [Dormann et al., 2013](#)). The functional neighbourhood of the plant community of each target ramet was characterized by two types of metrics: the community weighted mean (CWM) ([Lavorel et al., 2007](#)) of each trait calculated using each species cover and mean trait values at the pond level (we expected plant traits to differ between ponds with different abiotic conditions), and the functional dispersion of traits (then referred as FDis), calculated using the *fdisp* function of package FD ([Laliberté & Legendre, 2010](#)), of each of the three trait categories (aerial, clonal, and root traits).

#### Data analyses

The means of daily (day and night) water temperatures and light intensity from February 2020 to March 2021 were calculated for each pond, and all abiotic variables were averaged at the pond scale. Abiotic dimensions describing pond conditions were reduced to the first-three axes of a Principal Component Analysis (PCA) performed on abiotic variables, and in which data were centered and standardized by standard deviation (Figure S2).

#### *Association between interactions between neighbours and their local spatial arrangement*

Firstly, we used linear models to test for the effects of local spatial arrangements between neighbours at the community scale (between a target species<sub>*i*</sub> and all its neighbouring species) and pond abiotic conditions on the biomass LRR for five out of the six macrophyte species (*L. australis* omitted due to a lack of points). We included LSA and the first three axes of the PCA performed on abiotic variables as explanatory variables in the full model. Then we applied a stepwise model selection based on the AIC criteria (MuMIn package), and selected the most parsimonious model using an ANOVA test (type II). The same procedure was applied to test relationships between biomass LRR of target species *i* and LSA calculated at the species level (*i.e.* between species *i* and *j*). To that purpose, we only chose biomass LRR values calculated for ramets of species *i* having species *j* in their neighbourhood.

#### *Responses of interactions between neighbours to their traits*

We tested the response of biomass LRR for three out of the six macrophyte species (due to a lack of points), to its functional neighbourhood at community level. That is, the CWM of the traits of all neighbours and FDis of aerial, clonal, and root traits, together with pond abiotic conditions (first-three axes of the PCA performed on pond abiotic variables), and bare soil (to take into account the overall interaction intensity) using linear models. We started with the full model and then applied a model selection procedure through a stepwise selection based on AIC criteria (see previous model).

#### *Direct and indirect associations between abiotic and biotic variables and macrophyte community biomass*

Macrophyte community biomass, was calculated at the pond level using the sum of the mean ramet biomass per species, and the cover of each species at the pond scale (total

number of cells in which the species occur / total number of cells, considering all quadrats). We used Structural Equation Modeling (SEM) (Grace, Anderson, Olff, & Scheiner, 2010) to decipher direct and indirect effects of abiotic and biotic variables on community biomass. We included variables thought to affect macrophyte community biomass, either directly or through the modulation of interactions between neighbours. The variables were: nutrient concentration in water and sediments (Dar et al., 2014; Schneider, Cunha, Marchese, & Thomaz, 2015), pond morphometry [pond area (Rolon & Maltchik, 2006), water depth (Wang, Zhang, Xu, & Yu, 2016)], and water quality variables [electric conductivity (Lévesque, Hudon, James, & Legendre, 2017), O<sub>2</sub> concentration (Morris, Harrison, Bailey, & Boon, 2004), mean temperature (Dar et al., 2014), light intensity (Su et al., 2019)]. We added chlorophyll a concentration to reflect competition between macrophytes and phytoplankton (Phillips, Willby, & Moss, 2016). Distance to the closest pond was also included as a proxy of the degree of proximity between ponds, as this is known to impact plant species dispersal, and thus plant community richness and functional diversity (Favre-Bac, Mony, Burel, Seimandi-Corda, & Ernoult, 2017). Finally, biotic variables such as richness, FDis, and LSA allowed us to quantify macrophyte community structure and test for an association with biomass (Hooper et al., 2005; Monzeglio & Stoll, 2005; Qi et al., 2021). All possible relationships between variables were built based on the literature (Figure S3).

To build these relationships, LSA was calculated at the pond scale, taking the total number of co-occurrences between all pairs of species at the pond scale into account. FDis was calculated at the pond scale (calculated by pooling all lattices), including all measured traits and species cover. Nutrient concentrations in water (N-NH<sub>4</sub><sup>+</sup>, N-NO<sub>3</sub><sup>-</sup>, P-PO<sub>4</sub><sup>3-</sup>) and in sediments (C:N ratio, bioavailable P) were each reduced to the first axis of a PCA analysis, in which data were

centered and standardized. Variables were normalized (log or square-root transformations) and standardized before analysis. We performed a path analysis with the lavaan package (Rosseel, 2012) and reduced the full model by variable selection based on AIC values. All statistical analyses were carried out with R 4.0.3.

## Results

A Principal Component Analysis (PCA) was performed on abiotic parameters measured at the pond level to reduce abiotic dimensions (Figure S2). PCA Axis 1 was positively related to the light intensity in ponds which was highest when nutrient availability in sediments was low. PCA Axis 2 was positively related to the concentration of N-NH<sub>4</sub><sup>+</sup> in the water column and negatively to the density of phytoplankton (represented by the concentration of chlorophyll a per mL of water), especially when habitat temperatures were cold. PCA Axis 3 was positively related to N-NO<sub>3</sub><sup>-</sup> concentration in water and conductivity.

### *Local spatial arrangements between neighbours did not reflect their interactions*

At the community scale (interactions with all species in neighbourhood), we found no significant relationship between biomass LRR and LSA in all species (“All” in Table 1). Pond abiotic conditions, however, significantly explained biomass LRR in two out of the five species tested, either positively or negatively. Water nutrient concentration (PCA Axes 2 and 3) was strongly associated with interactions for *C. antarctica* and *R. moseleyi* (Table 1). At the species scale (LSA

**Table 1.** Results of ANOVAs performed on the most probable models determined based on the AIC selection method, and relationships between biomass LRR of each target species and the local spatial arrangements calculated between this target species and (i) all species in its neighbourhood without distinction (community scale), or (ii) one particular neighbouring species (species scale). See Materials and Methods section for more details on the calculation of local spatial arrangements between neighbours. To characterize the abiotic conditions of the ponds and test their effects on biomass LRR (without interactions with LSA), we used the first-three axes of a PCA performed on abiotic variables (Figure S2). Some species pairwise combinations were not tested because of a lack of observations, and thus do not appear in the table.

Biomass LRR of the target species	Neighbouring species	Explanatory variables of selected model					
		<i>n</i>	Predictor	F	d.f.	Model coefficient and its significance	Local spatial arrangements between the target species and neighbouring species
<i>C. ant</i>	All	21	<b>Axis2</b>	29.4	1	0.21***	None
	<i>J. sch</i>	18	<b>Axis2</b>	24.07	1	0.30***	None
	<i>R. bit</i>	16	<b>Axis2</b>	28.42	1	0.18***	None
<i>J. sch</i>	All	30	Axis2	2.73	1	-0.17 (n.s.)	None
	<i>C. ant</i>	15	<b>Axis2</b>	7.62	1	-0.29*	None
	<i>R. bit</i>	30	Axis2	4.09	1	-0.19.	None
	<i>R. mos</i>	8	<b>LSA</b>	13.03	1	0.14*	<b>Aggregation</b>
	<i>R. pseudo</i>	8	x	x	x	x	None
<i>R. bit</i>	All	28	x	x	x	x	None
	<i>C. ant</i>	13	x	x	x	x	None
	<i>J. sch</i>	30	x	x	x	x	None
	<i>R. mos</i>	8	x	x	x	x	None
	<i>R. pseudo</i>	10	<b>Axis3</b>	21.41	1	0.33**	None
<i>R. mos</i>	All	8	<b>Axis3</b>	8.94	1	-0.81*	None
	<i>J. sch</i>	8	<b>Axis3</b>	8.94	1	-0.81*	None
	<i>R. bit</i>	7	<b>Axis3</b>	11.44	1	-0.78*	None
<i>R. pseudo</i>	All	8	x	x	x	x	None
	<i>J. sch</i>	8	x	x	x	x	None
	<i>R. bit</i>	9	x	x	x	x	None

Notes: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ ; ‘.’  $0.05 < p < 0.1$ ; n.s. = not significant ( $p > 0.1$ ). ‘x’ none of the tested predictors actually influenced the response variable (model selection). *C. ant* = *C. antarctica*; *J. sch* = *J. scheuchzerioides*; *R. bit* = *R. biternatus*; *R. mos* = *R. moseleyi*; *R. pseudo* = *R. pseudotrullifolius*. ‘LSA’ local spatial arrangements. ‘n’ number of points to calculate relationship

of pairwise combinations of species, including the target species), biomass LRR was significantly associated with LSA (species aggregation or segregation) for only

one out of the five target species (Table 1). In *J. scheuchzerioides*, spatial aggregation had a positive effect on the biomass LRR of *R. moseleyi*. Biomass LRR was nevertheless

mostly predicted by pond abiotic conditions in the tested species, except in *R. pseudotrullifolius* (Table 1). In particular, biomass LRR of *C. antarctica* and *J. scheuchzerioides* were predicted by the dissolved N-NH<sub>4</sub><sup>+</sup> concentration (PCA Axis 2), likely depending on the presence of phytoplankton. Conversely, biomass LRR of *R. biternatus* and *R. moseleyi* was impacted by the water N-NO<sub>3</sub><sup>-</sup> concentration and electric conductivity (PCA Axis 3).

### *Interactions depend on the functional characteristics of neighbours*

Biomass LRR significantly responded to functional characteristics of neighbours in two out of the three target species (Table 2). Indeed, CWM of the neighbours' traits explained a total of 23.5% of biomass LRR variations in *J. scheuchzerioides*, and FDis of neighbours' traits contributed to 76.2% of biomass LRR variations in *R. biternatus*. More specifically, biomass LRR of these two species was only associated with CWM of aerial traits (Table 2), which had positive (describing facilitation) and negative (describing competition) effects, depending

**Table 2.** Results of ANOVAs performed on the most probable models determined based on AIC selection method, and testing responses of biomass LRR calculated for each target species to functional characteristics (i.e. CWM and FDis of traits) of their neighbours. Predictors in bold characters were significantly associated with biomass LRR. Functional characteristics were calculated on ramets within the 20cm neighbourhood of each target ramet, and included the CWM of seven traits and FDis calculated for three types of traits (aerial, root, and clonal). To characterize abiotic conditions and to test for their effects on biomass LRR (without interactions with functional characteristics), we used the first-three axes of a PCA performed on abiotic variables (Figure S2). Biomass LRR response was not tested in three species (*L. australis*, *R. moseleyi*, and *R. pseudotrullifolius*), because of a lack of observations (n=4), thus these species are not presented in the table.

Biomass LRR of the target species	n	Explanatory variables of selected model				
		Predictor	F	d.f.	Model coefficient and its significance	Part of explained variance (%)
<i>C. ant</i>	24	CWM max. root length	3.31	1	0.05.	7.91
		<b>Axis2</b>	14.0	1	0.31**	33.39
		<b>Bare soil</b>	4.61	1	0.01*	11.01
		Residuals		20		47.69
<i>J. sch</i>	24	<b>CWM height</b>	8.07	1	0.11**	23.51
		<b>Bare soil</b>	5.26	1	0.008*	15.33
		Residuals		21		61.16
<i>R. bit</i>	27	<b>CWM SLA</b>	5.17	1	-0.02*	3.56
		<b>CWM LDMC</b>	5.44	1	-0.006*	3.74
		<b>FDis aerial traits</b>	47.14	1	2.61***	32.43
		<b>FDis root traits</b>	55.89	1	-2.55***	36.45
		<b>Axis3</b>	13.63	1	0.28**	9.38
		Residuals		21		14.44

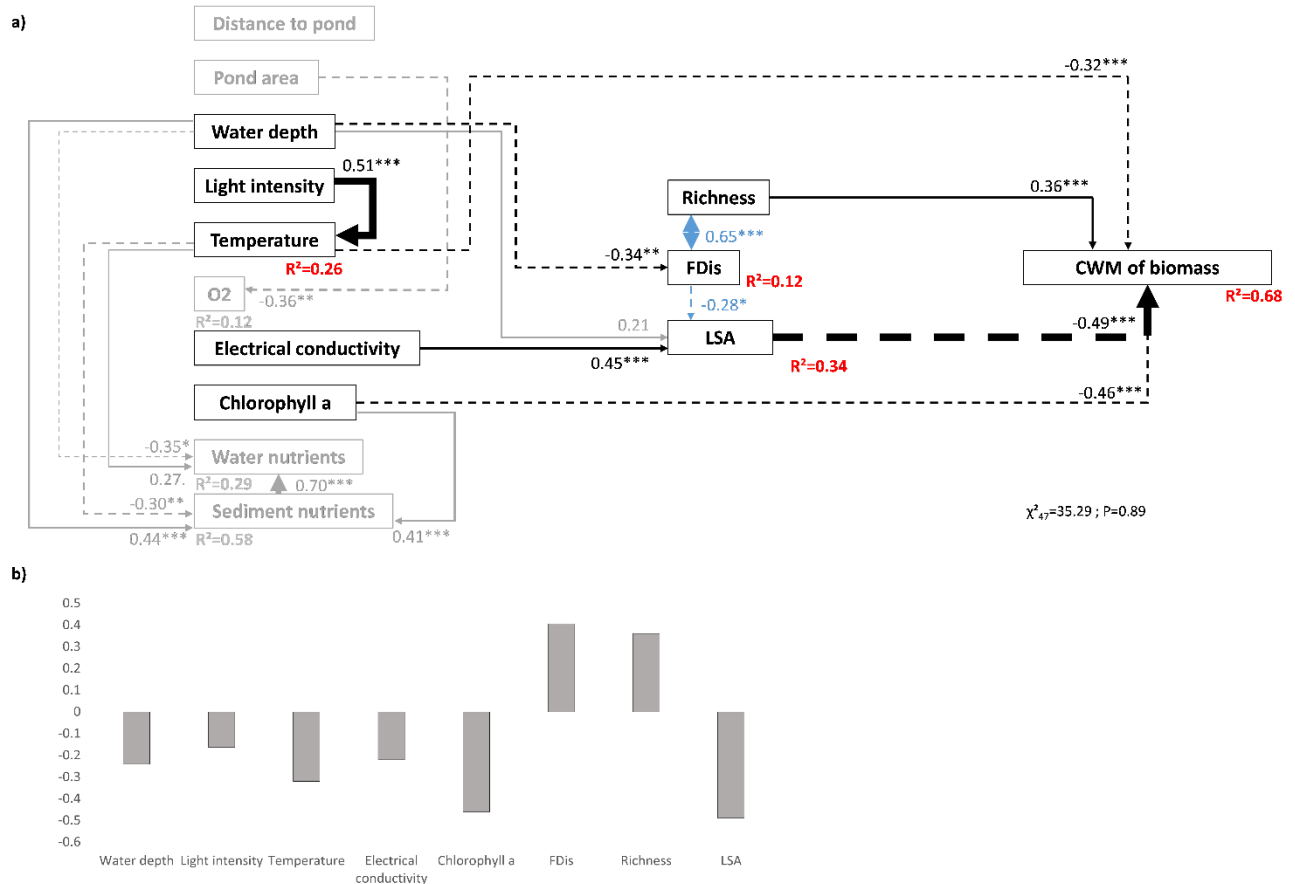
Notes: \* p < 0.05; \*\* p < 0.01; \*\*\* p < 0.001; '.' 0.05 < p < 0.1. 'x' none of the tested predictors actually influenced the response variable (model selection). *C. ant* = *C. antarctica*; *J. sch* = *J. scheuchzerioides*; *R. bit* = *R. biternatus*; *R. mos* = *R. moseleyi*; *R. pseudo* = *R. pseudotrullifolius*. Max. root length = maximum root length. 'n' number of points to calculate relationship.

on the target species. However, this effect was limited in *R. biternatus* (tCWM\_SLA= -0.02\*, tCWM\_LDMC= -0.006\*, both traits explaining about 3.5% of biomass LRR variations). Much of biomass LRR variations in *R. biternatus* were actually explained by FDis (68.88%). More precisely, FDis of aerial and root traits displayed respectively positive (t=2.61\*\*\*) and negative effects (t=-

2.55\*\*\*) on *R. biternatus* biomass LRR (Table 2).

*Direct and indirect effects of abiotic and biotic variables characterizing ponds on macrophyte community biomass*

Five out of the 13 variables tested did not have any direct or indirect effects on



**Figure 2.** a) Structural equation model representing the direct and indirect effects of abiotic and biotic variables characterizing ponds, on macrophyte community biomass. The initial model is presented in the Supplementary Information and was reduced with lavaan package through variable selection based on AIC criteria. All variables were calculated at pond level. CWM biomass was calculated based on the mean of biomass per species and their cover at pond level. Water and sediment nutrient dimensions were each reduced to the first axis of a PCA analysis. Single dark headed arrows indicate direct effects. Double headed blue arrows indicate correlation between two model variables. Standardized path coefficients are given in blue for correlations and in black for direct effects with their p-values: \*\*\*p < 0.001; \*\*p < 0.01; ‘.’ 0.05 < p < 0.1; no asterisk p ≥ 0.1 not significant. The widths of the lines are proportional to the strength of relationships (values of path coefficients). Solid and dashed lines respectively indicated positive or negative direct effects. Grey paths and grey variables indicated paths and variables that did not have significant direct or indirect effects on CWM biomass. R<sup>2</sup> values were the variance proportion of response variables explained by their explanatory variables. Local spatial arrangements between neighbours were calculated at pond scale, taking into account the total number of co-occurrences between all pairs of species. FDis was calculated at pond scale (taking into account all present species per pond), including aerial, clonal and root traits. b) Absolute direct and indirect effects of abiotic and biotic variables on macrophyte community biomass.



macrophyte CWM biomass (*i.e.* community biomass) (Fig. 2): distance to pond (*i.e.* between-pond proximity), pond area, and concentrations of dissolved O<sub>2</sub>, water and sediment nutrients. Regarding the eight variables that were significantly associated with community biomass, four had direct effects: water temperature (-0.32\*\*\*), chlorophyll a (-0.46\*\*\*), richness (0.36\*\*\*) and LSA (-0.49\*\*\*). A negative association between LSA macrophyte community biomass indicated that the more species were aggregated, the lower the community biomass.

There were also multiple indirect effects on community biomass. Firstly, several abiotic variables modulated the effect of other abiotic variables. For example, light intensity increased water temperature (0.51\*\*\*), thereby indirectly decreasing macrophyte community biomass. Secondly, biotic variables modulated each other, amplifying indirect biotic effects (Fig. 2). FDis was correlated with species richness (0.65\*\*\*) and had a negative effect on LSA (-0.28\*), thereby indirectly increasing community biomass. In addition, biotic variables were influenced by abiotic variables, strengthening indirect abiotic effects on macrophyte community biomass (Fig. 2). FDis was negatively affected by water depth (-0.34\*\*), while LSA was positively affected by electric conductivity (0.45\*\*\*). Ultimately, water depth and electric conductivity indirectly decreased macrophyte community biomass.

## Discussion

*Interactions between neighbours depend on abiotic variables and their functional characteristics in polar ponds*

Interactions between neighbours shape plant communities, and thus drive variations in their biomass. Indeed, a reduction in competitive interactions, or an increase in facilitative interactions between species, can lead to complementary effects, subsequently increasing community biomass (Callaway,

2007; Mulder, Uliassi, & Doak, 2001). We observed that interactions between neighbours depend on the functional traits of the target ramet and of its neighbours, as well as on abiotic variables (Schneider et al., 2015; Zhang et al., 2020).

In these sub-polar ponds, the direction and strength of interactions were mostly associated with patterns in abiotic variables, reemphasizing the need to consider abiotic factors as major influences on interactions between neighbours (Biswas & Wagner, 2014; Eränen & Kozlov, 2008). Changes in the net outcome of interactions caused by abiotic stressors could be inferred from fine scale observations of species spatial co-occurrences within communities (Kikvidze et al., 2005). Similarly, we expected interactions between the different species and their neighbours to be inferred from their LSA, both at the community and species scales. However, LSA did not reflect changes in the interactions between neighbours at very small scales, neither at the community (multispecies interactions) nor the species level. Our results are in line with Delalandre & Montesinos-Navarro (2018), who showed that LSA does not capture the underlying processes involving pairwise interactions at patch scale (about 0.05m<sup>2</sup>). Several non-exclusive hypotheses may explain these results. Firstly, the very low species richness of the Ile Kerguelen macrophyte community (four species at most) might cause more species segregation (Delalandre & Montesinos-Navarro, 2018). Indeed, we showed that more than 70% of the significant LSA at the pond scale represented species segregations (Table S5). Secondly, different processes may generate similar LSA *in situ* (MacKenzie, Bailey, & Nichols, 2004; McIntire & Fajardo, 2009; Rayburn & Monaco, 2011). Segregation may indeed reflect competitive interactions but also habitat heterogeneity, allowing species with different abiotic preferences to establish within different suitable micro-sites. Similarly, aggregation is usually interpreted as facilitation but can also indicate species aggregation within the same, most suitable

micro-site in an heterogeneous habitat (Blanchet et al., 2020). Finally, LSA calculation *in situ* has limitations. For example, if two species have opposite effects on each other (*i.e.* one species is facilitated by another that in turn competes with the first one), these will result in null LSA (we recorded 53 null LSA out of the 156 tested ones, Table S5). Moreover, the indirect effect of a third species on pairwise species interactions (Castillo, Verdu, & Valiente-Banuet, 2010; Christian Schöb, Armas, & Pugnaire, 2013) or asymmetric interactions (Delalandre & Montesinos-Navarro, 2018) are not measurable despite affecting the outcome of interactions between neighbours, and thus the resulting patterns of co-occurrence.

In abiotically constrained habitats, high functional convergence between species is expected, resulting from habitat filtering (Cornwell et al., 2006; Grime, 2006). Yet, coexistence within a community (*i.e.* the outcome of interactions) could be due to two possible processes, both based on differences in trait values between species: limiting similarity (Kraft, Godoy, & Levine, 2015; Turcotte & Levine, 2016) and the competitive hierarchy (Chesson, 2000; Mayfield & Levine, 2010). As expected, vertical traits (*i.e.* aerial and root traits related to resource acquisition) appeared to play a stronger role in interactions between neighbours than horizontal traits (clonal traits), in two out of the three species. Originally, we highlighted that there are two possible processes of species coexistence occurring within macrophyte communities, based on different traits and relationships with interacting species identities. Furthermore, these results indicate that the balance between competition and facilitation within abiotically constrained habitat, results from functional characteristics of neighbours related to resource acquisition, not just from functional characteristics of target species. More specifically, CWM of height had positive effects on *J. scheuchzerioides* biomass LRR (explaining 24% of its variation), that is, tall neighbours have facilitative effects on this species.

*Juncus scheuchzerioides* stands among the tallest species, and its neighbourhood is mostly composed of conspecifics ( $34.8 \pm 18.1\%$ , Figure S4). Since most contacts between *J. scheuchzerioides* ramets are intra-specific, and likely intracolonial, we conclude that intraspecific facilitation or even intracolonial cooperation [physiological integration (Wang et al., 2021)] are important for this species. In *R. biternatus*, ramets responded more to the variability of aerial and root traits than to their average within the neighbourhood (68.88% against 7.3% of biomass LRR variation). More precisely, *R. biternatus* is facilitated by a high aerial and a low root functional diversity, indicating above-ground resource partitioning (*i.e.* niche differentiation along the aerial trait axis). Thus, functionally redundant species can coexist at the community scale if their neighbourhood comprises species displaying different trait values (Maire et al., 2012). For example, *R. moseleyi* and *R. pseudotrullifolius*, two species closely related to *R. biternatus* and sharing similar resource use and functional roles, are very rare in its neighbourhood composition (Figure S4).

In conclusion, we confirmed that both abiotic and biotic characteristics are related to interactions between neighbours at species level. Multiple assembly processes operate simultaneously within the macrophyte community (Spasojevic & Suding, 2012) either through community weighted mean or neighbour dissimilarity (Copeland & Harrison, 2017) depending on traits. Ultimately, this shows the importance of multi-trait approaches to better infer community assembly processes (Kraft, Godoy, & Levine, 2015). Plus, we emphasize that LSA does not reflect interactions between neighbours. Therefore, interpreting significant spatial co-occurrences as evidence of interactions between neighbours should be done cautiously. By specifically focusing on interactions, mesocosm experiments are one way to control for multiple abiotic factors and environmental heterogeneity that can modulate interactions between neighbours and produce similar LSA (Bittebiere, Saiz, &

Mony, 2019; Brazeau & Schamp, 2019). Consequently, community-level characterization of LSA is needed as well as pairwise relationships. Furthermore, biotic and abiotic variables, either jointly or separately, should indirectly influence community biomass through their modulations of interactions between neighbours, and thereby also influence species biomasses.

#### *Joint effects of biotic and abiotic variables on macrophyte community biomass*

Five out of the 13 abiotic and biotic variables tested had no direct or indirect effect on macrophyte community biomass, confirming the need to study pond systems as a whole. The distance to the closest pond (*i.e.* between-pond connectivity), pond area, dissolved O<sub>2</sub> concentration, and (contrary to our expectations) water and sediment nutrient concentrations, do not have any direct or indirect effects on macrophyte community biomass. Ponds may not be limited by nutrients, since inputs by marine fauna are frequent, especially during summer (Smith, 2008), leading to minimal impact on biomass. Indeed, the species studied tended to have relatively high SLA and low LDMC (Figure S5), making them nutrient acquisitive, in line with similar studies of systems with high resource availability (Stanisci et al., 2020).

Our holistic approach confirmed our third hypothesis, demonstrating that abiotic variables were associated with macrophyte community biomass, either directly or through the modulation of inextricably connected biotic variables (*i.e.* the local spatial arrangement of the macrophyte community and its functional diversity, also related to its species richness). This is consistent with Sanaei, Sayer, Saiz, Yuan, & Ali (2021), who showed that biotic and abiotic variables are important drivers of plant assemblages and community biomass in relationships with nutrients and spatial co-occurrences within arid systems (semi-steppe rangelands). In our case, abiotic and biotic

variables had negative and positive effects on community biomass, respectively.

We demonstrated that few variables were directly associated with macrophyte community biomass: water temperatures, phytoplankton quantity (chlorophyll a), species richness, and the LSA. Spatial structure with segregated species supports macrophyte community biomass by limiting competitive interactions with superior competitors (Porensky, Vaughn, & Young, 2012). Furthermore, richness was positively associated with the macrophyte community biomass. Several studies have already demonstrated that higher species richness leads to higher community biomass because of the complementary use of resources among species, and of the sampling effect (increased probability of sampling highly productive species) (Engelhardt & Ritchie, 2001; Loreau & Hector, 2001; Schmid, 2002; Tilman, Lehman, & Thomson, 1997a). In addition, higher species richness leads to better ecosystem functioning (Loreau et al., 2001; Schwartz et al., 2000; Tilman, Knops, et al., 1997b), and maintains some abiotic conditions beneficial to the growth of macrophytes. Importantly, macrophyte community biomass is negatively affected by increased water temperatures. The importance of water temperature is not surprising since macrophyte species in the sub-Antarctic are adapted to cold temperatures. Indeed, although rising water temperatures can stimulate increases in macrophyte community biomass within the optimum thermal range (Dar et al., 2014), their negative impact suggests that this optimal thermal range has already been exceeded at the Iles Kerguelen (Frenot et al., 2006). As water temperatures continue to warm, the consequences for macrophyte community structure and its biomass will likely be severe. We found that light intensity increased water temperatures leading to an indirect negative impact on macrophyte community biomass. This observation calls into question results from the literature where only the positive direct effect of light intensity on plant growth rate in aquatic

ecosystems was considered, and thus effects on community biomass were not reported (Jin, Ibrahim, Muhammad, Khan, & Li, 2020). Furthermore, since macrophytes greatly influence ecosystem-level processes in ponds (Iacarella, Barrow, Giani, Beisner, & Gregory-Eaves, 2018; Lürig, Best, Dakos, & Matthews, 2021; Mo, Deng, Gao, Guo, & Yu, 2015), climate warming could negatively affect trophic chains and ecosystem function (Gutt et al., 2021).

Finally, very few studies in freshwater ecosystems have thoroughly assessed both abiotic and biotic variables in habitats (but see Wood, Stillman, Clarke, Daunt, & O'Hare, 2012 and Liu et al., 2020). This gap in the literature limits our understanding of the fate of macrophyte species concomitantly exposed to abiotic and biotic filters, especially in a context of climate change. The interconnection between abiotic and biotic variables shown here raises questions about the sequential influence of abiotic and biotic filters on plant community assembly (Keddy, 1992; Violle et al., 2012; but see Cadotte & Tucker, 2017). In addition, we provide strong evidence for the urgent need to approach biodiversity structure and its influence on ecosystem function, by jointly integrating biotic and abiotic variables in multivariate analyses (Chalmandrier et al. 2022).

## Conclusion

Our study brings new insights into the mechanisms involved in interactions between neighbours that supports species coexistence within freshwater ecosystems and other abiotically constrained habitats. In particular, we showed that abiotic variables had a stronger effect on species interactions than the spatial structure of macrophyte communities. In addition, we provided new evidence that biotic and abiotic variables influencing the assembly of macrophyte communities are interconnected, and we encourage researchers to consider their combined effects in future studies to get a better picture of the processes underlying plant community assembly. Longer-term

studies will be needed to better assess changes in plant communities, especially within poorly studied freshwater systems vulnerable to climate changes.

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## Conflict of interest

The authors declare that they have no conflict of interest.

## Data availability statement

All data are available in figshare (<https://doi.org/10.6084/m9.figshare.21187183.v1>).

## Author Contributions

Conceptualization: P.D., H.S., M-L.B., A-K.B. Developing methods: H.S., M-L.B., A-K.B. Conducting the research: P.D., F.M-B., L.S., F.V., Y.O., M.F., A-K.B. Data analysis and interpretation: P.D., H.S., M-L.B., A-K.B. Preparation figures and tables, and writing: P.D., H.S., M-L.B., F.M-B., L.S., D.R., F.V., Y.O., M.F., A-K.B.

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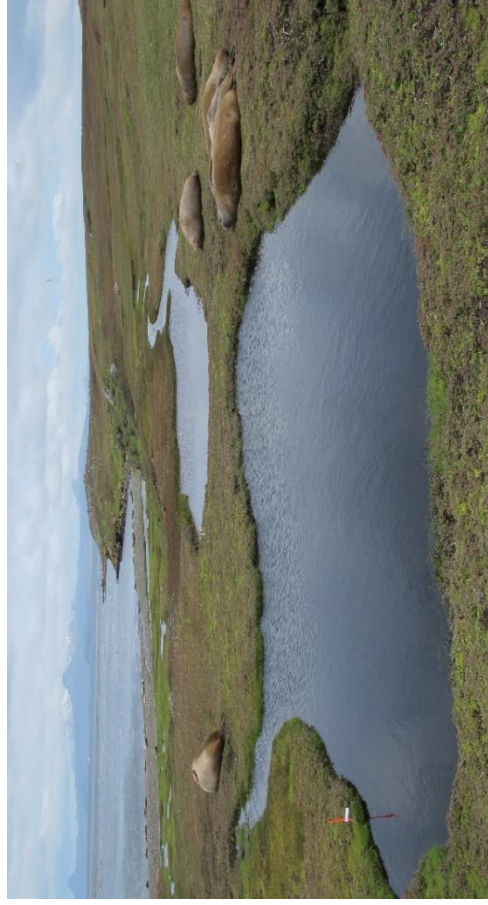
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## Supporting Information

**Table S1.** Mean ( $\pm$  SD) abiotic parameters measured in the ponds between November 2019 and March 2021.

Pond area (m <sup>2</sup> )	181.57 $\pm$ 382.39 except for one 180800
Water depth (cm)	19.03 $\pm$ 9.12
Mean water temperature (°C)	6.9 $\pm$ 0.57
Light intensity (Lux)	5373.1 $\pm$ 3771.49
Electrical conductivity ( $\mu$ S.cm <sup>-1</sup> )	196.88 $\pm$ 54.63
Dissolved oxygen (mg.L <sup>-1</sup> )	11.26 $\pm$ 2.49
Chlorophyll a ( $\mu$ g.L <sup>-1</sup> )	42.84 $\pm$ 92.88
N-NH <sub>4</sub> <sup>+</sup> ( $\mu$ g.L <sup>-1</sup> )	384.39 $\pm$ 612.85
N-NO <sub>3</sub> <sup>-</sup> ( $\mu$ g.L <sup>-1</sup> )	137.29 $\pm$ 211.33
P-PO <sub>4</sub> <sup>3-</sup> ( $\mu$ g.L <sup>-1</sup> )	22.24 $\pm$ 35.95
Bioavailable P (mg.g <sup>-1</sup> )	0.61 $\pm$ 0.33
C:N	13.92 $\pm$ 1.34

(i)



(ii)



*C. antarctica*



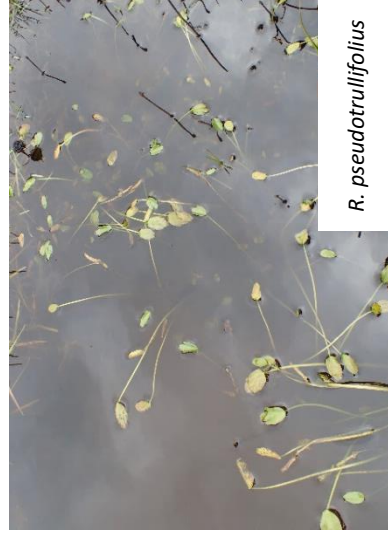
*J. scheuchzerioides* + *R. biternatus*



*L. australis*



*R. biternatus*



*R. pseudotrullifolius*



Pond harbouring *R. moseleyi* individuals

**Figure S1.** Photos of (i) of the studied pond systems, and (ii) of the six macrophyte species observed *in situ*.

**Table S2.** Results of ANOVAs (type II) performed on a linear model testing the relationship between the mean of daily light intensity in winter (recorded every half hour in each pond from May 2021 to October 2021) and the mean of daily light intensity in summer (recorded every half hour in each pond from November 2020 to April 2021) (n=43 ponds). This significant relationship allowed us to simulate the mean of daily light intensity in each pond from February 2020 to October 2020.

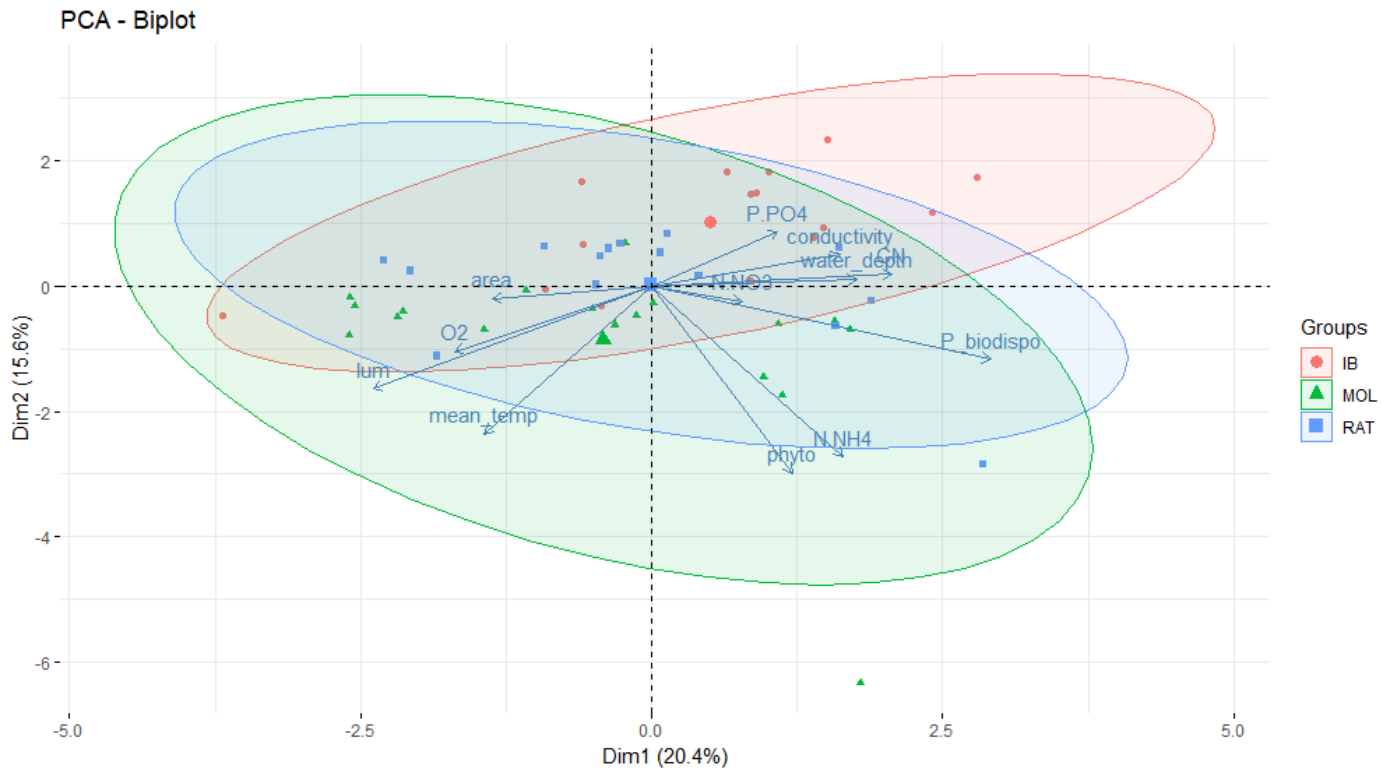
Model estimates	Estimate value	t value
Intercept	1396.1326	2.62*
Light intensity in summer	0.1779	3.31**

**Table S3.** Results of ANOVAs performed on the most probable models determined based on the AIC selection method, and testing the relationship between biomass LRR of each target species (control targets were individuals with less than 35% of neighborhood cover) and the local spatial arrangements (LSA) between this target species and one particular neighboring species. These results were complementary to Table 1 and provided evidences that we obtained similar results with a threshold of 10% and 35% of neighborhood cover to distinguish control and target ramets. LSA were calculated based on co-occurrences between the target species and one particular neighboring species (species scale). See Materials and Methods section for more details on the calculation of LSA. To characterize pond abiotic conditions and to test for their effects on biomass LRR (without interactions with LSA), we used the first-three axes of a PCA performed on abiotic parameters (Appendix 4). Some species pairwise combinations were not tested because of a lack of points, and did not appear in the table.

Biomass LRR of the target species	Neighbor species	Explanatory variables of selected model					
		<i>n</i>	Predictor	F	d.f.	Model coefficient and its significance	Local spatial arrangements between the target species and neighboring species
<i>C. ant</i>	<i>J. sch</i>	18	<b>Axis2</b>	8.81	1	0.18**	None
	<i>R. bit</i>	15	<b>Axis2</b>	3.73	1	0.13.	None
<i>J. sch</i>	<i>C. ant</i>	15	<b>Axis2</b>	7.82	1	-0.35*	None
	<i>R. bit</i>	29	Axis1	2.84	1	-0.12 n.s.	None
			<b>Axis2</b>	5.49	1	-0.30*	None
	<i>R. mos</i>	8	x	x	x	x	None
<i>R. pseudo</i>	9	<b>Axis2</b>	5.76	1	-0.31*	None	
<i>R. bit</i>	<i>C. ant</i>	13	x	x	x	x	None
	<i>J. sch</i>	26	x	x	x	x	None
	<i>R. mos</i>	8	x	x	x	x	None
	<i>R. pseudo</i>	10	<b>Axis3</b>	10.6	1	0.34*	None
<i>R. mos</i>	<i>J. sch</i>	8	x	x	x	x	None
	<i>R. bit</i>	8	x	x	x	x	None
<i>R. pseudo</i>	<i>J. sch</i>	7	x	x	x	x	None
	<i>R. bit</i>	8	x	x	x	x	None

Notes: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ ; ‘.’  $0.05 < p < 0.1$ ; n.s. = not significant ( $p > 0.1$ ). ‘x’ none of the tested predictors actually influenced the response variable (model selection). *C. ant* = *C. antarctica*; *J. sch* = *J. scheuchzerioides*; *R. bit* = *R. biternatus*; *R. mos* = *R. moseleyi*; *R. pseudo* = *R. pseudotrullifolius*. ‘n’ number of points to calculate relationship.

**Figure S2.** Correlation circle of a Principal Component Analysis (PCA) performed on abiotic parameters measured at the pond level. PCA Axis 1 was related to the trophic status of the pond: the light intensity increased when nutrients resources and probably water turbidity were low. PCA Axis 2 was positively related to the amount of available nutrients in water column that increased when the competition with phytoplankton (chlorophyll a) was low, especially in cold temperatures. PCA Axis 3 was positively related to water nutrients that increased the total dissolved solids concentration in the water column especially when the water depth was low, thus increasing electrical conductivity.

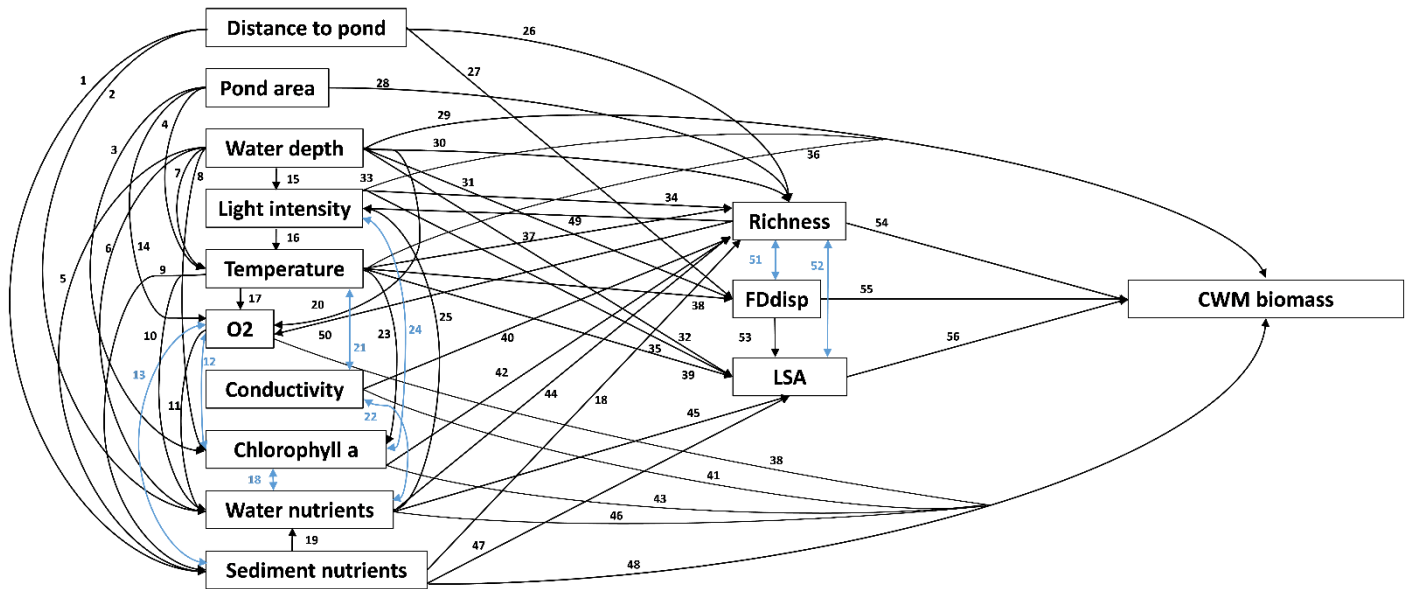


**Table S4.** Eigenvector scores for the first-three axes of a Principal Component Analysis (PCA) performed on abiotic parameters measured at the pond level. The three highest eigenvector scores for each PCA axis are indicated in bold. Variance accounted for by each axis is indicated into brackets. PCA Axis 1 was related to the trophic status of the pond: the light intensity increased when nutrients resources and probably water turbidity were low. PCA Axis 2 was positively related to the amount of available nutrients in water column that increased when the competition with phytoplankton (chlorophyll a) was low, especially in cold temperatures. PCA Axis 3 was positively related to water nutrients that increased the total dissolved solids concentration in the water column especially when the water depth was low, thus increasing electrical conductivity.

Abiotic variables	PCA 1 (20.43%)	PCA 2 (15.59%)	PCA 3 (13.62%)
Pond area	0.351	-0.051	0.214
Water depth	-0.454	0.029	<b>-0.693</b>
Mean water temperature	0.370	<b>-0.607</b>	-0.188
Light intensity	<b>0.616</b>	-0.422	0.124
Electrical conductivity	-0.415	0.129	<b>0.685</b>
O <sub>2</sub> (Dissolved oxygen)	0.436	-0.270	0.065
Chlorophyll a	-0.311	<b>-0.769</b>	-0.047
N-NH <sub>4</sub> <sup>+</sup>	-0.423	<b>0.701</b>	0.223
N-NO <sub>3</sub> <sup>-</sup>	-0.201	-0.062	<b>0.643</b>
P-PO <sub>4</sub> <sup>3-</sup>	-0.276	0.220	0.264
Bioavailable P	<b>-0.750</b>	-0.302	-0.037
C:N	<b>-0.532</b>	0.048	-0.214

**Figure S3.** Theoretical structural equation model representing the direct and indirect effects of abiotic and biotic variables measured on ponds, on macrophyte community biomass (CWM Biomass). This model was reduced with lavaan package through variable selection based on AIC criteria, and results are presented in Fig. 2. Water and sediment nutrients dimensions were each reduced to the first axis of a PCA analysis. Single dark headed arrows indicate direct effects. Double headed blue arrows indicate correlation between two model variables. All variables were calculated at pond level. Local spatial arrangements took into account the total number of co-occurrences between all pairs of species at pond scale (community scale). Numbers indicated literature references supporting each tested relations and correlations. 'LSA' local spatial arrangements.

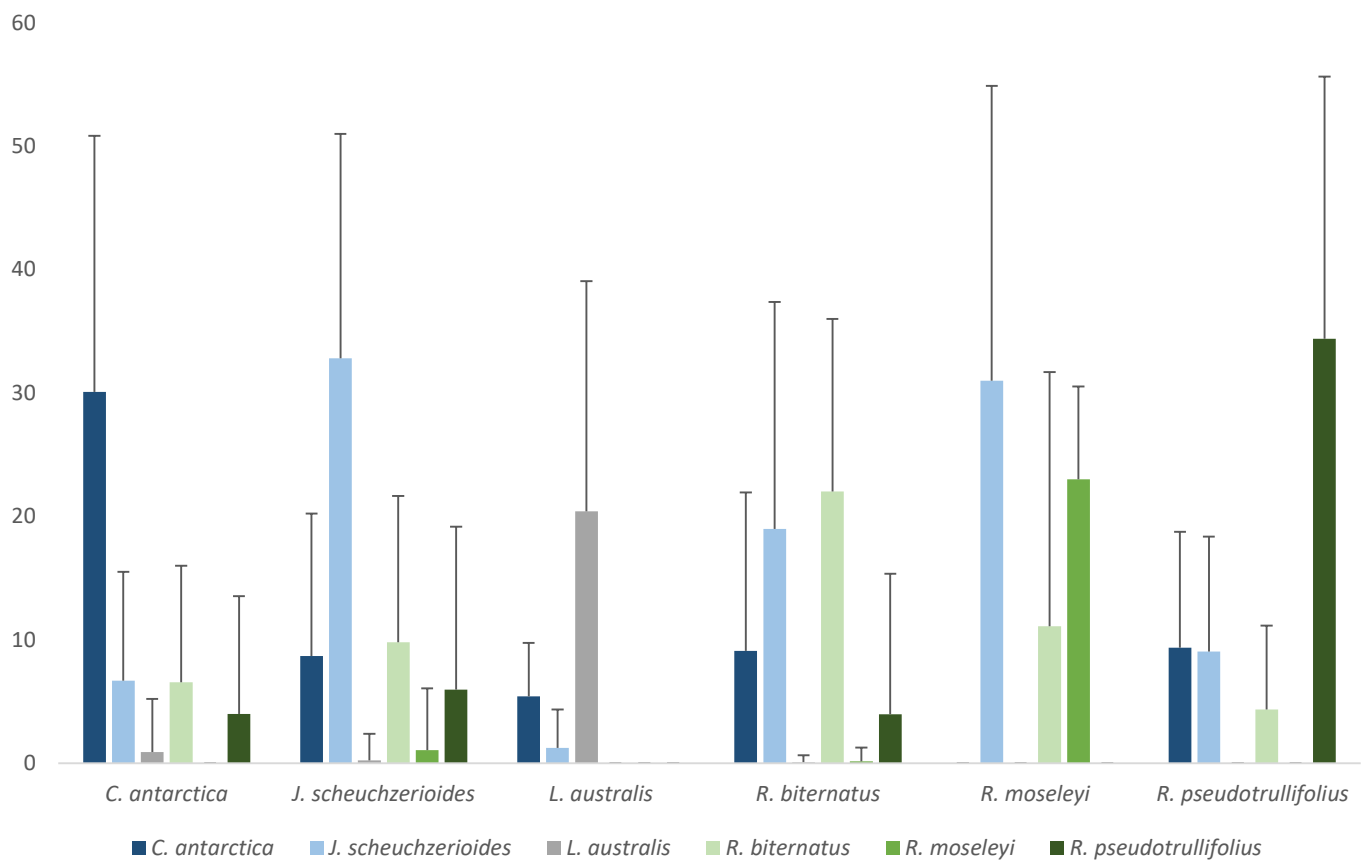




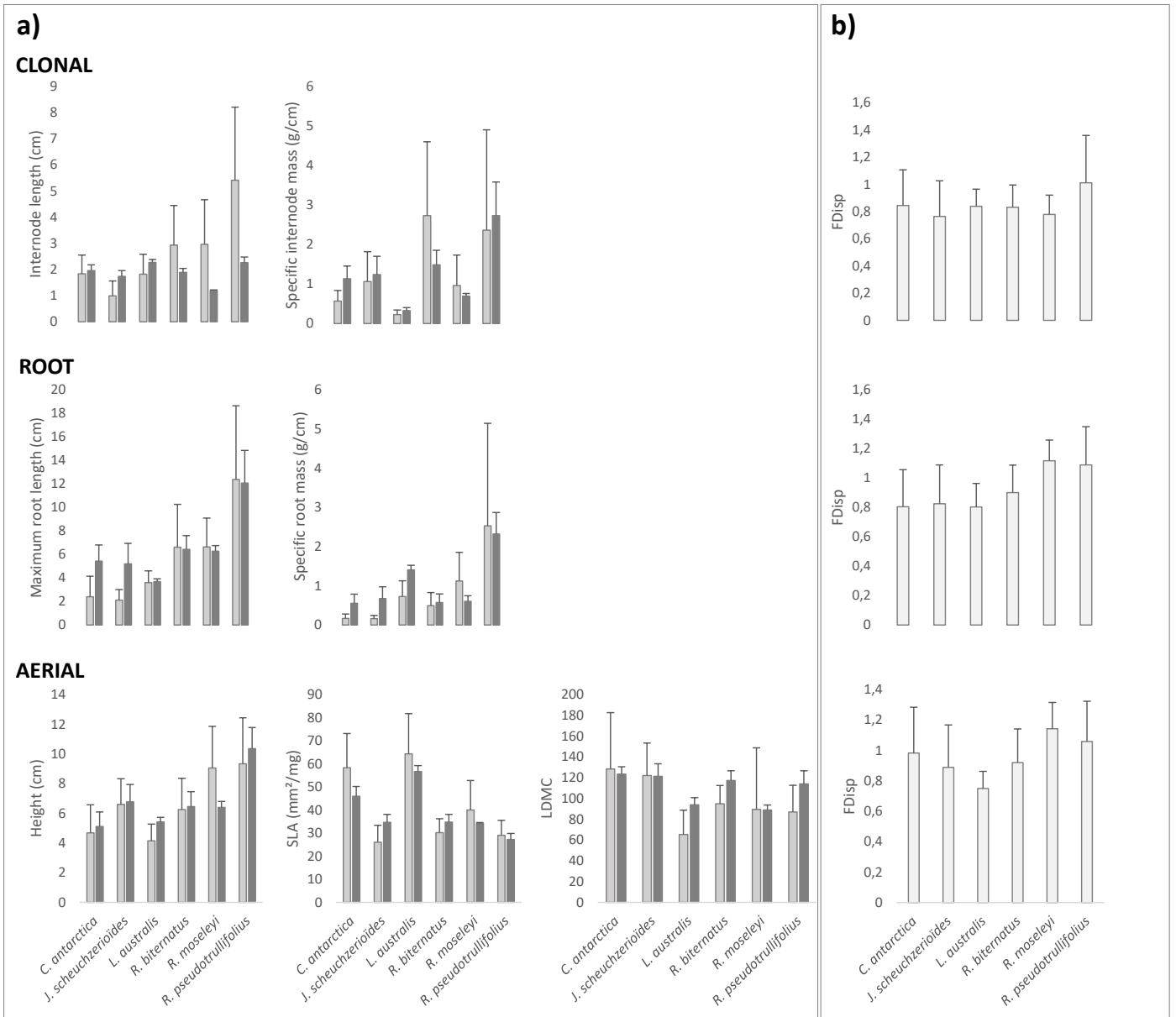
Notes: 1,2 Rooney, Carli, & Bayley, 2013 ; 3 Sand-Jensen & Borum, 1991 ; 4, 45, 47 Borner & Puijalon, 2011 ; 5 Steinman et al., 2012 ; 6 Mooij et al., 2005 ; (7 added to the test) ; 8 Jeppesen et al., 1997 ; 9, 56 Monzeglio & Stoll, 2005 ; 10 13, 19 Liikanen et al, 2002 ; 11 Wang et al, 2008 ; 12 Wallace et al, 2016 ; 14 Boyd, 1998; 15, 35, 44 Dar et al, 2014; 16 Idso & Foster, 1974 ; 17 Viet et al, s. d. ; 18, 24, 33 Su et al., 2019 ; 20 Beck et al, 2001; 21 Barron & Ashton, s. d. ; 22 Gaudet & Muthuri, 1981 ; 23 Coles & Jones, 2000 ; 25, 34 Liu et al., 2020 ; 26 Ward & Tockner, 2001 ; 27 Favre-Bac et al, 2017 ; 28, 40 Rolon & Maltchik, 2006 ; 29 Egertson et al, 2004 ; 30 Akasaka et al, 2010 ; 31 Hassall et al, 2011 ; 32 de Assis Murillo et al., 2019 ; 36, 48 P. Zhang et al., 2020 ; 37 Rosset et al, 2010; 38, 46 Schneider et al, 2015 ; 39, 52 Kikvidze et al., 2005 ; 41 Lévesque et al, 2017 ; 42 Hosper, 1989 ; 43 Phillips et al, 2016 ; (49 added to the test) ; 50 Zhang et al, 2019 ; 51 Petchey & Gaston, 2002 ; 53 Stubbs et al, 2004 ; 54 Qi et al., 2021 ; 55 Hooper et al., 2005.

**Table S5.** Local spatial arrangements (LSA) detected at the community scale. Significant differences between observed and expected co-occurrences indicated that local spatial arrangements (LSA) were significantly different from 0. These results were obtained through the Poisson probability function, with mean  $\lambda$  = expected number of co-occurrences at pond scale.  $LSA < 0$  indicates segregation, and  $LSA > 0$  indicates aggregation at community scale.

Observed LSA different from expected ?	LSA (Number of quadrats)
No	<0 (32) segregation =0 (11) random >0 (10) aggregation
Yes	<0 (75) segregation >0 (28) aggregation



**Figure S4.** Neighborhood composition i.e. mean ( $\pm$  SD) percentage of cover of each macrophyte species in the neighborhood of each target species.



**Figure S5.** a) Mean ( $\pm$  SD) traits of targets species and their neighbors (CWM values). Bars in light grey: values of target traits, bars in dark grey: CWM trait values of neighbors. \*  $p < 0.05$  (Wilcoxon signed-rank tests) b) Mean ( $\pm$  SD) of FDis of the three trait categories (aerial, clonal, and root) calculated on neighbors of each target species.

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CHAPITRE 2 : Réponses fonctionnelles des macrophytes  
à des modifications de filtres abiotiques  
dans un contexte d'interactions plantes-plantes

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## Préface

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Tout changement environnemental, dont l'augmentation des températures, peut renforcer ou modifier les filtres abiotiques mais aussi biotiques, notamment au travers de changements de la balance compétition / facilitation entre plantes (Ploughe et al., 2019 ; Souza et al., 2021).

La littérature montre que les réponses fonctionnelles des espèces végétales (y compris les macrophytes) sont généralement étudiées en considérant les facteurs biotiques et abiotiques indépendamment, alors que les espèces y sont soumises simultanément dans leur habitat. Les réponses à ces contraintes seraient pourtant antagonistes. En effet, il a été montré chez des plantes terrestres, que la compétition et le stress thermique induisent respectivement une augmentation (Novoplansky, 2009 ; Bittebiere et al., 2012) et une diminution (Shah & Paulsen, 2003 ; Chalanika De Silva & Asaeda, 2017) des valeurs moyennes de surface foliaire par exemple.

Dans ce chapitre, nous cherchons à déterminer les réponses fonctionnelles des espèces à des températures correspondant à leurs limites de tolérance thermique basse et haute, dans un contexte d'interactions plantes-plantes (**article V**). L'intensification des contraintes abiotiques en lien avec le changement climatique au cours du temps affecteraient les stratégies moyennes observées à l'échelle intra- mais aussi interspécifique *i.e.* à l'échelle de l'ensemble de la communauté (**article IV**). Pour tester cette hypothèse, nous avons utilisé une méthode basée sur le calcul d'hypervolumes (espace des valeurs de traits à n-dimensions) récemment développée par Blonder et al. (Blonder et al., 2014 ; Blonder, 2018) et permettant la prise en compte des variabilités inter- et intraspécifiques des traits fonctionnels et leurs réponses aux conditions environnementales. Cette méthode semble donc particulièrement appropriée pour étudier les effets des variations interannuelles des filtres abiotiques sur les communautés végétales, grâce à la comparaison d'hypervolumes. Notre étude serait alors l'une des premières (mais voir p. ex., Bjorkman et al., 2018) à tenir compte des variations temporelles des stratégies d'espèces au sein d'une communauté à travers leurs traits fonctionnels, en relation avec leurs variations d'habitat (**article IV**).

Le stress et les interactions plantes-plantes peuvent affecter simultanément la distribution des valeurs de traits à l'échelle intraspécifique, en terme de valeur moyenne et de



variabilité (**article V**). Les filtres biotiques et abiotiques sélectionnent les phénotypes / combinaisons de traits qui permettent aux individus de maintenir leurs performances. [Chalanika De Silva & Asaeda \(2017\)](#) ont montré notamment qu'une augmentation de la température au-delà de la gamme de tolérance de trois espèces de macrophytes, induit un stress oxydatif, une diminution moyenne de la croissance et de la concentration en pigments photosynthétiques. De plus, la croissance clonale confère aux macrophytes la capacité d'éviter ou de tolérer la compétition ([Bittebiere et al., 2012](#)) ou des conditions abiotiques stressantes ([Slade & Hutchings, 1987b](#)), en augmentant respectivement la longueur moyenne de leurs connexions ou le stockage (p. ex., des glucides). Par ailleurs, la variabilité phénotypique est également modifiée en fonction du type et de l'intensité des filtres. En effet, les contraintes abiotiques induisent une convergence des valeurs de trait, alors que les contraintes biotiques peuvent induire de la convergence ou de la divergence des valeurs de traits en lien avec les deux mécanismes de coexistence stable ([Chesson, 2000](#) ; [Grime, 2006](#) ; [Nagashima & Hikosaka, 2011](#) ; [Kraft et al., 2015b](#)). En cas de processus de filtrage intense, les patrons de réponse des traits (moyenne et variabilité) à l'échelle intraspécifique devraient se retrouver à l'échelle de la communauté entière (à l'échelle interspécifique également) (**article IV**).

Par ailleurs, il est généralement admis que les individus ne peuvent soutenir deux stratégies opposées qui nécessitent trop d'énergie ([Wright et al., 2004](#) ; [Reich, 2014](#) ; [Díaz et al., 2016](#)), par exemple maximiser l'aptitude compétitive et résister au stress thermique. Pour pallier à cela, les individus coordonnent différentes fonctions afin de maximiser leur performance avec un investissement minimal ([Murren, 2002](#) ; [De Kroon et al., 2005](#)) grâce aux co-variations de leurs traits à l'échelle de l'individu. Cela implique des compromis entre des traits liés à différentes stratégies ou des co-variations positives entre des traits qui soutiennent la même stratégie. Ces co-variations sont habituellement étudiées entre les espèces ([Wright et al., 2004](#) ; [Koehler et al., 2012](#) ; [Bucher et al., 2019](#) ; [Maccagni & Willi, 2022](#)), et rarement à l'échelle intraspécifique, pourtant nécessaire pour la prise en compte des mécanismes de plasticité phénotypique, en particulier chez les plantes clonales. Ainsi, étant donné que les modifications des stratégies des espèces en réponse à des changements environnementaux reposent sur les modifications des valeurs de traits, le signe et l'intensité de leurs co-variations sont susceptibles d'être modifiés en retour (**article V**) ([Reich et al., 2003](#) ; [Wright et al., 2004, 2005](#) ; [Sgrò & Hoffmann, 2004](#) ; [Pellissier et al., 2018](#) ; [Maccagni & Willi, 2022](#)), bien que les études demeurent rares à ce sujet. *In fine*, les variations de valeurs de traits et leur modulation

devraient impacter les performances des individus/espèces et donc la dynamique de la communauté végétale.

Ce deuxième chapitre vise donc à déterminer les réponses fonctionnelles des macrophytes à des modifications de filtres abiotiques dans un contexte d'interactions plantes-plantes. Pour cela, nous avons mis en place une expérimentation en conditions contrôlées permettant d'appréhender les mécanismes opérant à l'échelle spécifique en réponse à des températures extrêmes (**article V**), ainsi qu'une étude *in situ* pour décrire les variations temporelles de réponses observées à l'échelle de la communauté sur quatre années, face à des conditions environnementales changeantes (**article IV**). Les questions posées étaient les suivantes :

- Quelles sont les réponses fonctionnelles observées chez trois espèces de macrophytes à un gradient de température, les exposant à leurs limites de tolérance basse et haute, dans un contexte variable d'interactions plantes-plantes ? (**article V**). Nous avons émis les hypothèses suivantes :
  - Les traits aériens et racinaires devraient présenter des valeurs moyennes intermédiaires du fait de leur implication simultanée dans la résistance au stress thermique et le soutien à l'aptitude compétitive, tandis que les traits clonaux devraient subir une augmentation de leurs valeurs moyennes pour limiter la compétition et explorer des micro-sites plus favorables à leur maintien/survie.
  - Sous un stress thermique en situation d'interactions plantes-plantes, les traits aériens et racinaires devraient converger et les traits clonaux devraient diverger.
  - L'intensité et le sens des co-variations entre les traits devraient changer au sein des individus en fonction de la hausse des températures et des interactions plantes-plantes, en lien avec leurs stratégies de réponses à des conditions environnementales changeantes et impactant *in fine* leur performance.
- Face à des conditions environnementales changeantes, les communautés et les espèces qu'elles comportent, adoptent-elles des stratégies de réponse similaires à moyen terme (4 ans) ? Quels traits participent à la mise en place de ces patrons de réponses et quels sont les facteurs abiotiques qui induisent des modifications de stratégie chez les espèces ? (**article IV**). Les hypothèses étaient les suivantes :

- L'intensité du filtrage abiotique devrait déterminer les valeurs moyennes des traits (*i.e.* centroïdes des hypervolumes) verticaux (hauteur et traits foliaires) et horizontaux (clonaux). Ainsi, un processus de filtrage moins intense, devrait entraîner respectivement une augmentation et une diminution des valeurs moyennes des traits verticaux et horizontaux. Des patrons de réponses inverses sont attendus en cas d'intensification du filtrage abiotique.
- Les traits verticaux et clonaux convergeraient alors vers des valeurs moyennes qui permettraient aux individus de mieux résister aux changements environnementaux.
- Des filtres abiotiques intenses, en particulier l'élévation des températures, devraient conduire à des stratégies de réponse similaires entre les communautés (*i.e.* un espace multidimensionnel de traits similaire entre les communautés). En outre, les filtres abiotiques devraient également induire une diminution de la variabilité globale des stratégies des individus au sein de chaque communauté, reflétant des mécanismes de sélection stabilisante (*i.e.* une diminution de taille des hypervolumes).

## Using multidimensional trait space to study responses in aquatic plant community to modifications of abiotic filtering in the sub-Antarctic ponds.

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Article Informations	Abstract
<p><i>Article history:</i></p> <p>In prep</p> <hr/> <p><i>Keywords:</i></p> <p>Functional traits</p> <p>Hypervolume calculation</p> <p>Community assembly</p> <p>Trait variability</p> <p>Nutrient</p> <p>Temperature</p> <p>pH</p> <p>Oximetry</p>	<p>In the current context of climate change that cause strong habitat variations, understanding the mechanisms underlying plant community dynamics appears crucial to predict their fate. Taking the inter- and intraspecific trait variability into account would help us to identify these mechanisms. Recently, a method involving the calculation of hypervolumes (n-dimensional space of trait values) has been developed to study plant responses to their environment. Based on this method (hypervolume comparisons), we studied the effects of interannual variations in the abiotic filter on plant communities. We focused on the aquatic plant communities living in ponds of the Iles Kerguelen, in the sub-Antarctic region. This model is particularly relevant to test questions about the consequences of habitat variations related to climate changes, as aquatic plant communities are adapted to cold and overall stable habitat conditions, while climate is rapidly changing there. We conducted a field sampling over four years, in 45 ponds distributed within three sites. On all aquatic species, we measured five foliar, shoot, and clonal traits characterizing individual growth strategies, that are likely to respond to the variations in the abiotic filter. In parallel, we measured 10 abiotic variables to characterize plant habitat within ponds every three months during the duration of our survey. Hypervolumes were calculated within each site, for each year, to determine variations in aquatic plant strategies at the community level. We showed (i) the importance of spatio-temporal gradients of nutrient availability, temperature, and pH and oximetry for the functional structure of aquatic plant communities, (ii) that the shape of its mean response was trait dependent, with traits related to plant metabolism (SLA, specific internode mass) and to 3D space exploration (height, internode length) respectively displaying a quadratic or a linear response to the three spatio-temporal abiotic gradients, and (iii) selection pressures were especially high on vertical traits compared to the horizontal ones. We conclude that interannual abiotic variations over four years are already sufficient to detect rapid responses towards resistance (tolerance or avoidance), likely relying on phenotypic plasticity. Besides, our study may inform on future functional changes in aquatic plant communities of the Iles Kerguelen, and more widely of the whole sub-Antarctic region where similar species can be found.</p>

## Introduction

In the current context of climate change that cause strong habitat variations (e.g. more frequent episodes of higher temperatures, lower precipitations, higher nutrient availability...) (Franklin et al., 2016; Chaudhry and Sidhu, 2022), understanding the mechanisms underlying plant community dynamics appears crucial to predict the fate of plant species over time. Among these mechanisms, abiotic filters operate on individual traits and determine the community composition, by eliminating traits combinations that do not fit the habitat constraints (Keddy, 1992; Chase, 2003; Violle et al., 2007). Trait based approaches have then been suggested to rebuild community ecology and produce general principles on assembly mechanisms (Mcgill et al., 2006). Plant functional traits correspond to any morphological, physiological, and phenological characteristics that impacts individual performance either directly or through the individual growth, reproduction or survival (Violle et al., 2007). Historically, studies focused on interspecific trait variations in response to changing environments. More recently however, intraspecific trait variability, resulting from plasticity or local adaptation (Garnier et al., 2004; Choler, 2005; Mcgill et al., 2006; Quétier et al., 2007), was showed to play a major role in maintaining plant biodiversity by enabling different species to express varying phenotypes, allowing them to resist to environmental filters (Messier et al., 2010; Jung et al., 2010; Albert et al., 2010a; Nicotra et al., 2010; Violle et al., 2012). Taking the inter- and intraspecific trait variability into account would thus help us refine the mechanisms underlying plant community assembly over time, in particular under climate change.

A method involving the calculation of hypervolumes (n-dimensional space of trait values), recently developed by Blonder et al. (2014, 2018), allows the consideration of inter- and intraspecific trait variability in a multi-trait approach. This method has been

used so far at the interspecific level to highlight the influence of abiotic filters on functional traits (Lamanna et al., 2014), at the intraspecific level to study the response of clonal species to competition (Bittebiere et al., 2019) or at both levels to understand plant species invasiveness (Helsen et al., 2020, 2021). This method seems therefore particularly suitable for studying the response of plant individuals to the variations of their habitat filtering processes. Studies of species and community responses to habitat variations require the analysis of temporal series of trait data (Bjorkman et al., 2018). In this study, we propose to adapt Blonder et al. (2014; 2018) approach to study the effects of interannual variations in the abiotic filter on plant communities, based on hypervolume comparisons. This study would then be one of the first (but see e.g. Bjorkman et al., 2018) to consider the temporal variations of species strategies within a community through their traits, in relationship with their habitat variations.

Aquatic habitats are among the most abiotically constrained (Santamaría, 2002). Within aquatic plant communities, species are generally clonal *i.e.* able to produce genetically identical and potentially independent ramets (an erected shoot with its leaves and roots) connected through plagiotropic stems, and forming a clone (van Groenendael et al., 1996). Their resistance to variations in the aquatic habitat usually relies on modifications of their traits in the vertical (shoot and foliar traits), and in the horizontal directions (clonal traits) (van Groenendael et al., 1996; Klimeš et al., 1997; Ye et al., 2014). Over the years, variations in the aquatic habitat conditions would lead to more or less stringent abiotic filtering process. Under initially cold and humid climates, less stringent abiotic filter correspond to a slight increase in temperatures that could decrease the risk for plant species to be exposed to their lower limit of thermal tolerance and stimulate photosynthesis and growth (Barko et al., 1986; Silveira and Thiébaud, 2017) *i.e.* higher individual Specific Leaf Area, height (Riis et al., 2012), and elongation in roots (Kaspar and

Bland, 1992; Pregitzer et al., 2000). Precipitations would remain high, affecting the resource acquiring organs of plants *i.e.* aerial and root traits, through water level (Chagas et al., 2012; de Assis Murillo et al., 2019) and the nutrient availability in water and sediments (James et al., 2005; Barker et al., 2008). These milder habitat conditions should reduce the need of resource storage in connections (Suzuki and Stuefer, 1999), while ramets should aggregate in this favorable habitat through shorter internode length (van Groenendael et al., 1996; Halassy et al., 2005). On the contrary, with the strengthening of the abiotic filter, plant species could now be exposed to their higher limits of thermal tolerance. Thermal stress usually lead to decrease in height, leaf area (Shah and Paulsen, 2003; Chalanika De Silva and Asaeda, 2017), and root length (Pregitzer et al., 2000). Moreover, less abundant precipitations can decrease water depth, ultimately altering plant morphology to withstand hydric stress (*i.e.* lower SLA, and higher LDMC and specific root length, Luo and Xie, 2009; Gao et al., 2021; Han et al., 2021). Besides, under unfavorable conditions, clonal plants invest more in the length of their connections (escape behavior; Slade and Hutchings, 1987), and in their resource storage for future growth (Cheplick and Gutierrez, 2000). Thus the stringency of abiotic filtering would determine the average values of both vertical and horizontal traits (*i.e.* hypervolume centroid positions). Less stringent abiotic filtering would result in respectively higher or lower average values of vertical and horizontal traits, and conversely in case of abiotic filter strengthening.

Overall, these intraspecific variations of traits would lead to modifications of plant strategies at the community scale, and more precisely, of the plant phenotype variability. Under loose abiotic filters, strategies among and within species are quite variable to limit the occurrence of similar trait values, leading to divergent distributions of traits in realized assemblages (Weiher et al., 1999; Grime, 2006; Bello et al., 2009). On the contrary, communities under strong abiotic filters

harbor individuals with similar trait values to develop a stress tolerance or avoidance strategy (Jacobsen et al., 2009; Read et al., 2014; Pierce et al., 2017). Vertical and horizontal traits then converge towards values maximizing individual performance (Cornwell and Ackerly, 2009; Read et al., 2014). Variations in the strength of the abiotic filtering process over time, should then lead to modifications in the variability of species strategies (volume of the hypervolume), in the functional similarity between communities of the same region, and in the importance of horizontal and vertical trait for the strategy (as showed by the contributions to the hypervolume shaping).

In this study, we focused on the aquatic plant communities living in particular freshwater ecosystems *i.e.* the ponds of the Iles Kerguelen, in the sub-Antarctic region. This model is particularly relevant to test questions about the consequences of habitat variations related to climate changes, as (i) their effects are especially severe in aquatic ecosystems (Lacoul and Freedman, 2006), and (ii) aquatic plant communities from the sub-Antarctic region are adapted to cold and overall stable habitat conditions (Walther et al., 2002; Lebouvier et al., 2011). We conducted a field sampling over four years, in 45 ponds distributed within three sites. On all aquatic species, we measured five foliar, shoot, and clonal traits characterizing individual growth strategies, that are likely to respond to the variations in the abiotic filter over time. In parallel, we measured 10 abiotic variables that are known to affect plant growth and survival. Hypervolumes were calculated within each site, for each year, to determine plant strategy variations (Blonder et al., 2014; Blonder, 2018). Through this field sampling approach, we tested the following hypotheses:

- The stringency of abiotic filtering would determine the average values of both vertical (growth and light acquiring) and horizontal (space exploration, and resource storage) traits *i.e.* hypervolume centroid positions. Less stringent abiotic filtering, in particular the shift away from

the lower thermal limits of communities, would result in respectively higher or lower average values of vertical and horizontal traits. In case of abiotic filter strengthening, the opposite pattern of response is expected.

- Strong abiotic filters, in particular thermal stress, should lead to (i) similar adaptive strategies among communities, inferred from similar multidimensional trait space at aquatic plant community level, (ii) a decrease in the overall variability of individual strategies (lower hypervolume size), and (iii) vertical and clonal trait convergence towards values that allow individuals to better cope with environmental changes.

## Materials and methods

### Study area

This study was conducted on the main island of the Iles Kerguelen located in the sub-Antarctic region (South Indian Ocean) (48°30'–50°00'S, 68°27'–70°35'E). The climate is characterized by cold temperatures (annual mean of 4.6 °C with few variations over the year, from 2.1 °C to 7.7 °C - [Frenot et al., 2001, 2006; Lebouvier, 2007](#)), and low to abundant precipitations *i.e.* ranging from 500 mm to 3200 mm per year along an East-West gradient ([Frenot et al., 1998](#)).

We focused on the shallow freshwater ponds located nearby the shore line. These ponds are being supplied with water from rainfall and with nutrients from marine animal dejections (mostly elephant seals and birds) ([Smith, 2008](#)). The ponds are the main habitat of the aquatic plant species of the sub-Antarctic region ([Douce et al., submitted](#)), on which our study focuses: *Limosella australis* R.Br. (Scrophulariaceae), *Callitriche antarctica* Engelm (Plantaginaceae), *Juncus scheuchzerioides* Gaudich. (Juncaceae), together with three Ranunculaceae species: *Ranunculus biternatus* Smith, *R. pseudotrullifolius* Skotts., and *R. moseleyi* Hook.f. *C. antarctica* display a floating canopy, while the other species harbor either

a rosette architecture or erected shoots (*J. scheuchzerioides*) and are rooted in the sediments. These species are able to horizontally propagate through clonal growth *i.e.* they produce new and genetically identical ramets connected through plagiotropic stems (connections) (van Groenendael et al., 1996).

### Field survey

Sampling was conducted once a year in November (beginning of the growth season) from 2018 to 2021, at three locations of the main island of the Kerguelen archipelago. The locations were distributed along a West-East gradient: Molloy, Isthme Bas, and Cap Ratmanoff. At each location, fifteen ponds were randomly selected to describe a gradient of pond sizes.

Within each pond, we randomly positioned several 1 m<sup>2</sup>-quadrats to measure a range of biotic and abiotic parameters. The number of quadrats depended on the pond size: five quadrats were realized for ponds whose surface was >5m<sup>2</sup>, while three to four quadrats were used for ponds <5m<sup>2</sup>. Within each quadrat, we collected one ramet (one node with its leaves and roots, and one connection internode) of the six target species when present, to measure their traits.

To characterize the composition of the aquatic plant communities, the abundances of the different species were estimated for each quadrat. In addition, ten physical and chemical parameters were measured. Within each quadrat, we measured the mean water depth (based on three measurements), pH, specific conductance, and mean dissolved oxygen concentration (calculated from three measurements performed near the surface, in the middle of the water column, and at the bottom of the pond; HQ20, HACH™, Dusseldorf, Germany). At each pond, one 30 mL-water sample, and one 50 mL-sediment sample were also collected for further nutrient analyses in the lab. For these two samples, water and sediments were collected from several points within the pond to account for

possible heterogeneity in nutrient distribution.

### *Nutrient analyses*

After collection, water and sediment samples were stored at 6 °C and brought within 24h to the laboratory. Water samples were further filtered through Whatman GF/F filters (pore size: 0.7µm, Cytiva, Amersham, United Kingdom). All samples (water and sediments) were then stored at -20 °C for several weeks before chemical analyses. N-NH<sub>4</sub><sup>+</sup>, N-NO<sub>3</sub><sup>-</sup> and P-PO<sub>4</sub><sup>3-</sup> concentrations were determined based on standard colorimetric methods (Grasshoff et al., 1999) using a sequential analyzer (SmartChem200, AMSAlliance, Barsanti, Italy).

Nitrogen and carbon sediment concentrations were measured following the capsule method (Brodie et al., 2011). Specifically, an amount of five milligrams (± 10%) of homogeneous sediment was acidified with HCl in silver capsules to eliminate carbonates. Liquids were then evaporated on a 65 °C hot plate for 12 hours, before the entire drying out of capsules at 80 °C for a few days. Carbon and nitrogen nutrient analyses were then performed using an elementary analyzer (FlashEA 1112 NC Analyzers®, Thermo Fisher Scientific, Waltham, Massachusetts, USA). Following Ni, Wang and Wang (2016), available organic phosphorus was extracted from 50 mg of dry sediment samples with 5 ml of NaOH (1 M). After extraction during 16 hours on a rotatory shaker at room temperature, the supernatant was collected, and its pH was stabilized at 7 with addition of HCl (4 M). The extracted P that has been converted into orthophosphate was quantified using the molybdate/ascorbic acid blue method (Murphy and Riley, 1962), and results were reported in mg of available P per g of dry sediment.

### *Water temperature simulation*

Water temperature was recorded every half hour (HOBO Pendant MX2202, ONSET™,

Cape Cod, Massachusetts, USA) from September 2020 to October 2021, in the middle of the water column of each pond. We performed linear regression analyses to determine the relationship between water temperature within each pond and air temperature recorded at the meteorological station of the Kerguelen (Météo France 2020-2021 records, Port-aux-Français), after confirming normality of the distribution of model residuals. All relationships between air and water temperatures were significant ( $R^2 \geq 0.55$ ;  $P < 0.05$ ), with the exception of two ponds (see Douce et al., submitted for more details). These relationships were then used to infer water temperature occurring from November 2017 to August 2020 based on Météo France 2017-2020 records.

From these simulated and observed data, we calculated the mean water temperature of each year from November to October (*i.e.*, a period of one year preceding sampling), at the pond and at the site scales.

### *Trait measurements*

Traits were measured in the lab, on the sampled ramets of the six target species, within the 24 hours after sampling (ramets were stored at 4 °C during this period). These traits were chosen to characterize species growth strategies in the horizontal and vertical directions. Vertical traits included height, Specific Leaf Area, and Leaf Dry Matter Content. These two foliar traits were measured following Cornelissen et al. (2003), on one healthy and mature leaf randomly selected per ramet. We additionally measured two clonal traits: internode length and specific internode mass, calculated as the ratio between internode dry mass and length ( $\text{g}\cdot\text{cm}^{-1}$ ). Measurements of dry masses were performed after drying plant parts for 48 hours in oven at 65 °C. All plants were cleaned before any measurements.

### *Data analyses*

*Characterization of the habitats of plant species* - Before statistical analyses, abiotic



parameters and species abundances recorded from different quadrats per pond were averaged for each sampling date. To characterize the habitat of plant species, we ran a Principal Component Analysis (PCA) on the pond abiotic parameters using the R package *FactoMineR* (Lê et al., 2008). The first three axes explained 53.2% of total variance (Fig. S1a & S1b). The first axis (PCA1) described the trophic status of ponds based on water and sediment nutrient concentrations (Fig. S1c), the second axis (PCA2) was related to temperature (32,8%), water depth, and nitrogen and carbon sediment concentrations, while the third axis (PCA3) was associated to pH and dissolved oxygen concentration. The pond score on the first three axes of the PCA was then averaged by site\*year (Fig. S2).

As composition of pond communities was overall stable across space and time during our survey (Douce *et al.*, submitted), we do not expect an effect of species abundance variations on multidimensional trait space. Nevertheless, we calculated the Simpson diversity index for each pond using the *vegan* R package (Oksanen *et al.*, 2015), and averaged the values by site\*year (Fig. S3), to use it in our analyses to control for potential effect.

*Construction of five-dimensional hypervolumes* - The five-dimensional trait spaces of the aquatic plant communities were built through space and time, using a multidimensional kernel density estimation procedure (Blonder *et al.*, 2014; Blonder, 2018). One hypervolume for each site (Molloy, Isthme Bas, and Cap Ratmanoff) and for each year was built (see Fig.S4 for proportion of available individuals of each species for each hypervolume) using a kernel based on the Silverman estimator (Silverman, 2017) *i.e.* 12 hypervolumes in total. Before analysis, redundancy between traits was checked and no correlations with coefficients higher than |0.5| were found (Dormann *et al.*, 2013). Trait data were standardized using the mean and standard deviation of all the data simultaneously (Blonder *et al.*, 2014). For

reduced and centered data, volumes of hypervolumes are given in  $SD^n$  (n number of axes *i.e.* traits). All hypervolumes were built using the *hypervolume* R package (Blonder *et al.*, 2014).

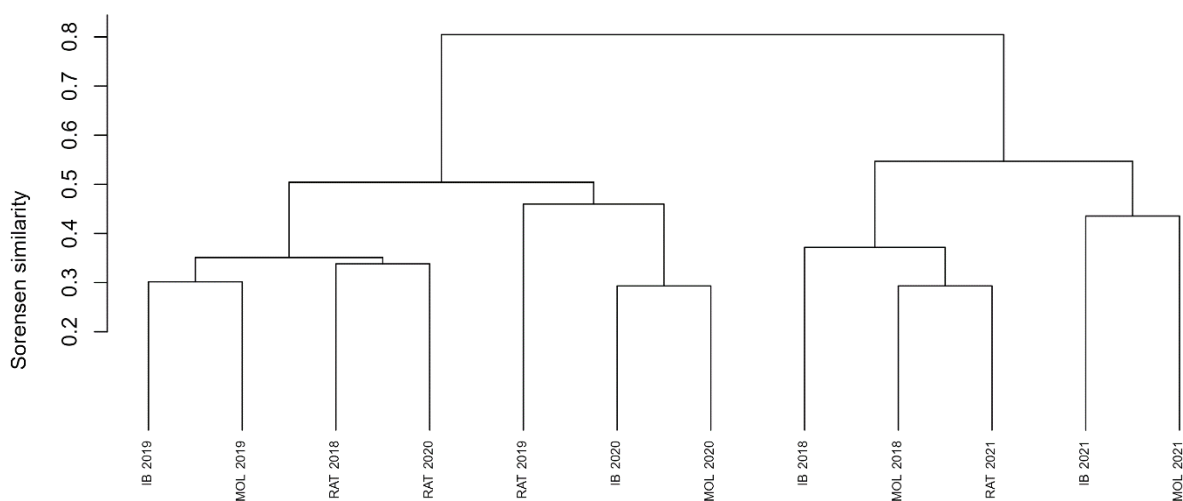
*Influence of habitat on similarity between aquatic plant communities through space and time* - To analyze the effect of habitat on similarity between aquatic plant communities through space and time, we calculated the overlap between each pair of hypervolumes. The overlap between two hypervolumes measured the intersection of the hypervolumes in the five-dimensional space defined by the traits. It was calculated following the Sorensen similarity index (Mammola, 2019):  $2 * \text{volume shared by hypervolume A and B} / \text{volume of hypervolume (A + B)}$ . Volume is a measure of hypervolume size, considering the range of values observed along each axis, *i.e.* the variability of all traits forming the hypervolume simultaneously. Similarities between pairs of hypervolume were then compared using a Ward's clustering method (Murtagh and Legendre, 2014), and then the effect of abiotic parameters and species abundances on similarities were assessed through Permutational Multivariate Analysis of Variance using the *Adonis* function of the *vegan* R package. A significant positive effect, means that communities with similar explanatory variables (*i.e.* abiotic parameters) correspond to communities with similar hypervolumes.

*Influence of habitat on the volume of multidimensional trait space* - To characterize the habitat effect on the functional strategies of species, the volume of the hypervolumes was calculated for each aquatic plant community through space and time. Since the volume is related to the number of individuals used to calculate the hypervolume (Blonder, 2018) and because there was only one hypervolume per aquatic plant community (no variability for comparing volumes), bootstrapping was used to simulate 100 hypervolumes to allow comparisons

(Bittebiere et al., 2019). Random selection of individuals with replacement was performed within each aquatic plant community, setting the used number of individuals to the lowest number of sampled individuals of all communities (*i.e.* 100 individuals). Then, volumes were used as response variables in Linear Mixed Effect models [*nlme* R package Pinheiro et al., 2013]. Specifically, the log-transformed volumes of hypervolumes were used as response variables, the first three PCA axes and the Simpson diversity index as main effects, and the aquatic plant community designation (depending on space and time) was included as random variable to control for non-independence between simulated hypervolumes. Quadratic terms were also included to test for potential non-linear effects. Every possible subset of this model was tested, and best-fitting combinations of variable displaying an Akaike's Information Criterion (AIC) < 2 were compiled by model averaging techniques [*MuMIN* R package Bartoń, 2013].

The same analysis was performed on each trait centroid coordinate (mean point positions on each axis) of the simulated hypervolumes.

*Modifications of traits' contributions to the hypervolumes' shape* - For each aquatic plant community through space and time, the contributions of the five traits to multidimensional trait space were calculated. Trait contribution is calculated as the ratio between the volumes of the hypervolume which considers all traits and of the hypervolume which considers all traits but the trait of interest. The trait contribution is thus related to its variability, relatively to other traits. Hypervolumes representing the potential multidimensional trait space of the communities were simulated by resampling 100 individuals within all sites and all years combined, 100 times. Then, the contribution of each trait, for each aquatic plant community, was compared to a 95% confidence interval built from the simulated data (*i.e.*, by selecting the 2.5 and 97.5 percentiles of simulated values). When the contribution of a trait was outside the confidence interval, it was significantly different from expected. All analyses were conducted with R-4.1.2.



**Figure 1.** Overlap between the hypervolumes of the aquatic plant communities calculated through space and time. The Y-axis represents 1-Sorensen similarity. Shorter branches represent communities with more similar hypervolumes. Dendrogram was created following Ward's clustering method (Murtagh & Legendre, 2014). MOL Molloy, IB Isthme Bas, RAT Cap Ratmanoff.

## Results

### *Influence of abiotic parameters on the multidimensional trait space*

Abiotic parameters had an influence on community multidimensional trait spaces. Indeed, the axes two (temperature) and three (pH and oxygen concentration) of the PCA had a significant effect on similarity between hypervolumes, and a tendency was observed for the first axis (nutrient availability) (Permanova, PCA1  $F_{df=1} = 2.290.$ ; PCA2  $F_{df=1} = 4.537^{**}$ ; PCA3  $F_{df=1} = 2.406^*$ ) *i.e.* more functionally similar communities have grown under more similar abiotic conditions (Fig.1). As expected, the Simpson diversity index had no effect on hypervolume similarity (Permanova,  $F_{df=1} = 0.682^{ns}$ ).

### *Reduction of multidimensional trait space with the strengthening of the abiotic filter*

As expected, an increase along the three PCA axes lead to a decrease in the volume of hypervolumes, *i.e.* a decrease in the variability of growth strategies at community scale (Fig.2, Table 1). This decrease was linear along the three PCA axes (quadratic effects were not significant, Table 1) with equivalent strength between the filters

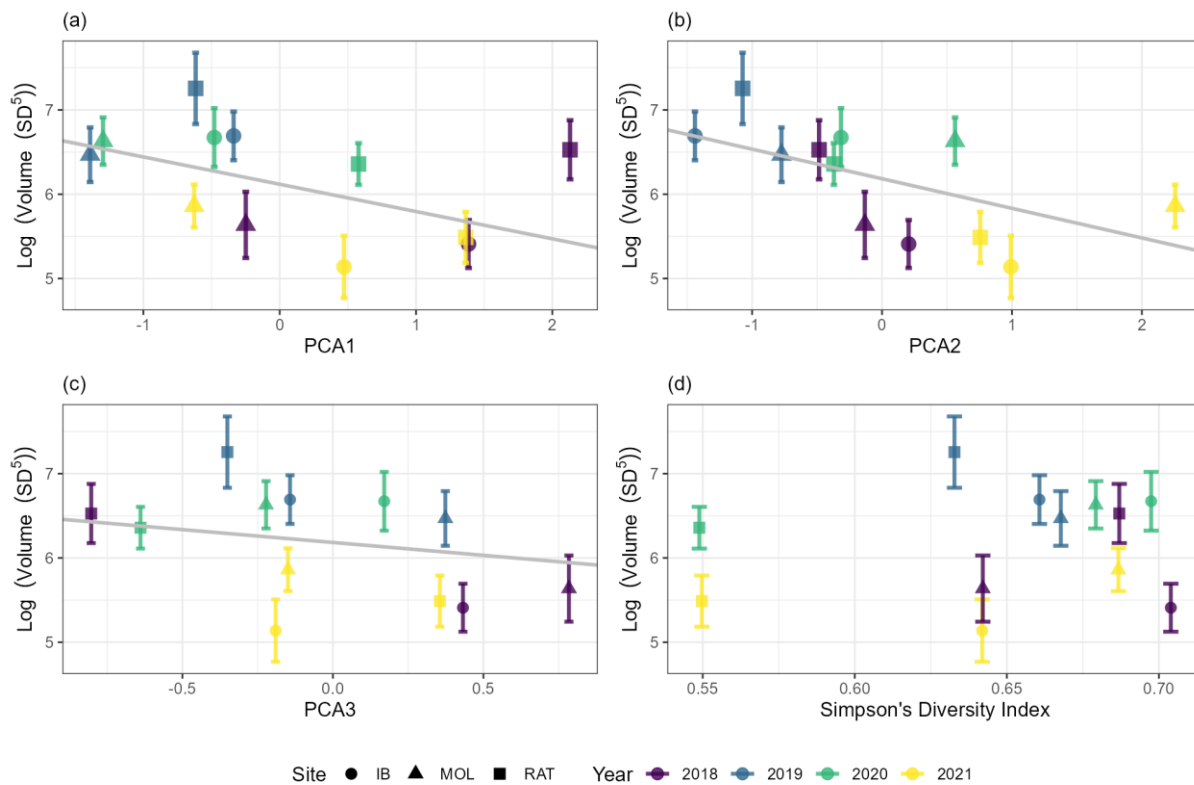
(similar slopes between the three PCA axes, Table 1). Simpson diversity index however, had no effect on the volume of hypervolumes.

### *Variations of traits' centroid and contributions to the hypervolume shape*

We found a significant effect of the second axis of the PCA on all traits except LDMC (Table 2, Fig.S5). Indeed, PCA2, which is related to temperature and water depth, had a negative linear impact on height, SLA and internode length, and displayed a negative bell-curve relationship with specific internode mass (maximal values at intermediate level on PCA2). The first axis, which described the trophic status of ponds and the third axis, associated to pH and dissolved oxygen concentration, both had a negative linear impact on height, and a positive quadratic effect on SLA (*i.e.* SLA was minimal for PCA1 and PCA3 intermediate values). As for PCA2, the response of specific internode mass to PCA3 followed a negative bell-curve (Table 2, Fig.S5). Contrary to our expectation, an effect of the Simpson diversity index was found but on height only (Table 2).

**Table 1.** Effects of PCA axes and Simpson diversity index on the volumes of hypervolumes. This table presents the results from the full averages of the best-fitting Linear Mixed Effects models selected through AIC comparison. Bold font indicates statistical significance. Std. Error standard error; Adjusted SE standard error; Z value: test statistic;  $Pr(>|z|)$ : p-value from the Z test. The “?” indicates the quadratic effect. PCA1 nutrient availability, PCA2 thermal conditions, PCA3 pH and oxygen concentration.

	Estimate	Std.Error	Adjusted SE	Z value	$Pr(> z )$
<b>PCA1</b>	<b>-0.323</b>	<b>0.089</b>	<b>0.105</b>	<b>3.056</b>	<b>0.002**</b>
PCA1 <sup>2</sup>	0.050	0.079	0.087	0.579	0.562
<b>PCA2</b>	<b>-0.351</b>	<b>0.084</b>	<b>0.101</b>	<b>3.464</b>	<b>&lt;0.001***</b>
PCA2 <sup>2</sup>	0.009	0.039	0.046	0.194	0.846
<b>PCA3</b>	<b>-0.304</b>	<b>0.083</b>	<b>0.100</b>	<b>3.042</b>	<b>0.002**</b>
Simpson diversity index	0.009	0.038	0.044	0.213	0.831



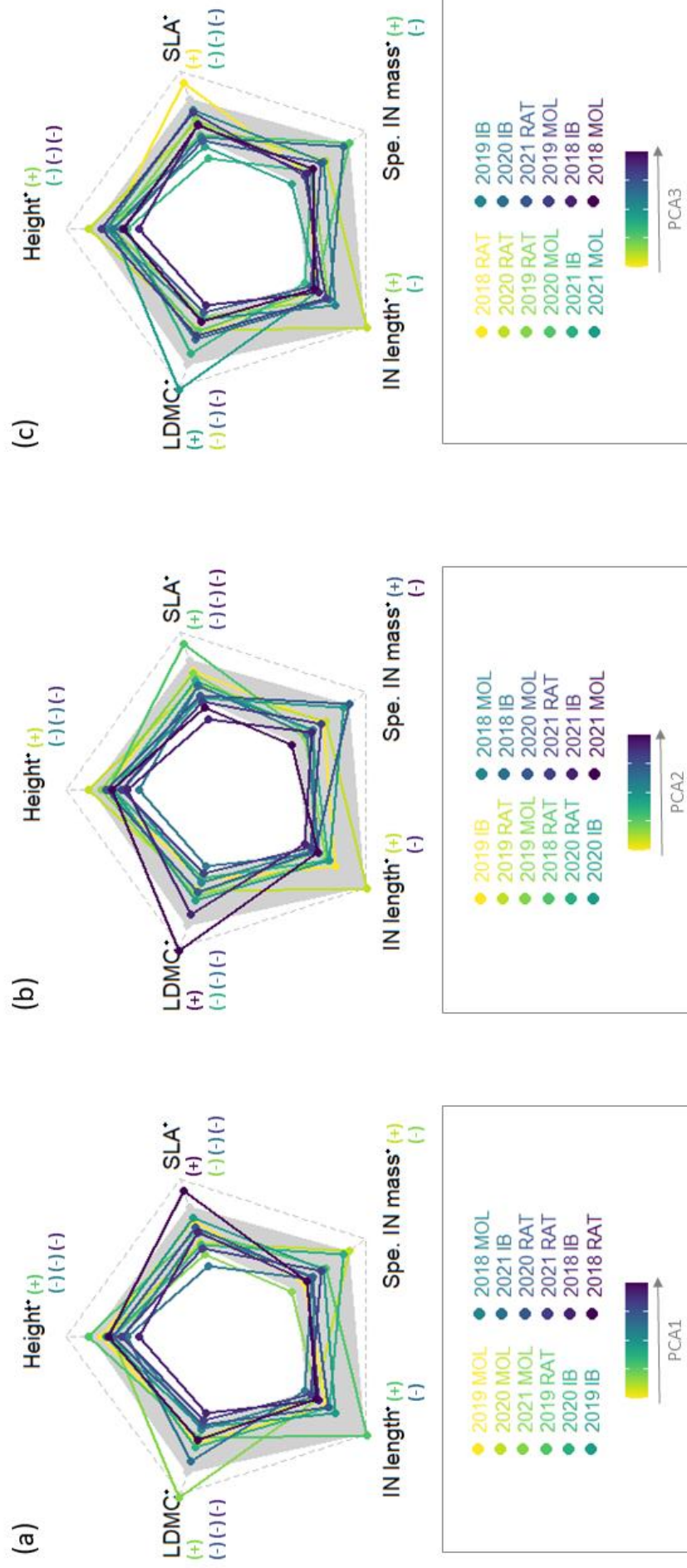
**Figure 2.** Relationships between volumes (mean of log-transformed values  $\pm$  SD) of the twelve hypervolumes calculated on aquatic plant communities through space and time, and (a-c) the three PCA axes describing abiotic conditions, (d) the Simpson diversity index. Volume indicates hypervolume size based on the five traits considered. Grey lines are the linear mixed-effect models fitted when the explanatory variable had a significant effect ( $p < 0.01$ ). PCA1 nutrient availability, PCA2 thermal conditions, PCA3 pH and oxygen concentration.

Vertical traits (*i.e.* height, SLA, and LDMC) had a contribution to hypervolume shape significantly different from null model in four aquatic plant communities through space and time, whereas it is only in two communities for horizontal traits (Fig. 3). The contribution of a trait to the shape of the hypervolume depended on the variability of that trait compared to the variability of the other traits that constituted the hypervolume. A trait that had a lower (or higher) contribution for an aquatic plant community compared to the null model was therefore significantly less (or more) variable for that community than for all the communities considered. Height contributed significantly more to hypervolume shape than expected for a community with low scores on the three PCA axes and conversely, less than expected for

communities with high scores on PCA axes 1-3 (Fig.3). LDMC contributed significantly more than expected for a community with low scores on PCA1 (nutrient availability) and high score on PCA2 (thermal conditions), and conversely less than expected for communities with high and low scores on PCA1 and PCA2 respectively (Fig.3a-b). The opposite pattern was observed for SLA, which contributed significantly more than expected for a community with high and low scores on PCA1 and PCA2 respectively, and conversely less than expected for communities with low and high scores on PCA1 and PCA2 respectively. Besides, no clear pattern of contribution to hypervolume shape was observed for horizontal traits (Fig. 3).

**Table 2.** Effects of PCA axes on centroid coordinates. IN length: internode length; Spe. IN mass: specific internode mass. This table presents the results from the full averages of the best-fitting Linear Mixed Effects models selected through AIC comparison. Bold font indicates statistical significance. Std. Error standard error; Adjusted SE standard error; Z value: test statistic; Pr(>|z|): p-value from the Z test. The “<sup>2</sup>” indicates the quadratic effect. PCA1 nutrient availability, PCA2 thermal conditions, PCA3 pH and oxygen concentration.

		Estimate	Std.Error	Adjusted SE	Z value	Pr(> z )
<b>Height</b>	<b>PCA1</b>	<b>-0.206</b>	<b>0.028</b>	<b>0.036</b>	<b>5.730</b>	<b>&lt; 0.001***</b>
	PCA1 <sup>2</sup>	0.042	0.032	0.037	1.118	0.263
	<b>PCA2</b>	<b>-0.086</b>	<b>0.026</b>	<b>0.033</b>	<b>2.626</b>	<b>0.008**</b>
	PCA2 <sup>2</sup>	0.009	0.017	0.020	0.453	0.651
	<b>PCA3</b>	<b>-0.157</b>	<b>0.026</b>	<b>0.032</b>	<b>4.804</b>	<b>&lt;0.001***</b>
	PCA3 <sup>2</sup>	-0.006	0.016	0.020	0.302	0.762
	<b>Simpson diversity index</b>	<b>-0.126</b>	<b>0.027</b>	<b>0.034</b>	<b>3.724</b>	<b>&lt;0.001</b>
<b>SLA</b>	PCA1	0.005	0.021	0.025	0.217	0.828
	<b>PCA1<sup>2</sup></b>	<b>0.131</b>	<b>0.034</b>	<b>0.041</b>	<b>3.206</b>	<b>0.001**</b>
	<b>PCA2</b>	<b>-0.215</b>	<b>0.037</b>	<b>0.044</b>	<b>4.864</b>	<b>&lt;0.001***</b>
	PCA2 <sup>2</sup>	0.021	0.028	0.031	0.682	0.495
	<b>PCA3<sup>2</sup></b>	<b>0.128</b>	<b>0.034</b>	<b>0.041</b>	<b>3.070</b>	<b>0.002</b>
	Simpson diversity index	0.004	0.018	0.021	0.202	0.839
<b>LDMC</b>	PCA1	-0.035	0.066	0.070	0.499	0.618
	PCA1 <sup>2</sup>	-0.063	0.077	0.083	0.765	0.444
	PCA2	0.037	0.064	0.069	0.543	0.587
	PCA2 <sup>2</sup>	0.065	0.061	0.066	0.984	0.325
	PCA3	0.004	0.025	0.028	0.171	0.864
	PCA3 <sup>2</sup>	-0.031	0.059	0.063	0.498	0.618
	Simpson diversity index	0.062	0.075	0.081	0.766	0.443
<b>IN length</b>	PCA1	-0.056	0.048	0.054	1.043	0.297
	PCA1 <sup>2</sup>	-0.042	0.044	0.049	0.867	0.385
	<b>PCA2</b>	<b>-0.156</b>	<b>0.045</b>	<b>0.053</b>	<b>2.899</b>	<b>0.003**</b>
	PCA2 <sup>2</sup>	0.063	0.038	0.043	1.445	0.148
	PCA3	-0.080	0.045	0.051	1.559	0.118
	Simpson diversity index	-0.008	0.023	0.027	0.319	0.749
<b>Spe. IN mass</b>	PCA1	-0.004	0.017	0.020	0.211	0.833
	PCA1 <sup>2</sup>	-0.003	0.015	0.017	0.193	0.847
	<b>PCA2<sup>2</sup></b>	<b>-0.095</b>	<b>0.026</b>	<b>0.031</b>	<b>3.090</b>	<b>0.002</b>
	PCA3	-0.043	0.038	0.042	1.015	0.310
	<b>PCA3<sup>2</sup></b>	<b>-0.161</b>	<b>0.034</b>	<b>0.041</b>	<b>3.926</b>	<b>&lt;0.001***</b>
	Simpson diversity index	0.001	0.011	0.014	0.080	0.937



**Figure 3.** Contributions of traits to hypervolume shaping. Each line corresponds to an aquatic plant community through space and time. Colors are attributed according to site\*year scores on a) PCA1, b) PCA2 and c) PCA3. Trait contribution to the shape of hypervolume is related to its variability relatively to the four other traits. The grey area corresponds to the confidence interval of trait values built from the simulated hypervolumes all years and site considered, by selecting the 2.5 and 97.5 percentiles of simulated values. Stars indicate when the observed value of trait contribution is significantly higher (+) or lower (-) than expected through simulations. IN length: internode length; Spe. IN mass: specific internode mass. PCA1 nutrient availability, PCA2 thermal conditions, PCA3 pH and oxygen concentration.

## Discussion

### *Convergence of community strategies along abiotic filter strengthening*

Through our study at the aquatic community level, we demonstrate as expected, an effect of the interannual variations in the abiotic filter on plant strategies based on hypervolume comparisons through space and time. In particular, the variability of strategies is affected (hypervolume size), together with the similarity between communities.

Reduction together with displacements in species multidimensional trait space have essentially been shown so far, at local scales and on the very short term (two years maximum) in response to water availability (Rodríguez-Alarcón, Tamme and Carmona, 2022, Carmona *et al.*, 2015, but see Rota *et al.*, 2017 for three years sampling), but never within aquatic systems. Through our approach, we demonstrate that aquatic communities under similar abiotic constraints display similar strategies, suggesting that individual functional responses are homogeneous at the regional and time scales studied (King *et al.*, 2017). This short-term response suggest the occurrence of trait plasticity rather than local adaptation, that would enable communities to respond to nutrient availability, rising temperatures, and increase in pH and O<sub>2</sub> concentration (Matesanz *et al.*, 2010; Arnold *et al.*, 2019). Indeed, previous studies showed a positive association between phenotypic plasticity and temporal variability in temperature and precipitation (Vázquez *et al.*, 2017), especially if it relates to inter-annual variations (Stotz *et al.*, 2021).

We highlight a linear decrease in strategies variability within communities (as reflected by the volume of their hypervolume) along spatio-temporal gradients of temperatures, nutrients availability, and pH and oximetry, with no additional effect of community diversity. In particular, the strengths of their effects (*i.e.* filter stringency) on strategies variability are similar. Indeed, we evidenced quite important variations

across sites\*years in temperatures (3.35 – 6.26°C), N–NH<sub>4</sub><sup>+</sup> concentration (45.97 - 1383.35 µg.L<sup>-1</sup>) and oximetry (6.19 - 12.96 mg.L<sup>-1</sup>). The aquatic system is therefore multi-constrained, which could explain its particular sensitivity to climate change through the modification of several abiotic parameters (Santamaría, 2002). Besides, we originally find that the relationships between strategies variability and filter stringencies are not quadratic but linear, suggesting a gradual response to the increasing values of temperatures, nutrient availability, pH and oximetry.

As a conclusion, hypervolumes are a powerful tool to infer community strategies in response to rapid environmental changes. Interannual abiotic variations during four years are already sufficient to detect rapid responses towards resistance (tolerance or avoidance), likely relying on phenotypic plasticity. In particular, we showed the importance of nutrient availability and temperature variations for the functional structure of aquatic plant communities. This result raises questions about the possible adaptation of communities at longer term, especially under a scenario where extreme temperatures get more frequent, along with a decrease in precipitations, as already observed in the Iles Kerguelen (*i.e.* abiotic filters strengthening). Indeed, several studies have found positive relationships between phenotypic plasticity and mean annual temperatures, meaning that plants from cold regions are less able to cope with the increasing frequency of extreme climatic events (Stotz *et al.*, 2021). Furthermore, the decrease in strategies variability in response to the intensities of the three detected abiotic filters suggests the existence of an adaptive phenotype in response to each of them. Therefore, one could wonder about the possibility of developing a phenotype that can enable species to respond to their simultaneous strengthening.

*Importance of traits related to plant metabolism in response to rising temperatures, nutrients availability and water chemistry*

Hypervolumes can help to precise the functional response of individuals to abiotic filters within communities. The response of traits to the three evidenced spatio-temporal gradients of abiotic parameters (*i.e.* temperature, nutrient availability, and pH and dissolved oxygen concentration) does not confirm our initial hypothesis stating that the mean values of vertical and horizontal traits would respectively decrease and increase with abiotic filter strengthening, and conversely with less stringent abiotic filter. The shape of mean response is actually trait-dependent, with no connection with the trait category (*i.e.* clonal or shoot/foiar). It appears instead that traits related to plant metabolism (SLA, specific internode mass) and to 3D space exploration (height, internode length) respectively display a quadratic or a linear response to the three spatio-temporal abiotic gradients (with the exception of the linear relationship between SLA and temperature).

First, the evidenced quadratic relationships between SLA and specific internode mass and abiotic filters would be due to the efficiency of underlying enzymatic reactions of metabolism, which usually display optimums depending on habitat conditions (Foyer et al., 2002; Salvucci and Crafts-Brandner, 2004). In the literature, SLA is usually reported as increasing linearly with nutrient availability to allow individuals to switch towards an acquisitive strategy of resources (Poorter and de Jong, 1999). The decrease in SLA that we evidenced could actually rely on this principle and may be related to the balance between  $\text{N-NH}_4^+$  and  $\text{N-NO}_3^-$ . Indeed, although the overall nutrient availability was higher, this balance changed, with lower  $\text{NH}_4^+$  concentration, *i.e.* probably less bioavailable nitrogen for plant growth. Beyond the switch point of the relationship, nutrient concentration is very high if not extreme, causing turbid water, and explaining

the investment of individuals in larger leaves to support light acquisition, especially under higher nutrient availability as demonstrated by Freschet, Swart and Cornelissen (2015). Similarly, specific internode mass increases or decreases depending on whether temperature stimulates (mild temperature, higher carbohydrates storage) (Herrmann et al., 2019) or constraints metabolism efficiency (stressful temperature, lower carbohydrates storage) (Lippmann et al., 2019). Besides, SLA and specific internode mass are related to pH and oximetry, with an opposite pattern of response. It is generally agreed that pH controls the available forms of dissolved inorganic carbon ( $\text{CO}_2$  vs.  $\text{HCO}_3^-$ ) (Burton, 1987), thus affecting carbon uptake and photosynthesis (Titus and Stone, 1982). Since aquatic plants have higher affinities for  $\text{CO}_2$  than for  $\text{HCO}_3^-$  (Allen and Spence, 1981), higher pH induce stressful conditions resulting in higher SLA and resource storage in clonal internodes to tolerate them. However, higher oxygen concentration slows down the carbon fixation (Van et al., 1976), thus resulting in lower carbohydrates storage. As a consequence, individuals invest in higher SLA values to support carbon uptake through larger exchange areas.

Second, we do not evidence any positive effects of abiotic filters on height and internode length. Indeed, height linearly decreases in response to all abiotic filters, whereas internode length responded to temperature only. Overall, this suggests a reduced plant growth in all cases: rising temperatures, nutrient availability, pH and oximetry. As a consequence, it would decrease the light and space acquisition, leading to a loss of competitiveness of the species within communities (Grace and Tilman, 1990).

Third, we expected vertical and clonal trait convergence towards values that allow individuals to better cope with environmental changes. We confirm this hypothesis for height, but not for SLA and LDMC. Indeed, SLA values converged at higher temperatures and lower nutrient availability (and



conversely), whereas LDMC displays an opposite pattern of response. In clonal traits however, we do not evidence a clear pattern of variability. More precisely, the observed aerial traits responses are in line with previous studies (Cornwell and Ackerly, 2009; Read et al., 2014). Indeed, plant height is integrative of the response to the three tested gradients and follows the expectations of values divergence under mild conditions, and conversely, of values convergence when the constraint increases. We actually highlighted a convergence towards a smaller phenotype (height, SLA), probably related to a passive response of growth delay because of the limiting conditions (rather than an active avoidance strategy) (Jenks and Hasegawa, 2008; Seleiman, 2019; Gong et al., 2020). This convergence in SLA and height towards lower means in response to rising temperatures, is in line with previous studies stating that inter-annual climatic variations result in higher plasticity in traits related to size or allocation (Pigliucci et al., 1999; Alpert and Simms, 2002; Botero et al., 2015). Consequently, plasticity appears especially high on vertical traits compared to the horizontal ones in case of both rising temperatures and nutrient availability.

Furthermore, it would be interesting to determine whether the evidenced strategies are adaptive or not, by evaluating the consequences on aquatic community performances. Indeed, the response of aquatic plants to the abiotic filters strengthening should have important consequences for their performance. For instance, inter-annual temperature variability have been shown to cause differences of 45% to 1160% in plant biomass between two years, in boreal lakes (Rooney and Kalff, 2000).

## Conclusion

To conclude, our study may inform on future functional changes in aquatic plant communities of the Iles Kerguelen, and more widely of the whole sub-Antarctic region where similar species can be found (Bergstrom and Selkirk, 2000; Chau et al.,

2021), by explicitly relating nutrient availability, temperature, and pH and oxymetry and key functional traits. In particular, our study underlines the importance of accounting for the warming temperature (Khare et al., 2020; Harrison, 2020; Chaudhry and Sidhu, 2022), as it influences changes in varying traits either linearly or through quadratic relationships. The mechanism underlying the evidenced short-term variation in traits is likely to correspond to plasticity, but as temperatures keep warming up (Bernstein et al., 2008), we expect either local adaptation or population disappearance to ultimately occur. Extending the studied period would thus be interesting to observe emerging longer-term trends in the functional responses of aquatic plant communities. In addition, further investigations are needed to precise response strategies at the species level, and to get a better picture of the processes underlying plant community assembly in this context of abiotic filter strengthening.

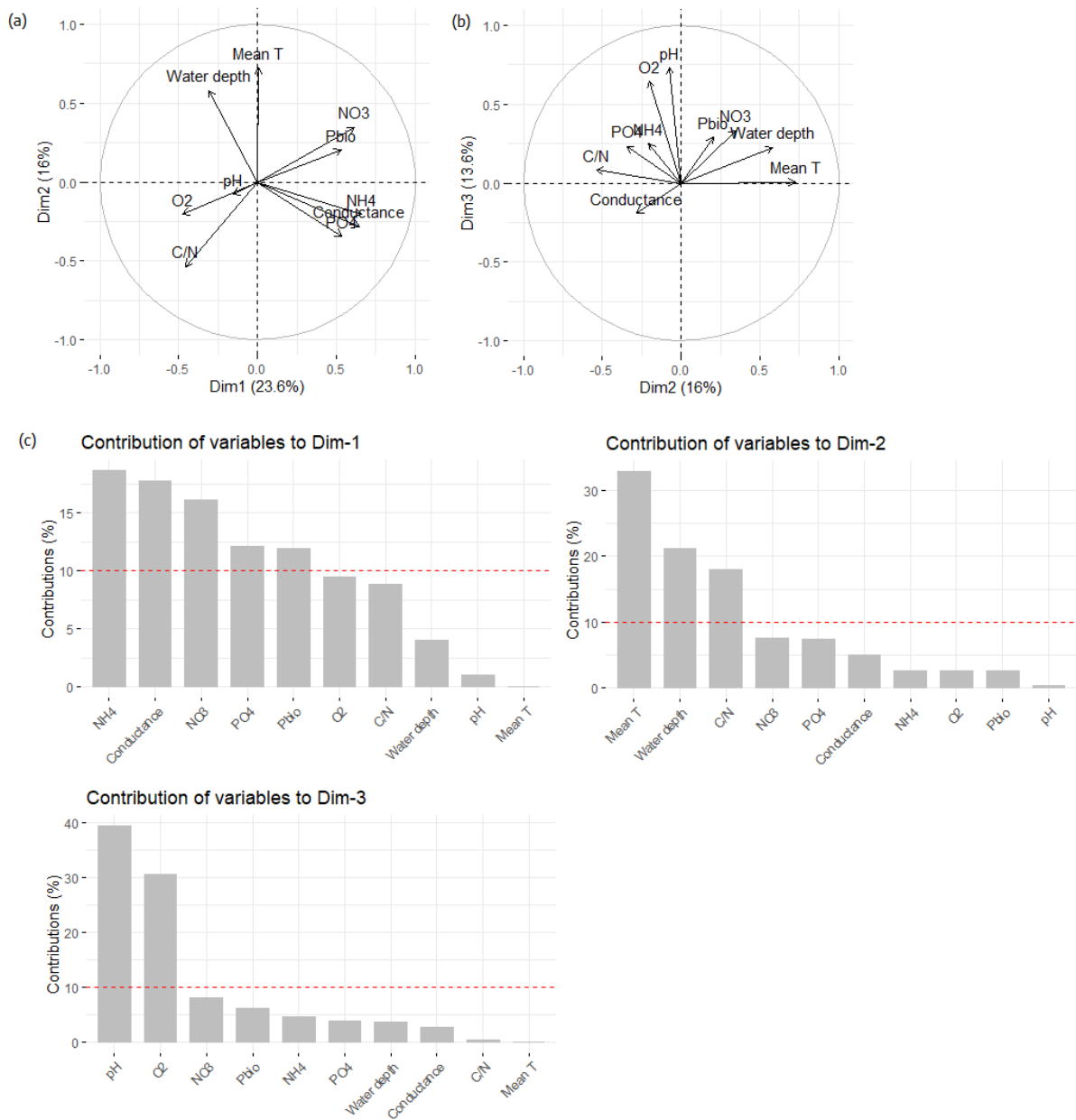
## Acknowledgements

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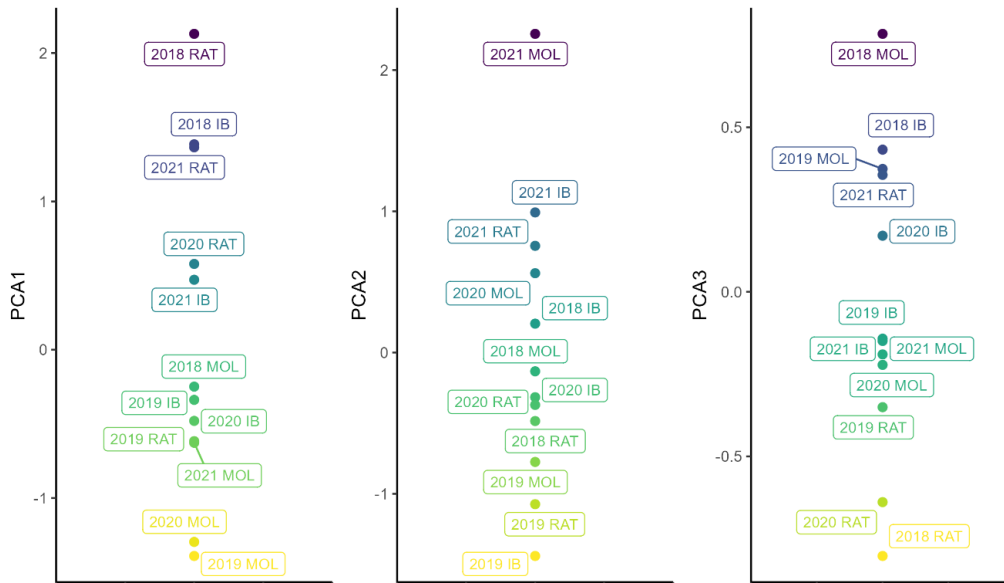
## Supplementary Information

**Table S1.** Mean abiotic parameters of ponds through space (site) and time (year). 'IB' Isthme Bas, 'MOL' Molloy, 'RAT' Cap Ratmanoff.

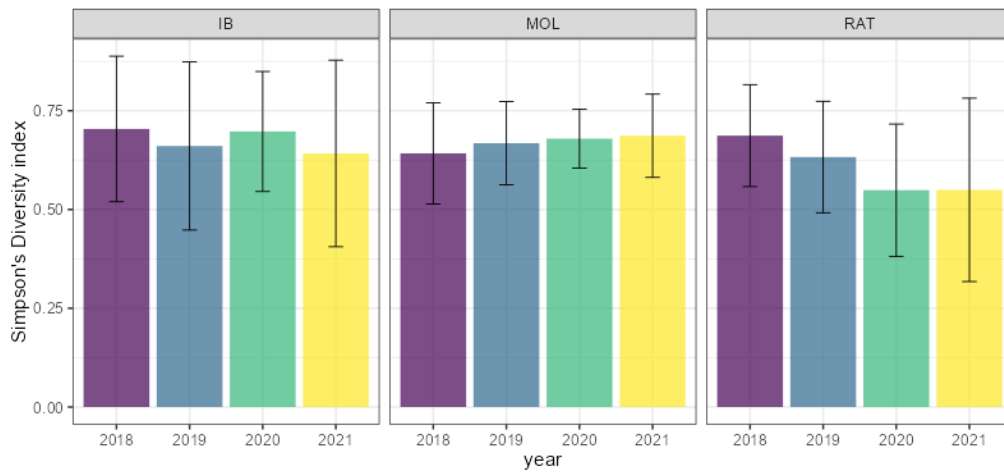
Year	Site	Mean Temp. (°C)	Water depth (cm)	pH	Conductance (mS.cm <sup>-1</sup> )	Dissolved oxygen (mg.L <sup>-1</sup> )	N- NH <sub>4</sub> <sup>+</sup> (µg.L <sup>-1</sup> )	N- NO <sub>3</sub> <sup>-</sup> (µg.L <sup>-1</sup> )	P- PO <sub>4</sub> <sup>3-</sup> (µg.L <sup>-1</sup> )	P <sub>bio</sub> (mg.g <sup>-1</sup> )	C/N
2018	IB	3.70	15.85	7.11	227.31	9.70	190.78	250.73	17.19	1.21	12.12
	MOL	3.35	14.36	7.22	132.54	12.96	126.11	164.20	3.50	1.06	12.98
	RAT	3.35	8.50	6.80	251.01	6.19	678.85	180.17	22.73	1.09	11.66
2019	IB	3.80	14.49	6.81	197.59	11.07	70.70	73.10	37.65	0.45	16.64
	MOL	3.50	16.95	6.94	89.72	12.96	102.53	59.50	9.26	0.79	16.33
	RAT	3.47	14.17	6.65	164.22	11.89	349.80	51.07	12.63	0.59	15.32
2020	IB	4.93	19.90	7.14	206.47	11.56	60.07	74.13	24.61	0.48	15.48
	MOL	4.74	23.13	6.82	112.74	11.57	45.97	35.17	4.15	0.56	13.71
	RAT	4.79	14.99	6.54	241.19	10.89	822.30	42.55	17.85	0.54	12.89
2021	IB	5.65	21.53	6.95	209.90	9.21	130.57	145.07	20.92	0.55	11.79
	MOL	6.26	27.73	6.56	83.05	10.41	91.00	154.04	7.82	0.62	11.80
	RAT	5.78	13.29	7.13	217.71	10.02	1383.35	170.07	23.03	0.81	11.11



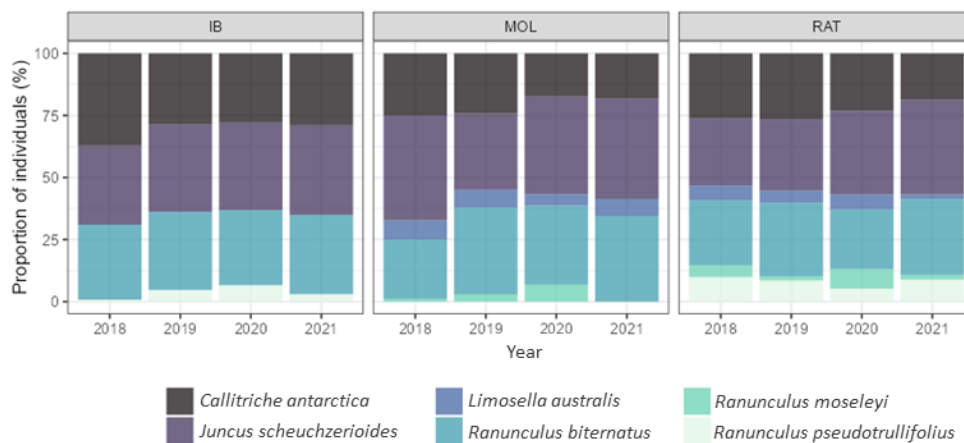
**Figure S1.** Principal Component Analysis performed on abiotic parameters, and showing their scores along a) axes 1 and 2, b) axes 2 and 3. c) Contributions of abiotic parameters to axes 1 to 3. Mean T – mean annual water temperature, O<sub>2</sub> – dissolved oxygen, P<sub>bio</sub> – bioavailable P. All abiotic data averaged at the pond scale were included (*i.e.* all sites and years combined) for the PCA, and then the abiotic parameter scores on the PCA axes were averaged at the site\*year scale.



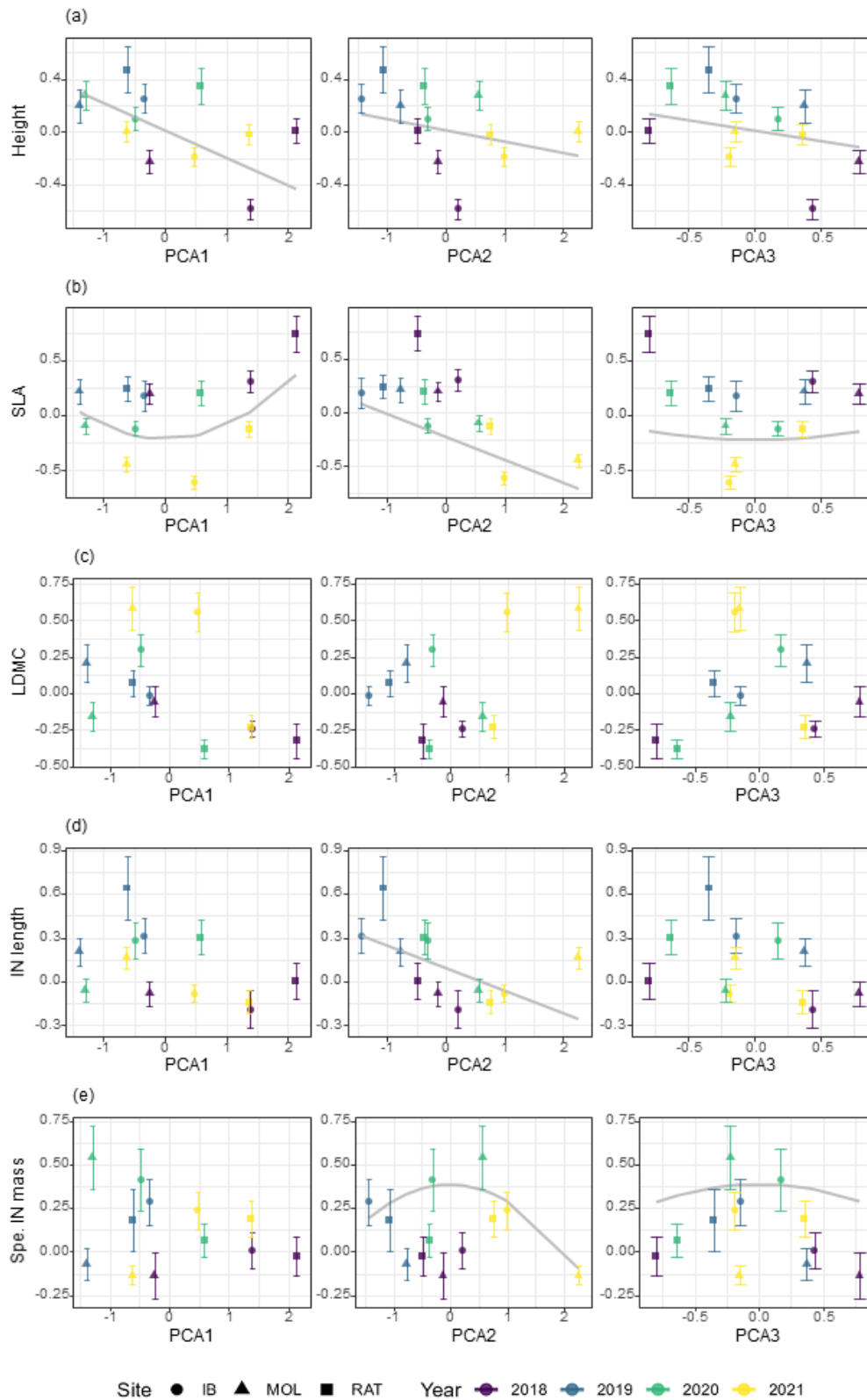
**Figure S2.** Mean coordinates of each site for each year along the PCA axes 1 to 3. PCA1 nutrient availability, PCA2 thermal conditions, PCA3 pH and oxygen concentration.



**Figure S3.** Mean Simpson diversity index of each site for each year.



**Figure S4.** Species proportions of individuals used to build the hypervolume of each site for each year.



**Figure S5.** Relationships between centroid coordinates (mean  $\pm$  SD of the simulated hypervolumes) of the twelve hypervolumes calculated on aquatic plant communities through space and time and the three PCA axes describing abiotic conditions. (a) height, (b) SLA, (c) LDMC, (d) IN length: internode length and (e) Spe. IN mass: specific internode mass. Grey lines are the results from the full averages of the best-fitting Linear Mixed Effects models selected through AIC comparison when the explanatory variable had a significant effect ( $p < 0.01$ ). PCA1 nutrient availability, PCA2 thermal conditions, PCA3 pH and O<sub>2</sub> concentration.

## Macrophyte strategies and performance in response to thermal constraints in a context of plant-plant interactions. The example of the plant species from the Iles Kerguelen.

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Article Informations	Abstract
Article history:	<p>Climate change is likely to alter directly the filter of thermal stress, and indirectly the filter of plant-plant interactions, both influencing the structure of plant communities especially within aquatic ecosystems that are especially sensitive to climate change. Plant responses to these two filters are usually studied separately in the literature although individuals are simultaneously facing these two constraints <i>in natura</i>. We thus suggest to study macrophyte response to temperature in a context of plant-plant interactions taking the mean and the variability of the response into account, together with the possible modifications in trait relationships. In this study, we investigated the responses to plant-plant interactions × temperature of three macrophyte species originating from the Iles Kerguelen, and living in pond ecosystems. Temperature warming is there especially rapid, while the species-poor communities of macrophytes, are remarkably adapted to cool temperatures. Ramets of the three target species were grown under different conditions of temperature × plant-plant interactions (no interaction, intra-, and interspecific interactions). We characterized species responses through different functional [vertical (<i>i.e.</i> leaf, and root) and horizontal (clonal)], and performance traits, and determined the variations of their mean and variability. Furthermore, we assessed the modifications in trait co-variations. Contrary to our expectations, we did not demonstrate an intermediate strategy between supporting competitive abilities and thermal resistance in aerial and root traits, and clone traits values did not increase. Modifications in individual strategies were mostly recorded in response to temperature only, and involved different traits depending on the species, showing that there is not universal strategy of resistance to thermal variations. We also highlighted that both coexistence mechanism and habitat filtering operated to determine the variability of individual strategies. Besides, the sign and the intensity of a few trait co-variations changed, but in response to either temperature or plant-plant interactions with no interactive effect of these two constraints. Finally, regarding clone performance, rising water temperatures up to 18°C did not either stimulate or prevent species dry mass production. As a conclusion, this study gives new insight about the thermal tolerance of species within communities and could serve as basis to improve prediction models of species redistribution in relationship with rising temperatures.</p>
In prep	
Keywords:	
Functional trait	
Individual performance	
Trait co-variations	
Intraspecific trait variability	

## Introduction

Rising temperatures affect ecosystems and cause a major crisis for biodiversity (Khare et al., 2020; Harrison, 2020). Understanding the mechanisms underlying the dynamics of plant communities appears crucial to predict their fate in this context (McGill et al., 2006). This climate change is likely to alter directly the filter of thermal stress, and indirectly the filter of plant-plant interactions which become unpredictable (*i.e.* does not support the Stress Gradient Hypothesis for instance, Ploughe et al., 2019; Souza et al., 2021). Both filters are known to structure plant communities by determining the individuals which display the functional traits (morphological, physiological, phenological characteristics - Violle et al., 2007) that enable them to hold in the community. As sessile organisms, plants are simultaneously subjected to both filters in their habitat, while their responses are generally studied separately in the literature (e.g. Greulich and Bornette, 1999; Riis et al., 2012; Bittebiere et al., 2019), subsequently limiting the explanatory power of studies regarding the response of plant species assemblages to climate change. In particular, intraspecific trait variability should highly contribute to the sustainability of plant communities (Sultan, 2000; Violle et al., 2012). Indeed, several studies have recently shown that intraspecific trait variability account for 30 to 40% of trait variance within a community, supporting species resistance to environmental filters (Jung et al., 2010; Albert et al., 2010a). Not taking this variability into account in community ecology studies, would then lead to false interpretations of community assembly mechanisms.

Most species in plant communities are clonal *i.e.* able of producing newly genetically identical ramets (an erected shoot with its leaves and roots) connected through plagiotropic stems (van Groenendael et al., 1996). Clonal plants can buffer the effects of thermal stress and negative biotic interactions through plastic modifications of their phenotypes in the vertical and horizontal

directions (Sultan and Bazzaz, 1993; Novoplansky, 2009). These modifications will first affect the average values of traits. Indeed, an increase in temperature beyond the tolerance range of ramets induces a decrease in height, leaf area, and concentration of photosynthetic pigments (Shah and Paulsen, 2003; Chalanika De Silva and Asaeda, 2017), whereas the opposite response is observed under competition (Novoplansky, 2009; Bittebiere et al., 2012). In the horizontal direction, elongation of connection internodes has been observed under stressful or competitive conditions as an escape behavior (Slade and Hutchings, 1987a; Bittebiere et al., 2012) together with increased storage (e.g. of carbohydrates) in connections for the growth of future ramets (Cheplick and Gutierrez, 2000). Thus, the intensification of thermal stress should lead to an increase in average values of horizontal traits, but to intermediate average values of vertical traits due to the antagonism of responses to thermal stress and plant-plant interactions.

Second, trait variability is also likely to be altered in response to temperature and plant-plant interactions (Cornwell and Ackerly, 2009). When the risk of exposure to the high thermal limits of plant individuals is high, thermal stress would reduce the diversity of performing phenotypes over time, which can be shown through the convergence of traits values within species (*i.e.* reduced trait variability) (Read et al., 2014; Michaletz et al., 2014). In response to plant-plant interactions, trait distributions at the intraspecific level, would either converge or diverge following two coexistence mechanisms: the fitness equalization or the niche stabilization. On the one hand, individuals invest in the maximization of trait values supporting their competitive ability such as high height or specific leaf area (reduced trait variability, *i.e.* fitness equalization) (Chesson, 2000; Mayfield and Levine, 2010; Nagashima and Hikosaka, 2011). On the other hand, individuals plastically modify their traits values to avoid niches overlapping (increased trait variability, *i.e.* niche stabilization) (Kraft et al., 2015a;

Turcotte and Levine, 2016). Both patterns of trait variability can be observed simultaneously in the vertical and horizontal directions. Indeed, Herben and Goldberg (2014) showed that within species-rich communities, individuals experienced a high variability of clonal traits (*e.g.* number of branches, internode length) related to the acquisition of space, together with a low variability of traits associated with growth and resource acquisition (*e.g.* height, leaf area). Thus, under rising temperatures in the context of plant-plant interactions, vertical traits (aerial and root traits) are expected to be less variable and converge towards values that confer thermal resistance and competitive abilities, whereas horizontal traits (clonal traits) values are expected to be more variable to colonize more favorable micro-habitats.

It is generally agreed that species cannot concomitantly support two opposite strategies that require too much energy (Wright et al., 2004). Individuals thus coordinate different functions to maximize their performance with a minimal energy investment (Murren, 2002; De Kroon et al., 2005) through the co-variations of their traits at the whole plant level (*i.e.* across plant organs within individuals). This implies trade-offs between traits related to different strategies (Wright et al., 2004; Koehler et al., 2012; Molina-Montenegro et al., 2012; Reich, 2014; Díaz et al., 2016; Bucher et al., 2019) or positive co-variation between traits that support the same strategy (Kerkhoff et al., 2006; Freschet et al., 2010; Liu et al., 2010). For instance, trade-off between traits related to frost tolerance and growth rate (Koehler et al., 2012; Molina-Montenegro et al., 2012; Bucher et al., 2019) results from the plant need to find an intermediate strategy between stress tolerance and competitive ability. Moreover, positive co-variations between aboveground and belowground organs, with respect to the acquisition, have been found in some studies (co-variation between SLA and specific length of roots, Withington et al., 2006; covariation between leaf nitrogen content and the amount of nitrogen in stems and roots, Kerkhoff et al., 2006; Liu et al.,

2010). The sign and the intensity of these co-variations are likely to change in response to environmental conditions, especially in connection with climate changes (Wright et al., 2004, 2005; Sgrò and Hoffmann, 2004; Pellissier et al., 2018; Maccagni and Willi, 2022), although studies remain rare. For instance, the intensity of leaf–root trait relationships can vary depending on the drought (Liu et al., 2010), and the soil freezing conditions (Craine et al., 2005). In addition, the sign of the relationships between pairs of traits can change depending on the habitat (Reich et al., 2003). Therefore, if plants have to adjust their thermal resistance while maintaining their competitive abilities, we can expect the intensity and the sign of their trait co-variations to be modified, to coordinate their responses and ultimately support their performances.

Aquatic systems have become one of the most vulnerable habitats to climate change (Sala et al., 2000; Lacoul and Freedman, 2006; Bates et al., 2008; Jin et al., 2009), while their communities of plants (*i.e.* macrophytes) are essential for a large variety of organisms (Keddy, 2010). In this study, we investigate the responses to plant-plant interactions  $\times$  temperature of three macrophyte species originating from the Iles Kerguelen, and living in pond ecosystems. Temperature warming is there especially rapid (Walther et al., 2002), while the species-poor communities of macrophytes, are remarkably adapted to cool and stable temperatures (Bergstrom and Chown, 1999). These communities would therefore be especially sensitive to current thermal changes, thus constituting a relevant model for our experimental study. Ramets of the three target species were grown under different regimes of temperature  $\times$  plant-plant interactions (no interaction, intra-, and interspecific interactions). We measured different functional [vertical (*i.e.* leaf, and root) and horizontal (clonal)], and performance traits, to determine the variations of their mean and variability. Furthermore, we assessed the modifications in trait co-variations. Based on this experimental



approach, we specifically tested the following hypotheses:

- (i) Clonal traits should experience an increase in their average values to limit competition and find more suitable abiotic conditions, while aerial and root traits should display intermediate values since they should simultaneously be involved in thermal resistance and competitive ability.
- (ii) Under plant-plant interactions  $\times$  temperatures, aerial and root trait values should converge, whereas clonal traits values should diverge.
- (iii) The intensity and the sign of co-variations between traits should change in response to both rising temperatures and plant-plant interactions, to adjust ramet strategies to their changing environment and maximize their performance.

## Materials and methods

### *Biological material*

We studied the responses to plant-plant interactions  $\times$  temperature of three aquatic plant species that can be found within the shallow freshwater ponds of the Iles Kerguelen (Southern Indian Ocean, 49°20'00''S, 69°20'00''E): the Plantaginaceae *Callitriche antarctica* Engelm, and two Ranunculaceae species: *Ranunculus pseudotrullifolius* Skottsbo., and *R. moseleyi* Hook.f.

Ramets of these three species were used as targets and neighbors in our experiment, while we additionally used ramets of the Scrophulariaceae *Limosella australis* R.Br., the Juncaceae *Juncus scheuchzerioides* Gaudich., and of *R. biternatus* as neighbors only. Target species are hydrophytes whereas the two other species are helophytes. Nevertheless, the six species can all locally co-occur in the field. These species are perennial plants displaying a clonal network structure, *i.e.* plants are composed of related ramets (shoots with

leaves and roots) that are connected through plagiotropic stems (van Groenendael et al., 1996). They display contrasted morphologies with the three *Ranunculus* species and *L. australis* forming rosettes, *J. scheuchzerioides* having erected stems, and *C. antarctica* showing floating canopies.

All plants were collected from the field at the start of the growing season in November 2020, from different localities, to maximize their genetic variability (Appendix 1). For each treatment and target species, a unique genotype was assigned to each replicate (10 genotypes per species in total) to control for genotype effect (de Kroon et al., 1994) and measure plasticity as genotype reaction norm. We then collected 10 clonal fragments per target species, composed of nine connected ramets. These were then cultivated in pots, on a substrate composed of 80% compost and 20% sand, and kept at 13°C with 12/12 h lighting for three weeks, to suppress potential maternal effects on their growth.

All plants were washed and standardized in size before planting. For all species, the planted unit consisted in one adult ramet with its roots and leaves, and one internode of connection that contained reserves to facilitate the early growth (Stuefer and Huber, 1999).

### *Experimental treatments*

This experiment aims at determining in the three target species, the functional responses of plants concomitantly submitted to interactions with their neighbors and to a temperature gradient, and how these responses ultimately affect plant performances.

To fulfill these objectives, we set up three types of plant cultures for each studied species *i.e.* two with interactions (either intra- or interspecific), and a no-interaction control. Each type of plant culture was grown at three water temperatures: one control of 13 °C (mean water temperature recorded in the ponds of the Iles Kerguelen during the growth

season – see Douce et al. submitted), 8 °C (cold treatment) and 18 °C (heat treatment). In total, nine treatments were tested per target species (three temperatures × three interaction modalities). Each treatment was replicated 10 times.

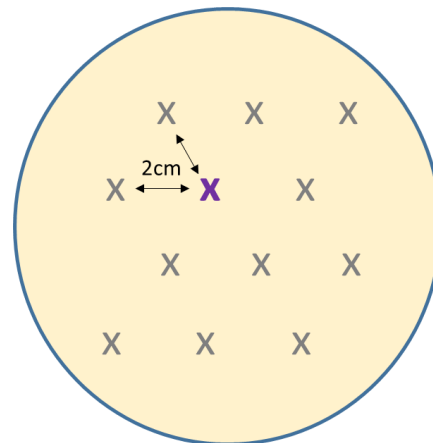
### Experimental design

For each target species, experimental cultures were conducted in pots (10.5 cm diameter × 8 cm height) on a substrate composed of 80% compost (N:250g/m<sup>3</sup>, P<sub>2</sub>O<sub>5</sub>: 120 g/m<sup>3</sup>, K<sub>2</sub>O: 80 g/m<sup>3</sup>) and 20% sand, in the climatic chambers of the experimental platform of the Iles Kerguelen. In the no-interaction control, one target ramet and its connection internode was planted alone in the center of the pot. Under interactions, 12 ramets were planted 2 cm apart of each other, following a hexagonal design that allows balanced interactions (Birch et al., 2007) (Fig. 1). The most central position was assigned to the target ramet, while the 11 other positions were occupied either by conspecific neighbors (*i.e.* monoculture, intraspecific interactions) or by ramets of the six studied species (interspecific interactions) with their positions being assigned in a balanced and random way (two ramets per species). Neighbors were planted 11 days before target ramets, so that they were well established. During this delay, cultures were kept at 13°C. After target ramet transplantation, cultures were left for two more days at 13°C, to allow their recovery from transplantation before they endure treatments.

Pots were randomized regularly during the course of the experiment. Cultures were maintained at 12/12 h lighting throughout the experiment. Water was changed every two weeks to avoid high level of nutrient concentrations due to nutrient leaching from substrate, and to better approach the pond nutrients conditions *in situ*. Water level was maintained throughout the experiment at one centimeter above the soil surface so that hydric conditions fit both hydrophyte and helophyte species.

### Trait measurements

Plants were harvested after 73 days of cultivation. At harvest, the transplanted target ramet had vegetatively propagated, to produce a whole clonal fragment *i.e.* related ramets connected through horizontal stems. All plants were carefully washed before measurements.



**Figure 1.** Ramets plantation following a hexagonal pattern in pots. In violet: target ramet. Neighbors (in grey) were either conspecific (intraspecific interactions) or heterospecific (interspecific interactions)

For each target species, different trait measurements were performed at both the clonal fragment and the ramet levels.

- 1- Clonal fragment level – We measured both the number of connected ramets, and the total dry mass of the clonal fragment to evaluate the clone performance.
- 2- Ramet level – One mature and newly produced ramet was randomly selected to measure functional and performance traits. The functional traits were chosen to characterize ramet growth response to both temperature and plant-plant interactions (Hutchings et al., 1997; Cornelissen et al., 2003; Butterfield and Callaway, 2013; Bittebiere and Mony, 2015; Meng et al., 2015; Gray and Brady, 2016; Loughnan and Gilbert, 2017; Wang et al., 2018; Bittebiere et al., 2019; Colom and Baucom, 2020; Dostálek et al., 2020). Different categories of traits were investigated, that is (i) aerial traits with height, Specific Leaf Area (SLA), and

Leaf Dry Matter Content (LDMC) to estimate the resource acquisition; (ii) clonal traits with internode length and specific internode mass (ratio of the dry mass and the length of one internode) to evaluate both space exploration and occupation, and resource storage; (iii) and root traits with maximum root length and specific root mass (ratio of the dry mass and the length of root) to evaluate the resource acquisition and conservation. One mature and healthy leaf of the selected ramet was randomly chosen to assess SLA and LDMC following (Cornelissen et al., 2003). We also measured ramet performance resulting from its growth through its total dry mass.

All dry masses were measured after drying plant parts for 48 hours in oven at 65 °C.

### Data analyses

#### *Responses of trait mean and variability to temperature × plant-plant interactions*

We aimed to determine which traits were involved in the biotic and abiotic resistance of the three target species. On the one hand, we tested for the interactive effects of temperature and plant-plant interactions (both categorical variables), on the values of functional and performance trait, based on a linear model procedure [glm.nb function for the number of ramets (“MASS” package, Ripley et al., 2018), and lm function for all other traits (“stats” package, Bolar, 2019)]. Trait data were previously normalized (log or square-root transformations) when needed. We applied a stepwise model reduction based on the AIC criteria (MuMIn package, Bartoń, 2013) on the full model to select the most parsimonious one, on which we performed the ANOVA test (type II). On the other hand, the exact same procedure was applied to test for the response of trait variability to temperature × plant-plant interactions, using residuals that were manually calculated as response variable (*i.e.* the difference between each trait value and the mean value of the corresponding culture treatment). In addition,

when the effects of temperature and plant-plant interactions were significant, differences in trait means and variability among treatments were determined using *post-hoc* tests based on the glht function (“multcomp” package, Hothorn et al., 2022).

#### *Temperature × plant-plant effects on co-variations between traits*

We aimed to assess in each target species, the combined effects of temperature and plant-plant interactions on the relationships between all pairs of the studied functional traits (in terms of direction and intensity). In particular, to assess the co-variations between trait A and trait B, we tested for the response of trait B to the interaction between trait A, temperature and plant-plant interactions; and reciprocally with trait B as explanatory variable. Trait data were previously normalized (log or square-root transformations) when needed. We performed an ANCOVA test (type II) on the most parsimonious model that was determined based on the AIC criteria (MuMIn package).

All statistical analyses were carried out with R 4.0.3.

## Results

### *Trait mean and variability responded to either temperature or plant-plant interactions depending on the species*

On the one hand, with the exception of LDMC, we observed a mean plastic response of aerial, root, or clonal traits depending on the species, to either plant-plant interactions (specific root mass only, in *Ranunculus moseleyi*) or temperature, with no significant interactions of these two factors (Table 1). More specifically, we did not confirm our hypothesis stating that vertical (aerial and root) and clonal traits should respectively display intermediate and higher means with increasing temperatures under plant-plant interactions. Most detected plastic responses were related to temperature influence only, involving different categories of traits

**Table 1.** Responses of the trait mean and variability to temperature  $\times$  plant-plant interactions. Responses were assessed through ANOVAs performed on the most probable models determined based on the AIC selection method, and testing the interactive effects of temperature and plant-plant interactions in each target species, and for each trait on (i) its mean values, and on (ii) its residuals (to evaluate the response of trait variability). Some relationships were not tested because of a lack of observations (ramet mortality), and thus do not appear in the table.

Trait	<i>n</i>	Species	(i) Explanatory variables of selected model Values differences			(ii) Explanatory variables of selected model Residuals differences		
			Temperature	Plant-plant interactions	Temperature $\times$ Plant-plant interactions	Temperature	Plant-plant interactions	Temperature $\times$ Plant-plant interactions
<i>Aerial traits</i>								
Height	59	<i>C. antarctica</i>	-	-	-	-	-	-
	53	<i>R. moseleyi</i>	<b>8.03<sub>1</sub>***</b>	-	-	-	-	-
	49	<i>R. pseudotrullifolius</i>	-	-	-	<b>14.15<sub>2</sub>***</b>	<b>3.99<sub>2</sub>*</b>	-
SLA	56	<i>C. antarctica</i>	-	-	-	-	-	-
	46	<i>R. moseleyi</i>	<b>9.50<sub>1</sub>**</b>	-	-	-	<b>3.11<sub>2</sub>.</b>	-
	48	<i>R. pseudotrullifolius</i>	<b>5.76<sub>1</sub>**</b>	-	-	-	-	-
LDMC	55	<i>C. antarctica</i>	<b>2.70<sub>2</sub>.</b>	-	-	<b>3.76<sub>2</sub>*</b>	-	-
	49	<i>R. moseleyi</i>	-	<b>2.39<sub>2</sub><sup>n.s.</sup></b>	-	-	-	-
	47	<i>R. pseudotrullifolius</i>	-	-	-	-	-	-
<i>Clonal traits</i>								
Internode length	50	<i>C. antarctica</i>	-	-	-	-	-	-
			<b>3.52<sub>2</sub>*</b>					

Specific internode mass	53	<i>C. antarctica</i>	4.67 <sub>2</sub> *	-	-	13.35 <sub>2</sub> ***	1.91 <sub>2</sub>	6.77 <sub>4</sub> ***
<i>Root traits</i>								
Maximum root length	51	<i>C. antarctica</i>	3.26 <sub>2</sub> *	-	-	1.19 <sub>2</sub> <sup>n.s.</sup>	2.41 <sub>2</sub> <sup>n.s.</sup>	6.15 <sub>4</sub> ***
	52	<i>R. moseleyi</i>	-	-	-	-	4.60 <sub>2</sub> *	-
	47	<i>R. pseudotrullifolius</i>	-	-	-	7.14 <sub>2</sub> **	3.67 <sub>2</sub> *	-
Specific root mass	45	<i>C. antarctica</i>	5.39 <sub>2</sub> **	-	-	-	-	-
	46	<i>R. moseleyi</i>	-	4.41 <sub>2</sub> *	-	-	-	-
	43	<i>R. pseudotrullifolius</i>	-	-	-	5.89 <sub>2</sub> ***	-	-
<i>Performance traits</i>								
Ramet dry mass	58	<i>C. antarctica</i>	-	-	-	-	-	-
	49	<i>R. moseleyi</i>	4.26 <sub>1</sub> *	-	-	-	-	-
	45	<i>R. pseudotrullifolius</i>	-	-	-	9.38 <sub>2</sub> ***	-	-
Clone dry mass	60	<i>C. antarctica</i>	-	-	-	-	-	-
	48	<i>R. moseleyi</i>	21.44 <sub>1</sub> ***	4.35 <sub>2</sub> *	-	5.84 <sub>1</sub> *	2.65 <sub>2</sub> .	-
	47	<i>R. pseudotrullifolius</i>	7.77 <sub>2</sub> **	-	-	8.21 <sub>2</sub> ***	-	-
Number of ramets	60	<i>C. antarctica</i>	20.58 <sub>2</sub> ***	8.18 <sub>2</sub> *	11.82 <sub>4</sub> *	18.88 <sub>2</sub> ***	8.76 <sub>2</sub> ***	3.61 <sub>4</sub> *
	53	<i>R. moseleyi</i>	5.28 <sub>1</sub> *	-	-	-	-	-
	50	<i>R. pseudotrullifolius</i>	16.46 <sub>2</sub> ***	-	-	31.93 <sub>2</sub> ***	-	-

Notes: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ ; ' '  $0.05 < p < 0.1$ ; n.s. = not significant ( $p > 0.1$ ). ' ' the tested predictors did not influence the response variable and was removed from the selected model. 'n' number of points to calculate relationship. Indicated values correspond to the F statistics with the degree of freedom (as subscript).

according to the species. For instance, *C. antarctica* ramets displayed higher internode length and specific internode mass at 13°C than at 18°C (with intermediate values at 8°C), while specific root mass was higher at 18°C than at 8°C and 13°C. In *R. moseleyi* and *R. pseudotrullifolius*, only aerial traits showed a response to temperature. Indeed, *R. moseleyi* and *R. pseudotrullifolius* experienced significantly higher SLA at 13°C (than at 8°C) and 18°C (than at 8°C with intermediate values at 13°C) respectively, and mean values of height were higher at 13°C than 8°C in *R. moseleyi*.

On the other hand, regarding the variability in plastic responses of functional traits, we only found interactive effects of temperature and plant-plant interactions in *C. antarctica* maximum root length and specific internode mass (Table 1, Fig. 2). Indeed, in absence of plant-plant interactions, along the tested gradient of temperatures, the variability of maximum root length remained constant whereas the variability of specific internode mass decreased. However, plant-plant interactions modified this response pattern of the trait variability. For example, under intraspecific interactions, values of maximum root length converged gradually from 8°C to 18°C, while values of specific internode mass diverged more at 13°C than at 18°C, with an intermediate divergence at 8°C. For all other traits with the exception of SLA and internode length, trait variability responded either to temperature or plant-plant interactions, or to their additive effects. Nevertheless, the variability in the observed plastic responses was trait and species dependent, regardless of the trait category (aerial, root, or clonal) contrary to our expectations. For instance, temperature and plant-plant interactions had additive effects on height variability in *R. pseudotrullifolius* that experienced more convergent values at 18°C than at 8°C and 13°C (Fig. 2), while LDMC in *C. antarctica* responded to temperature only, with more convergent values at 13°C than at 18°C (with intermediate variability at 8°C) (Fig. 2). Besides, root trait variability was altered by plant-plant interactions (maximum root

length) and temperature (maximum root length, specific root mass) in the *Ranunculus* species.

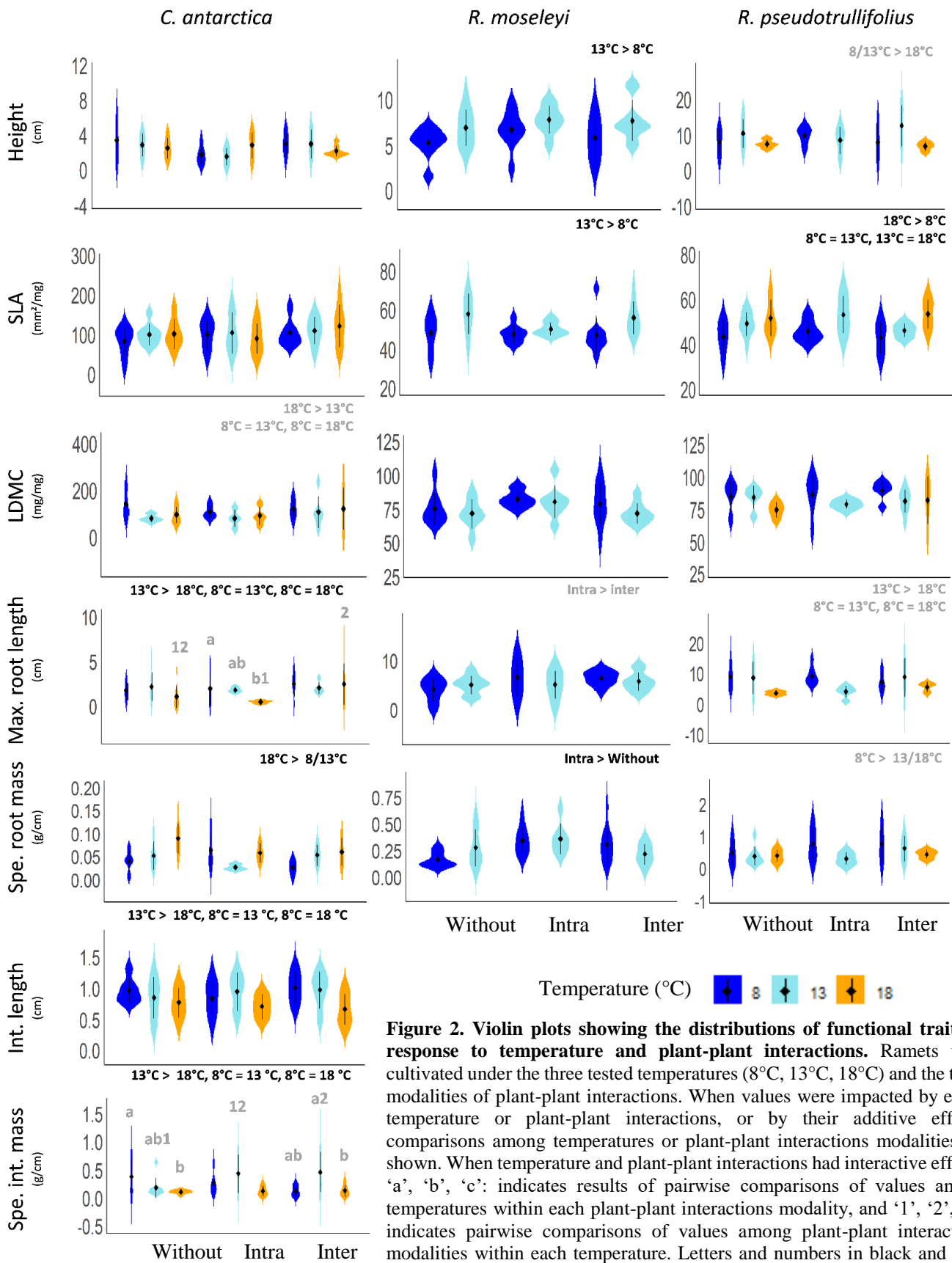
The growth conditions and the plastic functional responses that we evidenced, mostly lead to variations in the number of ramets as compared to ramet and clone dry masses (Table 1, Fig. 3). Indeed, in *R. pseudotrullifolius*, clonal multiplication was more efficient and more variable at 13°C than at 8°C or at 18°C, while in *R. moseleyi*, we noticed a higher clonal multiplication at 13°C than at 8°C. In *C. antarctica*, temperature and plant-plant interactions had an interactive effect on both the mean and the variability of the number of ramets. More specifically, in absence of plant-plant interaction, clonal growth was more efficient and more variable at 13°C and 18°C than at 8°C. Nevertheless, the mean and variability of ramet production differed between temperatures under intra- and interspecific interactions. Ramet dry mass appeared mostly unresponsive to the tested factors, with the exception of responses to temperature in its mean and variability detected respectively in *R. moseleyi* and *R. pseudotrullifolius*. Finally, responses in the number of ramets seemed to subsequently impact mean clone dry mass, excepted in *C. antarctica*. Indeed, in *R. pseudotrullifolius*, clones experienced higher mean biomass at 13°C than at 8°C (with intermediate values at 18°C). In *R. moseleyi*, mean clone dry mass differed among both temperature and plant-plant interaction treatments, but its variability differed among temperatures only. In particular, clone dry mass tended to converge towards lower values at 8°C compared to 13°C.

*Either temperature or plant-plant interactions affected co-variations between traits*

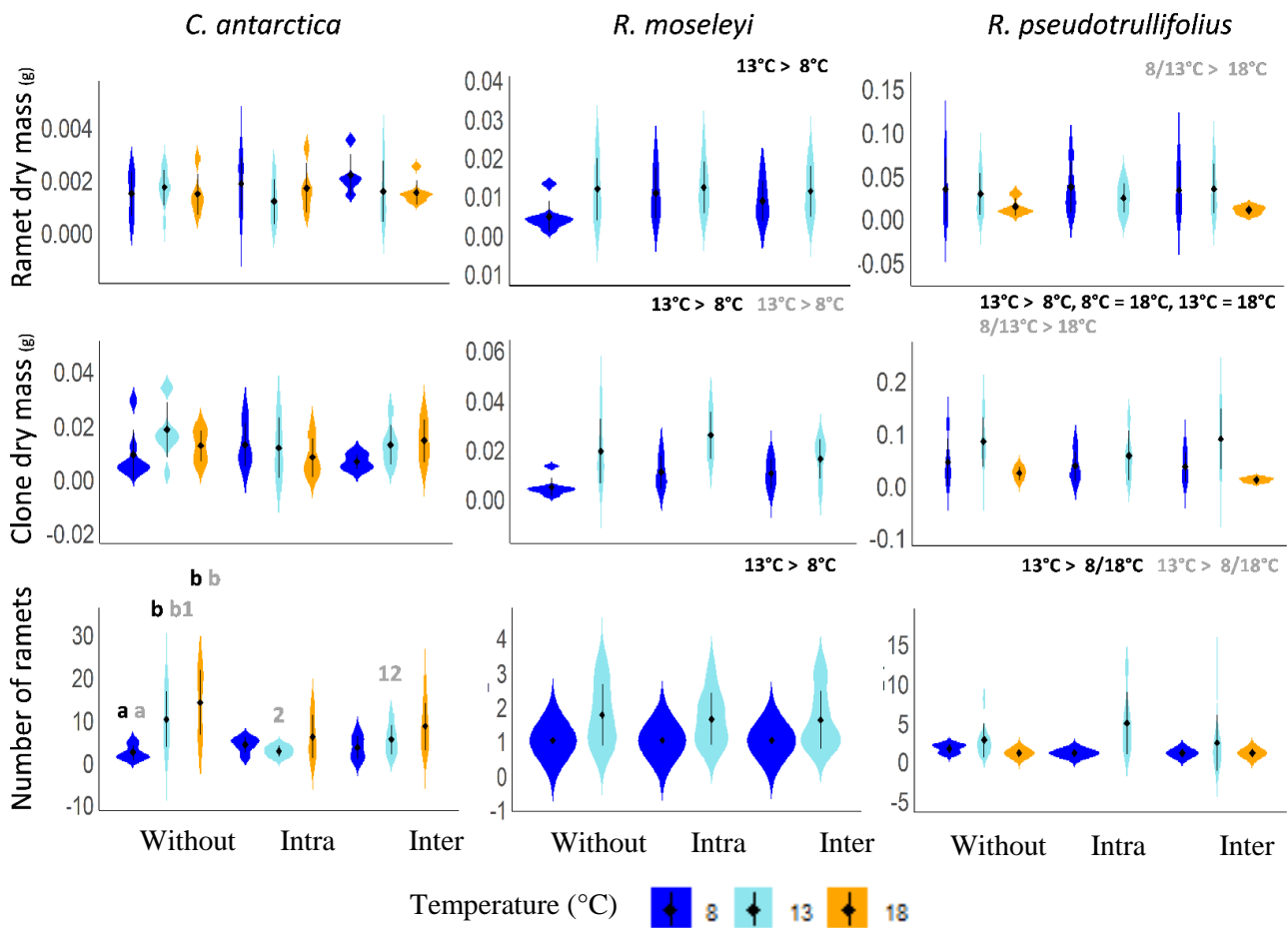
Contrary to our expectations, we found no interactive effects of temperature and plant-plant interactions on trait co-variations (Table 2). However, temperature and/or plant-plant interactions impacted the co-variations of two pairs of traits (height vs. maximum root

length, and SLA vs. LDMC) in two out of the three target species (no response of trait co-variation found in *C. antarctica*) (Table 2). Either the intensity or the direction of the relationships was modified depending on the species and the trait considered (Fig. 4). Indeed, the co-variation between SLA and LDMC was affected by the temperature in *R. moseleyi* (intensity, the relationship was more intense at 13°C than at 8°C, Fig. 4), and by the temperature and plant-plant interactions in *R. pseudotrullifolius* (direction, at 8°C we found

either a positive relationship without interactions, or a negative one with inter-/intraspecific interactions, Fig. 4). In addition, the co-variations between height and maximum root length responded to plant-plant interactions in *R. moseleyi* (intensity, the relationship was more intense in monocultures than in the two others plant-plant interactions treatments Fig. 4), and to temperature in *R. pseudotrullifolius* (intensity, the relationship was more intense at 13°C than at 8°C and 18°C, Fig. 4).





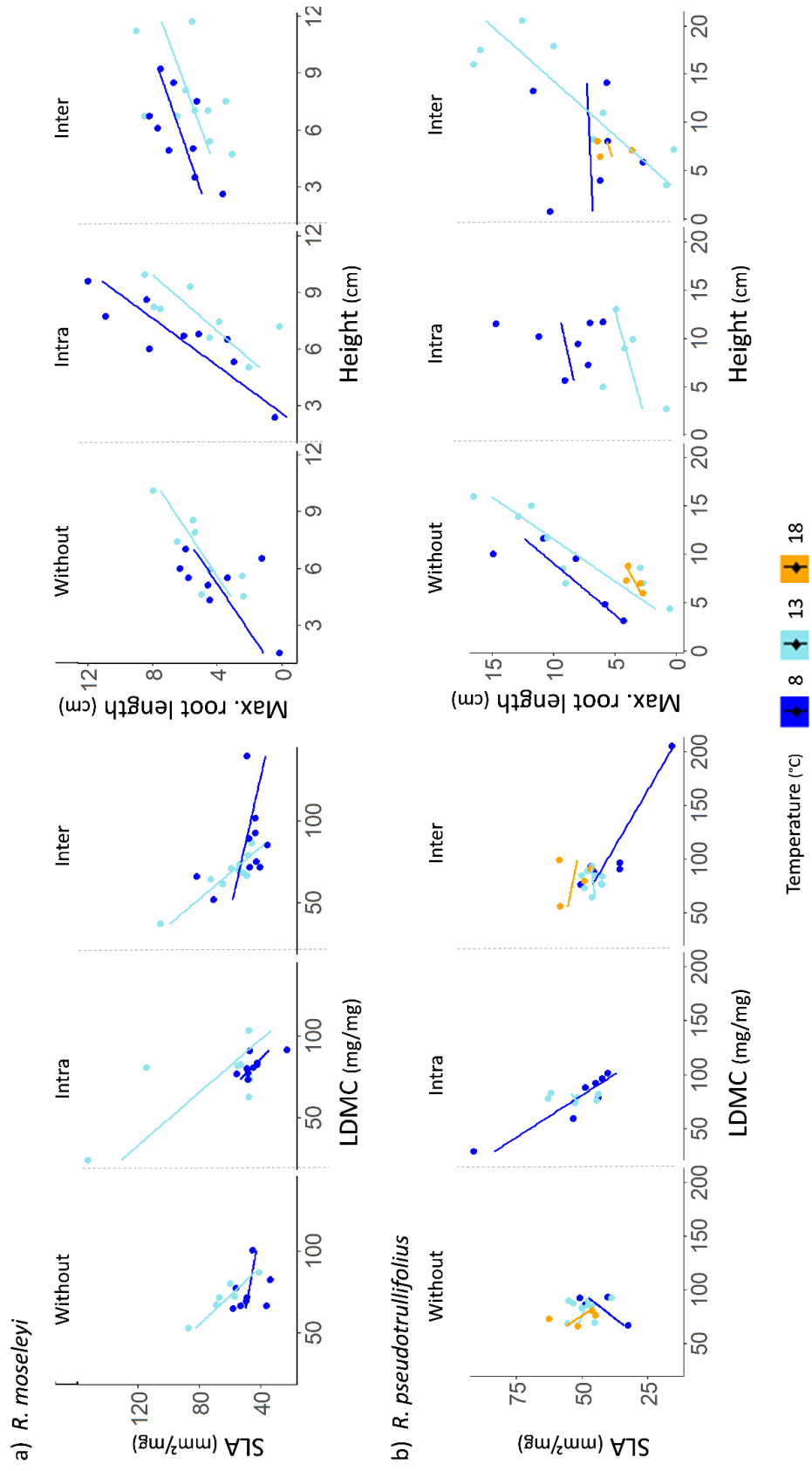


**Figure 3. Violin plots showing the distributions of performance trait values in response to temperature and plant-plant interactions.** These individuals were cultivated under the three tested temperatures (8°C, 13°C, 18°C) and the three modalities of plant-plant interactions. When values were impacted by either temperature or plant-plant interactions, or by their additive effects, comparisons among temperatures or plant-plant interactions modalities are shown. When temperature and plant-plant interactions had interactive effects: ‘a’, ‘b’, ‘c’: indicates results of pairwise comparisons of values among temperatures within each plant-plant interactions modality, and ‘1’, ‘2’, ‘3’: indicates pairwise comparisons of values among plant-plant interactions modalities within each temperature. Letters and numbers in black and grey indicate significant differences respectively in mean traits, and in residual values. When letters or numbers are absent: no significant difference in mean values between treatments. Treatments can be absent due to high mortality. In black in the violin: mean  $\pm$  SD. ‘*R. pseudo*’ *R. pseudotrullifolius*. ‘Without’ without interaction, ‘Intra’ intraspecific interactions, ‘Inter’ interspecific interactions.

**Table 2. Responses of the trait relationships to temperature × plant-plant interactions.** Table 2 displays the results of the ANOVAs performed on the most probable models determined based on the AIC selection method, and testing the interactive effects of temperature and plant-plant interactions on the relationships between all pairs of traits, in each target species. Here, we reported only the trait relationships that were impacted by either temperature or plant-plant interactions. Temperature and plant-plant interactions never had interactive effects on traits co-variations.

Species	Dependent trait variable	Trait as covariate	n	Explanatory variables of selected model		
				Predictor	F	d.f.
<i>C. antarctica</i>	-	-	-	-	-	-
<i>R. moseleyi</i>	SLA	LDMC	52	<b>LDMC</b>	<b>20.56***</b>	1
				Temperature	<b>6.72*</b>	1
				<b>LDMC × temperature</b>	<b>5.72*</b>	1
	LDMC	SLA		<b>SLA</b>	<b>44.72***</b>	1
	Height	Max. root length	52	<b>Max. root length</b>	<b>38.60***</b>	1
				Temperature	<b>15.03***</b>	1
	Max. root length	Height		<b>Height</b>	<b>36.73***</b>	1
				Temperature	<b>7.09*</b>	1
				Interactions	1.58 <sup>n.s.</sup>	2
				<b>Height × interactions</b>	<b>5.65**</b>	1
<i>R. pseudotrullifolius</i>	SLA	LDMC	49	<b>LDMC</b>	<b>60.99***</b>	1
				<b>Temperature</b>	<b>4.28*</b>	2
				Interactions	2.01 <sup>n.s.</sup>	2
				<b>LDMC × interactions</b>	<b>4.57*</b>	1
	LDMC	SLA		<b>SLA</b>	<b>67.19***</b>	1
				Temperature	0.12 <sup>n.s.</sup>	2
				<b>SLA × temperature</b>	<b>7.67**</b>	1
	Height	Max. root length	47	<b>Max. root length</b>	<b>27.52***</b>	1
				Temperature	2.80.	2
	Max. root length	Height		<b>Height</b>	<b>40.81***</b>	1
Temperature				<b>5.57**</b>	2	
<b>Height × temperature</b>				<b>3.54*</b>	1	

Notes: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ ; ‘.’  $0.05 < p < 0.1$ ; n.s. = not significant ( $p > 0.1$ ). ‘-’ none of the tested co-variations were impacted by either temperature or plant-plant interactions. ‘n’ number of points to calculate relationship. ‘Max. root length’ maximum root length. ‘interactions’ plant-plant interaction treatments.



**Figure 4. Significant relationships between the two pairs of traits (SLA vs. LDMC, and height vs. maximum root length) that were impacted by temperature and/or plant-plant interactions in a) *R. moseleyi*, b) *R. pseudotrullifolius*.** ‘Max. root length’ maximum root length. When values at 18°C are absent: high rate of mortality. ‘Without’ without interaction, ‘Intra’ intraspecific interactions, ‘Inter’ interspecific interactions.

## Discussion

### *Both habitat filtering and coexistence mechanisms influence species strategies*

Processes of abiotic environmental filtering and plant coexistence mechanisms can be inferred *via* the trait mean and variability (Cornwell and Ackerly, 2009; Mouchet et al., 2010; Mason et al., 2013). We then studied both parameters in response to temperature  $\times$  plant-plant interactions.

On the one hand, contrary to our expectations, we do not demonstrate an intermediate strategy between supporting competitive abilities and thermal resistance in aerial and root traits, while clonal traits do not increase. We actually evidenced very little effects of plant-plant interactions on the studied traits, whereas temperature effect is predominant. Nevertheless, this temperature effect is species and trait dependent, showing that there is no universal strategy of resistance to thermal variations. Both *Ranunculus* species invested in aerial plasticity, since SLA experienced higher mean values at higher temperatures (18°C in *R. pseudotrullifolius*, and 13°C in *R. moseleyi*) than at 8°C. This is in line with previous studies stating that rising temperatures induce more resource acquisitive ramets (Poorter et al., 2009). However, given the high mortality rate observed in *R. moseleyi* at 18°C, this temperature could be considered as stressful (or even deadly) for this species. *C. antarctica* response relies on the plasticity of root and clonal traits, more precisely on those related to resource conservation. Indeed, ramets produce shorter and thicker roots, but also shorter clonal internodes with less resource storage at 18°C than 13°C (mild temperature). Resource storage thus switches towards roots instead of clonal connections, in response to temperature, perhaps reflecting a tolerance strategy (Grime, 2006).

On the other hand, although trait variability responds to either temperature or plant-plant interactions in *R. pseudotrullifolius*, only *C. antarctica* is influenced by their interactive effects, in particular in maximum root length and specific internode mass. More precisely, we partially confirm our hypothesis regarding vertical traits variability, but we invalidate our hypothesis regarding horizontal traits. Under mild conditions (13°C) which is indicative of the plant-plant interaction effects only (*i.e.* without habitat filtering), root length variation does not change with plant-plant interactions, whereas specific internode mass is more variable in ramets cultivated under interspecific interactions than in absence of interactions, with intermediate variations in monocultures. Thus, specific internode mass plays a role in the coexistence mechanisms to limit the intra- and interspecific competition by stabilizing niche differences between *C. antarctica* individuals and their neighbors (Chesson, 2000). However, we highlight that temperature modifies the role of traits in coexistence mechanisms. Indeed, the variability of specific internode mass is similar among plant-plant interaction treatments at 8°C and 18°C, which may indicate that cold and warm stresses constrain phenotype variability in response to plant-plant interactions and that the coexistence mechanism may be different at these temperatures.

To conclude, further experimentations are needed to better evaluate the responses of other macrophyte species, and to test for the effects of higher temperatures (above 18°C) that have already been recorded at Iles Kerguelen (Frenot et al., 2006). Indeed, climate change can dramatically impact cold areas through a general decrease in suitable habitats (Parmesan, 1996, 2006). Moreover, although these results on the joint effects of

plant-plant interactions and temperature are promising, the study suffered from the high mortality of cultivated ramets that decreased the quality of our results (especially at 18°C). This mortality may be due to species limits of thermal tolerance but more likely to the substrate used for experimental cultures that may have been too rich despite our precautions, compared to what is usually observed under natural conditions (Douce et al., submitted).

#### *Traits co-variations responded to temperature or plant-plant interactions*

To maintain optimal performance, ramet should present high co-variations among functionally related traits (high integration within functional unit), and lower co-variations among functionally different traits (among functional units), conferring flexibility yet coordination to ramets (Nicotra et al., 1997). Through our study, we demonstrate multiple trait co-variations (Appendix 2) but only two of them are actually impacted by either temperature or plant-plant interactions, or by their additive effect in the two *Ranunculus* species. However, no modification of trait co-variation is recorded in *C. antarctica*. Indeed, functional traits poorly respond to the tested factors, likely implying that their relationships remain also stable.

Whether the intensity or the direction of the co-variations are affected by the tested factors, depends on the species. We find SLA and LDMC to overall negatively co-vary in both *Ranunculus* species, in line with several studies (Garnier et al., 2001; Wright et al., 2004), excepted at low temperatures (8°C) in absence of interactions in *R. pseudotrullifolius*. Indeed, SLA and LDMC positively co-vary, showing that ramets maintain their photosynthetic abilities while adopting increased resistance to low temperatures, reflecting macrophyte species

adaptation to cold-temperatures in the sub-Antarctic region (Hennion and Walton, 1997b). In *R. pseudotrullifolius*, trait co-variations differ in intensity among temperatures, with stronger co-variations at 8°C than at 13°C, contrary to the results in *R. moseleyi*, where co-variations are stronger at 13°C than at 8°C. This observation supports the theory on the trade-off between growth rate and cold tolerance, stating that the acquisition of resources for cold acclimatization (high LDMC) would impose a cost in terms of resource allocation that results in lower growth rates (*i.e.* lower SLA) (Woodward et al., 1990; Howe et al., 2003; Koehler et al., 2012; Molina-Montenegro et al., 2012; Bucher et al., 2019).

Besides, height and maximum root length positively co-vary, but with varying intensities depending on temperature (in *R. pseudotrullifolius*) or plant-plant interactions (in *R. moseleyi*), suggesting a similar trait syndrome related to resources capture between above- and belowground compartments (Withington et al., 2006). Changes in co-variation intensities between traits would indicate alteration of the phenotypic integration (Gianoli and Palacio-López, 2009). As a consequence, in *R. moseleyi*, the stronger co-variations observed between both traits in monocultures compared to under interspecific interactions or the no-interaction treatments, would indicate that higher competitive ability relies on stronger phenotypic integration. Similarly, in *R. pseudotrullifolius*, the positive co-variations between both traits is more intense at 13°C than at 8°C or 18°C, suggesting a decrease in phenotypic integration.

To conclude, while numerous studies have focused on trait co-variations across species, we bring new insights on these co-variations at the intraspecific level, and on their modifications in response to biotic and abiotic factors. In particular, we highlighted

that the sign and the intensity of trait co-variations are likely to change in response to varying environmental conditions, particularly those related to climate changes (Wright et al., 2004, 2005; Sgrò and Hoffmann, 2004; Pellissier et al., 2018; Maccagni and Willi, 2022). Thus, intraspecific trait variability would offer species the opportunity to adjust their response to changing environment as a whole through traits co-variations.

#### *Temperature rather than plant-plant interactions affects clone performance*

The evidenced plastic responses in phenotypes to plant-plant interactions  $\times$  temperature subsequently affect their performances in both *Ranunculus* species, on the contrary to *C. antarctica*, in which clone performances remained constant among treatments.

In absence of plant-plant interactions, in both *Ranunculus* species, mild temperatures (13°C) stimulated ramet production of higher (in *R. moseleyi*) or similar (in *R. pseudotrullifolius*) dry mass, likely enabling the clone to rapidly colonize space (Fahrig et al., 1994; Stuefer et al., 2002) and to get more successful (as reflected by higher clone biomass), in comparison with cold temperature (8°C). In addition, at higher temperature (18°C), in *R. pseudotrullifolius*, clone biomass and ramet production do not differ from those observed at 8°C and 13°C, indicating that 18°C would not be as stressful as expected for its individuals, unlike *R. moseleyi*. In *C. antarctica*, in absence of plant-plant interaction, both clone and ramet dry masses remain constant among temperatures, even if ramet production is stimulated at warmer temperatures (from 13°C). This result highlights that its more resource conservative strategy allows *C. antarctica* to maintain its performance at 18°C.

Furthermore, under plant-plant interactions, clone dry mass is not different from without interactions in the three tested species at the three tested temperatures, implying that the ecological niche is here similar to the theoretical one. In addition, we do not detect changes in the balance between competition and facilitation in response to thermal constraint. Thus, 8°C and 18°C may not be distinct enough from optimal conditions to show a variation of the interaction balance as stated by the Stress Gradient Hypothesis (Ploughe et al., 2019; Souza et al., 2021).

As a conclusion, rising water temperatures up to 18°C do not either stimulate or prevent the performance in *R. pseudotrullifolius* and *C. antarctica*, even if functional responses have been evidenced. As for *R. moseleyi*, further studies are needed to better evaluate its response at 18°C and actually determine whether the observed mortality was due to the temperature or the inappropriate level of nutrients in the cultures. However, one could wonder about the community response to higher temperatures (up to 23°C), which have already been observed in the Iles Kerguelen (or in the nearby Marion Island, Nyakatyia and McGeoch, 2007). Indeed, temperature constraints play a major role in species distributions (Walther et al., 2002; Parmesan and Yohe, 2003; McLachlan et al., 2005). Thus, characterizing the ecological niche of each species in terms of thermal tolerance range would be a complementary approach to characterize the functional responses of these species to abiotic stress. Moreover, determining the specialist and generalist species should help to understand the role of water temperature in the spatio-temporal distribution of macrophyte species.

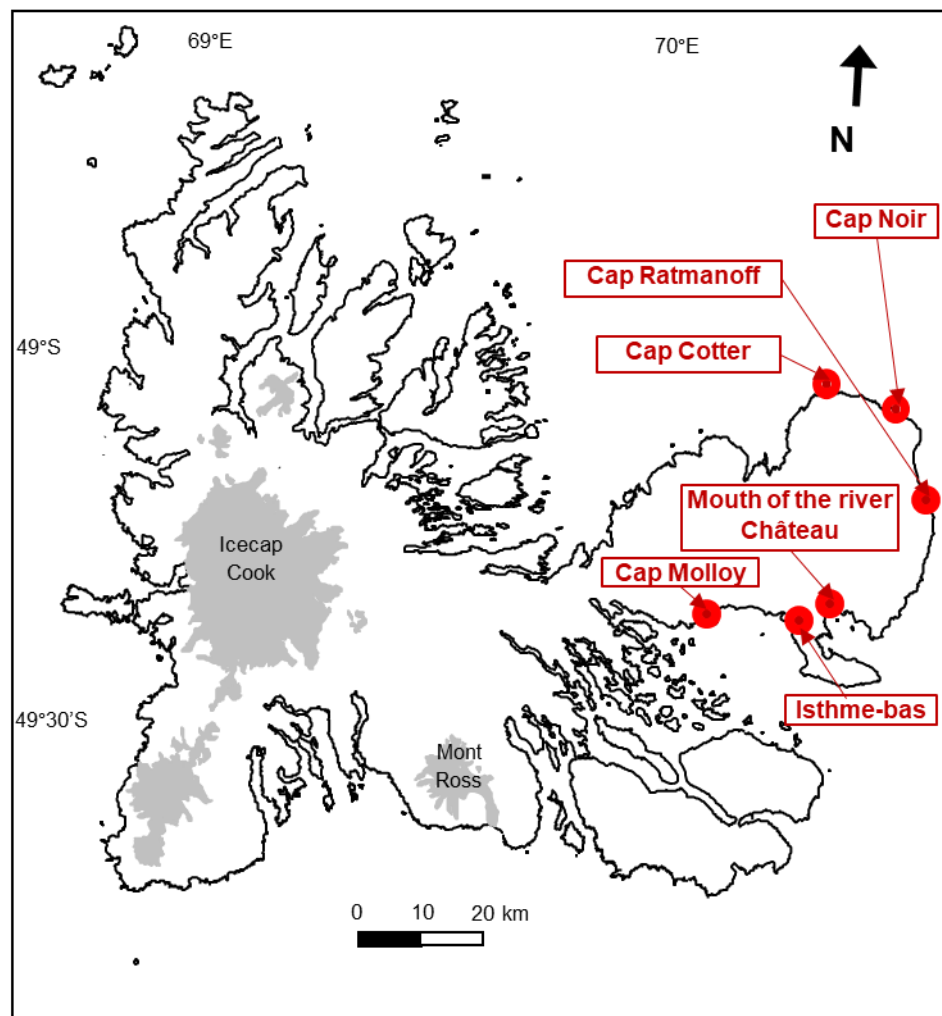
## Conclusion

Our study brings new insights on the mechanisms involved in thermal resistance in a context of plant-plant interactions within freshwater ecosystems and, more widely, within abiotically constrained habitats. In particular, we evidenced plastic responses that were trait and species dependent. This study could serve as a basis to improve the prediction models of species redistribution in response to warming temperatures with better realism since plant-plant interactions, which modulate responses to thermal stress, were here taken into account. In addition, the traits studied can be considered as response but also as effect traits for the functioning of the aquatic ecosystem. We thus expect that the evidenced responses can further impact ecosystem functions such as productivity or nutrient cycling.

## Acknowledgements

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## Supplementary Information



**Appendix 1.** Locations (red points) of the six sampled sites of ramets in the six macrophyte species on the French sub-Antarctic Iles Kerguelen (48°30–50°S, 68°27–70°35E).



**Appendix 2.** Responses of trait relationships to temperature × plant-plant interactions. Appendix 2 displays the results of the ANOVAs performed on the most probable models determined based on the AIC selection method, and testing the interactive effects of temperature and plant-plant interactions on the relationships between all pairs of traits, in each target species. Here, we reported only the significant trait relationships that do not include interactions between the covariate and the tested factors (reported in Table 2).

Species	Dependent trait variable	Trait as covariate	Explanatory variables of selected model			
			<i>n</i>	Predictor	F	d.f.
<i>C. antarctica</i>	Height	Specific internode mass	53	<b>Specific internode mass</b>	25.47**	1
	Specific internode mass	Height	53	<b>Height</b>	29.04***	1
				<b>Temperature</b>	6.96**	2
				Interactions	0.37	2
				<b>Temperature x interactions</b>	4.71**	4
	Internode length	Height	53	<b>Height</b>	5.19*	1
<b>Temperature</b>				4.76*	2	
SLA	LMDC	53	<b>LDMC</b>	9.34**	1	
LDMC	SLA	53	<b>SLA</b>	25.18***	1	
			<b>Temperature</b>	3.2*	2	
			Interactions	2.52.	2	
<i>R. moseleyi</i>	Height	Specific root mass	52	<b>Specific root mass</b>	21.81***	1
	Specific root mass	Height	52	<b>Temperature</b>	6.35*	1
				<b>Height</b>	16.54***	1
	Interactions	2.69	2			
Max. root length	Specific root mass	47	<b>Specific root mass</b>	12.64***	1	
Specific root mass	Max. root length	47	<b>Max. root length</b>	16.44***	1	
<i>R. pseudotrullifolius</i>	Height	Specific root mass	47	<b>Specific root mass</b>	6.09*	1
	Specific root mass	Height	47	<b>Height</b>	21.81***	1
	Specific root mass	Max. root length	47	<b>Max. root length</b>	7.82**	1

Notes: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ ; ‘.’  $0.05 < p < 0.1$ ; n.s. = not significant ( $p > 0.1$ ). ‘n’ number of points to calculate relationship. ‘Max. root length’ maximum root length. ‘interactions’ plant-plant interaction treatments.

CHAPITRE 3 : Boucles de rétroaction entre  
les réponses fonctionnelles des macrophytes  
et le fonctionnement des systèmes mares

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## Préface

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Dans ce chapitre, nous avons cherché à étudier l'impact du changement climatique, notamment thermique, sur le fonctionnement de l'écosystème aquatique « mare ».

Un nouveau champ disciplinaire a récemment vu le jour, mettant l'accent sur l'interdépendance des processus évolutifs et écologiques, en lien avec les boucles de rétroaction existantes entre ces deux processus, appelées « boucles éco-évolutives » (Hairston Jr et al., 2005 ; Urban & Skelly, 2006 ; Fussmann et al., 2007 ; Urban et al., 2008 ; Ellner et al., 2011 ; Schoener, 2011 ; Matthews et al., 2011 ; Shefferson & Salguero-Gómez, 2015 ; De Meester et al., 2016, 2019). En effet, certains facteurs abiotiques, de même que les interactions biotiques, constituent des pressions de sélection sur les phénotypes des individus végétaux. Les dynamiques écologiques peuvent donc moduler les dynamiques évolutives, défini comme la composante « Eco vers Evo » de la boucle éco-évolutive. Cette sélection et évolution phénotypique peuvent en retour impacter certaines propriétés écologiques, définissant ainsi une rétroaction des dynamiques évolutives sur les dynamiques écologiques, c'est alors la composante « Evo vers Eco ». Cependant, peu de recherches sur les dynamiques éco-évolutives prennent en compte la réalité complexe des interactions plantes-plantes qui opèrent au sein d'une communauté (Barraclough, 2015 ; De Meester et al., 2019). Pourtant, la prise en compte des interactions plantes-plantes est d'autant plus importante dans des systèmes paucispécifiques (Urban et al., 2008) ou isolés (Vanoverbeke et al., 2016 ; De Meester et al., 2016) au sein desquels les dynamiques évolutives seraient plus intenses. Par ailleurs, il semblerait que la boucle éco-évolutive complète n'ait jamais été étudiée au sein d'une communauté végétale à ce jour (De Meester et al., 2019).

Le travail présenté dans ce chapitre 3 participerait à faire progresser les connaissances sur les boucles de rétroaction Eco vers Evo et Evo vers Eco au sein d'une communauté végétale, dans l'hypothèse où les variations phénotypiques mises en évidence seraient hérissables. Dans le chapitre 2, nous avons démontré que les valeurs de traits foliaires étaient affectées par les facteurs biotiques (interactions plantes-plantes) et abiotiques (température). Ces traits de réponse constituent des traits d'effets sur le fonctionnement des écosystèmes. En particulier, les variations de valeurs de traits associés à la production primaire (Gutt et al., 2021) ou la composition chimique des individus (Swan & Kominoski, 2012), tels que la teneur en nutriments dans les feuilles ou encore la SLA ou le LDMC, peuvent impacter la qualité de la

litière qui en résulte, de même que sa facilité à être décomposée par les microorganismes et les détritivores, et donc *in fine* influencer les cycles du carbone et des nutriments (Aerts, 1997 ; Wedderburn & Carter, 1999 ; Santiago, 2007). De plus, les processus de décomposition dépendent également des activités enzymatiques microbiennes qui sont sensibles aux contraintes thermiques (Bragazza et al., 2013). Ainsi, il existerait un optimum de température pour les processus de décomposition, correspondant à une efficacité optimale des communautés microbiennes. Les modifications de taux de décomposition de la litière déterminent ensuite la quantité de nutriments minéralisés et donc biodisponibles pour les plantes (Kaye & Hart, 1997 ; Schimel & Bennett, 2004), ce qui pourrait affecter par rétroaction, la réponse fonctionnelle des plantes en termes de croissance et de valeurs de traits foliaires.

Ce troisième chapitre comprend l'**article VI** et vise à définir les rétroactions en jeu au sein des systèmes aquatiques, en se basant sur le modèle des mares des Iles Kerguelen et en les recréant à petite échelle en conditions contrôlées. L'étude porte sur l'espèce *Limosella australis*, qui est une hydrophyte observable dans les mares des Iles Kerguelen. En nous basant sur ce système expérimental en mésocosmes, nous avons abordé les questions suivantes :

- Quelles sont les réponses intraspécifiques des traits fonctionnels de l'espèce cible *Limosella australis* à la combinaison de l'élévation des températures et des interactions plantes-plantes ? Quelles conséquences sur la performance des individus ? L'hypothèse suivante a été testée :
  - Les individus devraient trouver une stratégie intermédiaire entre résistance à la contrainte thermique et aptitude compétitive à travers des valeurs intermédiaires de traits foliaires et de croissance, permettant un maintien de leur performance.
- Comment les variations de phénotypes peuvent influencer les processus de décomposition de litière et donc la fonction de recyclage des nutriments ? Nous avons émis les hypothèses suivantes :
  - Les individus avec une forte teneur foliaire en azote, une faible teneur en carbone et une faible LDMC devraient produire une litière de bonne qualité.
  - La décomposition de la litière devrait donc dépendre de la qualité de la litière mais également de la température à laquelle la litière se décompose. Plus précisément, une litière de bonne qualité devrait être rapidement décomposée, en particulier sous une température optimale pour les activités microbiennes.

- Comment la modification de ces processus écologiques peut affecter en retour les caractéristiques fonctionnelles de l'espèce cible *L. australis* dans un contexte d'élévation des températures ? (Boucle de rétroaction). Nous avons supposé les éléments suivants :
  - La modification des taux de décomposition affecterait la quantité de nutriments biodisponibles pour les plantes dans le système, ce qui conduirait *in fine* à une modification du phénotype et des performances des individus.

*N.B* : si ces variations phénotypiques s'avéraient héritables (cette hypothèse restant à tester), nous pourrions avoir mis en évidence une dynamique éco-évolutive au sein des systèmes étudiés.

**Temperature drives eco-evolutionary feedbacks within sub-Antarctic ponds: evidence from an experiment conducted at the community and ecosystem levels.**

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Article Informations	Abstract
<p><i>Article history:</i></p> <p>In prep</p> <hr/> <p><i>Keywords:</i></p> <p>Response and effect traits</p> <p>Plant-plant interactions</p> <p>Climate warming</p> <p>Eco-evolutionary dynamics</p> <p>Litter decomposition</p>	<p>1. There is now ample evidence that climate changes, in particular temperature increase, affect plant communities, ultimately threatening biodiversity. Within communities, plant individuals are additionally exposed to plant-plant interactions. However, in the literature, trait responses to these two constraints have usually been studied separately. Furthermore, trait response to environmental variations may influence processes at higher organizational levels, scaling-up from the community to the ecosystem. In turn, these ecological modifications may impact evolutionary dynamics of the occurring species. Thus, eco-evolutionary dynamics has become a popular conceptual framework as it proposes to determine how systems as a whole, respond to rapid environmental changes. Yet, studies considering both the evo-to-eco and the eco-to-evo side of the feedback have never been conducted so far, in particular at the plant community level.</p> <p>2. We developed an experimental approach based on the model of the macrophyte communities living in the ponds of the Iles Kerguelen, in the sub-Antarctic region. Effects of climate changes are severe in aquatic ecosystems, especially in the rapidly warming sub-Antarctic region where aquatic plant communities are remarkably species-poor and cold adapted. Specifically, we recreated at small scale (in mesocosms) conditions that are similar to pond ecosystem in the field. To that aim, individuals of the sub-Antarctic plant species <i>Limosella australis</i> were grown under different treatments of temperature × plant-plant interactions to assess their trait responses and create litters of varying qualities. These litters were then decomposed in the presence of a plant individual, at different temperatures to determine the resulting effects on ecosystem functioning, and potential feedbacks on plant trait values.</p> <p>3. Our results first highlighted that plants invested in different strategies to face rising temperatures depending on the plant-plant interactions. In particular, in absence of interactions, ramets invested in an escape strategy with resources acquisitive ramets. Under intraspecific interactions, ramets switched towards a tolerance strategy, whereas under interspecific interactions, ramets invested in an intermediate strategy by increasing competitive abilities to face the interspecific competition. Second, we found that the litter quality impacted the litter decomposition, depending on the temperatures. Thirdly, we evidenced a positive feedback of litter decomposition rate on leaf dry matter content, thus suggesting that variations in ecological properties could result in evolutionary changes of plant phenotypes.</p>

4. Our study overall leads to the following conclusions: (i) ecological and evolutionary dynamics can occur on similar timescales, and (ii) temperature can affect directly and indirectly the Eco-Evo dynamics. Therefore, our study brings new insights into the emerging concept of eco-evolutionary dynamics, especially in a community context which still remains poorly understood.

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## Introduction

There is now ample evidence that climate changes, in particular temperature increase, affect plant communities, ultimately threatening biodiversity (Halloy and Mark, 2003; Khare et al., 2020; Harrison, 2020). Functional ecology has then been proposed as a relevant approach to study the consequences of these changes (Mcgill et al., 2006) based on traits *i.e.* any morphological, phenological, or physiological feature measurable at the individual level (Violle et al., 2007). Modifications in trait values due to environmental variations may influence processes at higher organizational levels, scaling-up from community (response traits) to ecosystem (effect traits) for example (Lavorel and Garnier, 2002; Violle et al., 2007). Recently, integrative research provided growing evidence that ecological and evolutionary dynamics can occur on similar timescales and even interact (Matthews et al., 2011; De Meester et al., 2019). As such, eco-evolutionary dynamics has become a popular conceptual framework as it proposes to determine how systems as a whole, respond to rapid environmental changes (Bassar et al., 2021). These would indeed select adaptive phenotypes supporting individual survival in novel environment, resulting in evolutionary changes that can influence ecological properties of populations, communities, and even ecosystems (evo-to-eco feedback). In turn, these modifications in ecological processes can lead to selective pressures triggering species response (eco-to-evo feedback). Yet, studies considering both the evo-to-eco and the eco-to-evo side of the feedback have never been conducted so far, in particular at the plant community level.

Within plant communities, individuals are exposed to biotic and abiotic constraints simultaneously, although their trait responses have usually been studied separately (see e.g. Dudley and Schmitt, 1996; Greulich and Bornette, 1999; Suding et al., 2008; Riis et al., 2012). This literature gap underlies the need to consider complex systems integrating plant-plant interactions as they could alter species responses to thermal stress resulting from climate change. Thermal stress and plant-plant interactions (*i.e.* competition and facilitation) are filters ultimately shaping plant community composition based on individual phenotype (Keddy, 1992; Violle et al., 2007). Previous studies have highlighted the importance of intraspecific trait variability in species ability to overcome these filters (Jung et al., 2010; Violle et al., 2012). For instance, competition induces an increase in specific leaf area (Bittebiere et al., 2012), leaf phosphorus and nitrogen concentration (Novotny et al., 2007) and a decrease in plant height (Bittebiere and Mony, 2015; Yu et al., 2018) overall to support the competitive ability. The opposite trend happens under thermal stress (Wright et al., 2005; Moles et al., 2009; Pallardy, 2010; Reich, 2014; Zhang et al., 2016, 2019; Bjorkman et al., 2018) to favor the thermal stress tolerance. Overall, this antagonism between plant individual responses to plant-plant interaction and thermal stress suggests the existence of an intermediate strategy owing to traits involved in thermal resistance and competitive ability.

These potential evolutionary changes of plant phenotypes may result in modifications of ecological processes. As plants are primary producers, their responses to plant-plant interactions  $\times$  thermal stress can indeed scale up through their effect traits to the ecosystem level (Lavorel and Garnier,

2002; Eviner and Chapin III, 2003; Quétier et al., 2007), and affect its functioning *i.e.* the nutrient cycling. Intraspecific trait variability would thus play an important role in ecosystem functioning but it remains poorly studied so far (Pichon et al., 2022). Litter decomposability is known to be tightly related to its quality (Fortunel et al., 2009; Yang et al., 2022), that mostly relies on the “after-life effect” of leaf trait values (De Deyn et al., 2008; Makkonen et al., 2012). In particular, LDMC and leaf carbon content were found to be negatively correlated with litter decomposability, whereas the opposite effect was found for SLA and leaf nitrogen content (Lecerf and Chauvet, 2008; Cornwell et al., 2008; Freschet et al., 2013; Tao et al., 2019). Moreover, the litter decomposition depends not only on its quality but also on the environmental conditions which influence the activity of the decomposers, in particular the temperature. An increase in temperature would stimulate the decomposer community efficiency (Sulkava and Huhta, 2003), which could however experience a decrease in their efficiency above the stimulation temperature range, thus limiting the litter decomposition (Wetterstedt and Ågren, 2011). Therefore, litter decomposition would be determined by the temperature, either directly or indirectly through litter quality resulting from plant traits responses to warming.

Ecological properties would select phenotypes in response to multiple factors such as abiotic factors or biological interactions, possibly resulting in their evolution, if trait variations have a genetic basis (De Meester et al., 2019). Litter decomposition has been shown to be a key driver of nutrient cycling (Freschet et al., 2013), as it determines the dynamics of soil labile organic matter and influences nutrient release in the ecosystem (Kaye and Hart, 1997; Schimel and Bennett, 2004). Nutrient flows are also driven by temperature that accelerate nitrogen mineralization (Epstein et al., 2000; Rustad et al., 2001) and plant nutrient uptake (Bassirirad, 2000; Epstein et al., 2000), especially in cold biomes where decomposition is temperature limited (Hobbie

et al., 2002; Robinson, 2002). Consequently, these changes in nutrient availability and uptake should create a feedback towards the mineral nutrition of plants, subsequently affecting their growth and traits values (Wardle et al., 2004; Freschet et al., 2013). In particular, SLA and leaf nutrient concentration are known to increase in response to nutrient availability (Westoby et al., 2002; Cornelissen et al., 2003). As a consequence, plant traits values should be directly modified in response to temperature and/or litter decomposition rate that reflects nutrient availability.

In this study, we conducted an experimental approach based on the model of pond ecosystems from the sub-Antarctic region. This freshwater ecosystem constitutes a relevant model to test questions related to thermal stress, and its consequences on plant community dynamics and ecosystem processes. Indeed, effects of climate changes are severe in aquatic ecosystems (Lacoul and Freedman, 2006), especially in the rapidly warming sub-Antarctic region where aquatic plant communities are poor and adapted to cold temperatures (Lebouvier et al., 2011, Douce et al. *submitted*). We then recreated at small scale, in mesocosms, conditions that are similar to pond ecosystem in the field. Individuals of the sub-Antarctic plant species *Limosella australis* were then grown under different regimes of temperature × plant-plant interactions to assess their trait responses and create litters of varying qualities. These litters were then decomposed at different temperatures to determine the resulting effects on ecosystem functioning, and potential feedbacks on plant trait values. Through this experimental approach, we specifically tested the following hypotheses related to the evo-to-eco and to the eco-to-eco side of the feedback (Fig. 1):

- An intermediate strategy between competitive ability and thermal resistance should occur in response to both increasing temperatures and plant-plant interactions, determining in turn the litter quality. In particular,

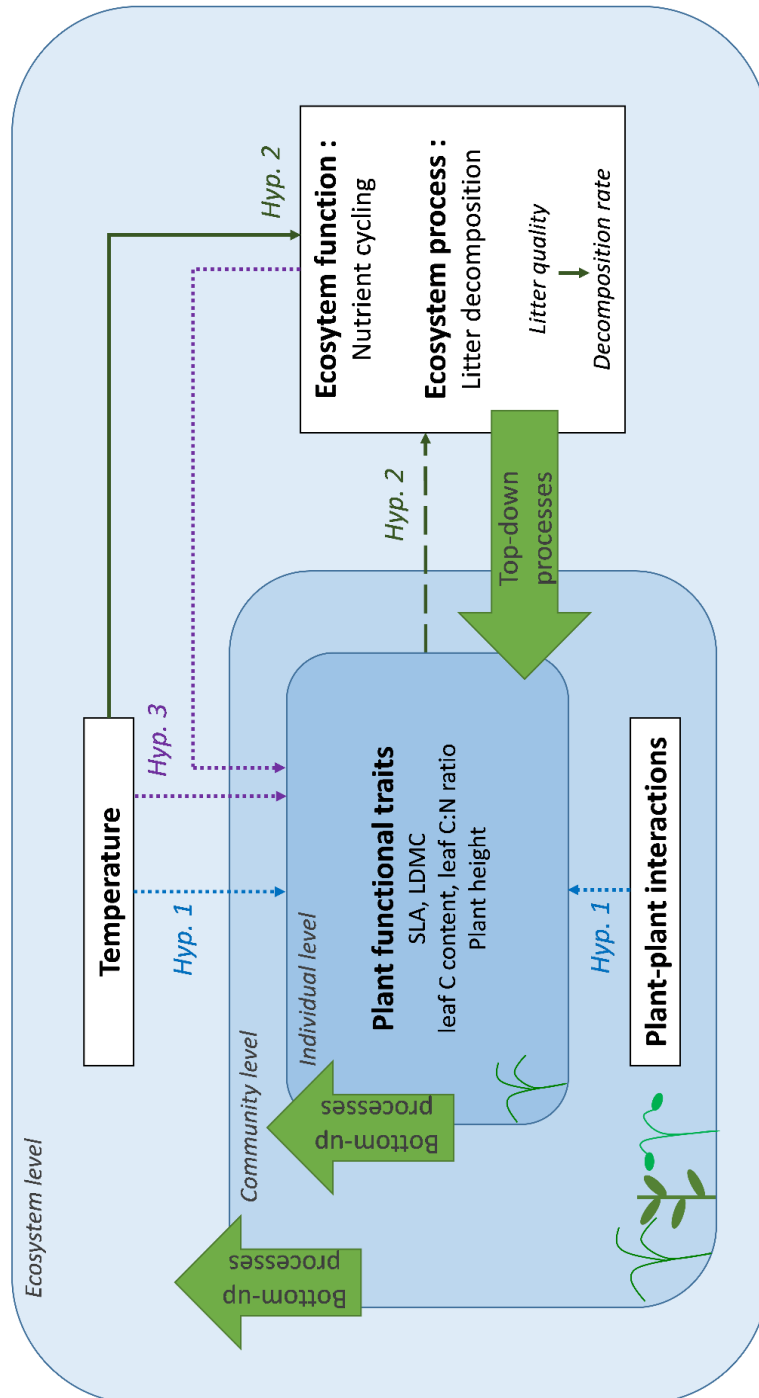


individuals with a high leaf nitrogen content, a low leaf carbon content and a low LDMC for instance, should produce a good litter quality.

- Litter decomposition should depend on both temperature and litter quality. In particular, high litter quality would result in higher decomposition rate, especially under temperatures that are

optimal for the decomposer community activity.

- Decomposition efficiency as measured by decomposition rate, combined with temperature, should ultimately affect plant traits value.



**Figure 1.** Tested hypotheses at the species and ecosystem levels. Dashed-dotted lines and dotted lines indicates Evo-to-Eco and Eco-to-Evo dynamics respectively. Blue, green and violet arrows indicate respectively the first, second and third hypotheses.

## Materials and methods

### *Studied system and species*

Our experimental study was conducted based on the model of the ponds of the Iles Kerguelen in the sub-Antarctic region (South Indian Ocean) (48°30–50°S, 68°27–70°35E). These ponds are shallow freshwater systems, supplied in water through rainfall and enriched by nutrient inputs from marine fauna like seabirds and sea elephants (Smith, 2008). Climate warming is particularly rapid in this region (Walther et al., 2002), while their native communities are well adapted to cold temperatures (mean air temperature = 4.6°C) (Frenot et al., 2006; Lebouvier, 2007) and abundant precipitations (range from 500 mm to 3200 mm along an East-West gradient – Frenot et al., 1998 and Meteo France). Plant communities being poor in terms of species number (simplified plant-plant interactions) and remaining free from anthropic influence, they constitute a relevant model to infer mechanisms of plant community assembly and ecosystem functioning, especially under climate change (Bergstrom and Chown, 1999).

Ponds provide habitats for aquatic plant communities (*i.e.* macrophytes) that are mainly composed of six native species that can all locally co-occur: *Limosella australis* R.Br. (Scrophulariaceae), *Callitriche antarctica* Engelm (Plantaginaceae), *Juncus scheuchzerioides* Gaudich. (Juncaceae), together with three Ranunculaceae species: *Ranunculus biternatus* Smith, *R. pseudotrullifolius* Skotts., and *R. moseleyi* Hook.f. All of these species are perennials. We choose *L. australis* as target species, because it was the most abundant hydrophyte species. The five other species were used as neighboring species. *L. australis* display a network architecture forming the clone, that is built from related ramets (short erected stems with leaves and roots) connected through stolons. This species additionally reproduces through autogamous sexual reproduction.

### *Biological material*

Prior to the experiments, seeds of *Limosella australis* and ramets of the five other macrophyte species were collected from different localities of the Iles Kerguelen, distributed throughout the main island to maximize the genetic variability of plant ramets (Appendix 1). Then, ramets of *L. australis* were grown from seeds and clonally multiplied under controlled conditions of substrate (50% sand and 50% compost, N: 250 g. m<sup>-3</sup>, P<sub>2</sub>O<sub>5</sub>: 120 g.m<sup>-3</sup>, K<sub>2</sub>O: 80 g.m<sup>-3</sup>), water supply, and temperatures (*i.e.* 13°C, which is the recorded mean temperature in Iles Kerguelen ponds during the growth season) with a monitored light regime of 12h/12h. This allowed us to limit maternal effects and to have ramets with similar growth history. In addition, clonal individuals produced new genetically identical ramets that will later be assigned to the treatment replicates of the two experiments, allowing us to control for genotypic effects on the measured responses.

For our experiments and for each species, ramets were cleaned and standardized before their transplant into mesocosms. We planted one adult ramet with one stolon internode (with reserves to facilitate the growth after the transplant, Stuefer and Huber, 1999) per ramet.

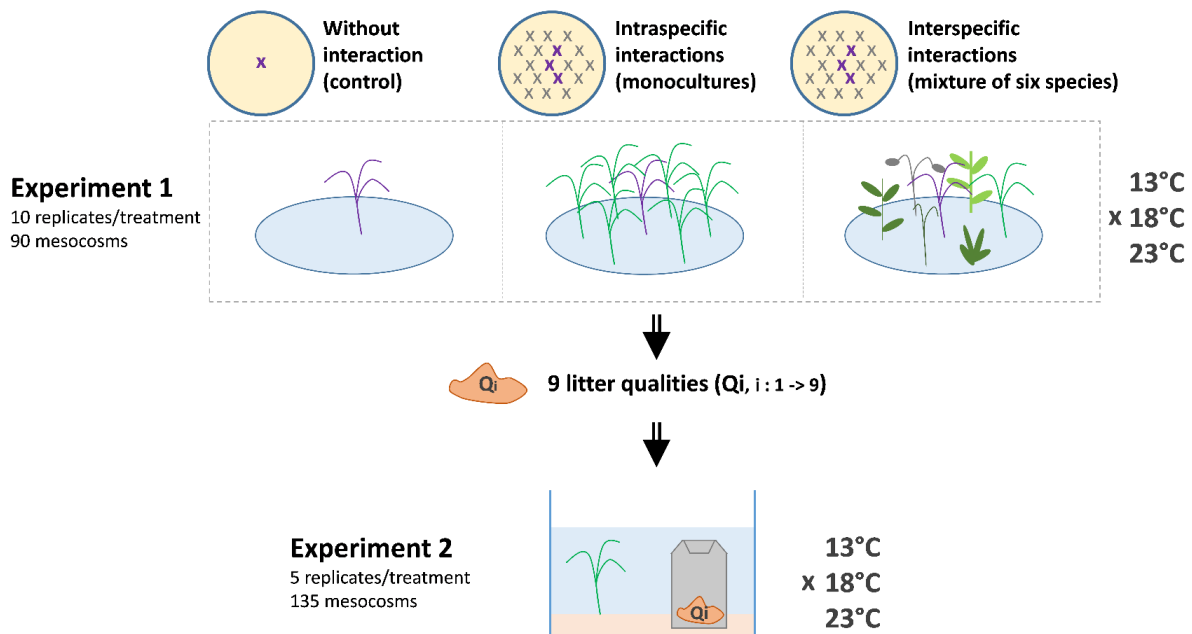
### *Responses of ramet traits and performances to temperatures × plant-plant interactions*

This first experiment was conducted in mesocosms within regulated rooms of the LEHNA laboratory, in Villeurbanne (France). The biological material obtained through prior cultures under controlled conditions, was used to build two different experimental assemblages with *Limosella australis* in monocultures, and in mixtures with the five other species occurring in ponds of the Iles Kerguelen. Additionally, one *L. australis* ramet was cultivated alone, *i.e.* without plant-

plant interactions. This design allowed us to assess the effects of intra. vs. interspecific plant-plant interactions on plant responses. To test for the impact of temperature increase on plant responses, all of these three plant-plant interaction treatments were cultivated at three temperatures (13°C – mean temperature in ponds during the growing season during the day, 18°C, and 23°C - extreme temperature observed in the Iles Kerguelen ponds). This temperature gradient is additionally based on the literature (Riis et al., 2012) and would allow us to detect ramet responses to temperature. Overall, we thus tested nine treatments in total (three temperatures x three plant-plant interactions treatments) (Fig. 2 Part 1).

In the interspecific and intraspecific treatments, ramets were planted following a hexagonal pattern (18 ramets per pot, Fig. 2 Part 1) as it allows balanced plant-plant interactions with neighbors (Birch et al., 2007), within pots (9 cm diameter, 8 cm height), on a substrate composed of 50% sand

and 50% compost [N: 250 g. m<sup>-3</sup>, P<sub>2</sub>O<sub>5</sub>: 120 g.m<sup>-3</sup>, K<sub>2</sub>O: 80 g.m<sup>-3</sup>]. This substrate composition was established through prior cultures of the target species under controlled conditions. Target *L. australis* ramets were planted so that they each have six neighbors (Fig. 2 Part 1). We planted three target ramets per pot, all having the same genotype. Neighboring ramets were equally distributed between the other occurring species (total density kept as constant) and their positions within the planting design were randomized. Neighbors were transplanted fifteen days before the target ramets of *L. australis*. During this period any dead neighbor was replaced. This delay allowed the neighbors to be well-established when targets were transplanted. Each combination of temperature and plant-plant interaction treatment was replicated ten times, resulting in 90 pots in total. One genotype has been assigned to one replicate to measure plastic responses as genotype reaction norms. Light conditions were set to a 12h/12h light regime.



**Figure 2.** Experimental design conducted in two phases. The first experiment aimed to determine the plant trait and performance responses to combined effects of temperature and plant-plant interactions. The second experiment sought to determine the combined effects of temperature and litter quality on litter decomposition rates, and the subsequent potential effects on plant growth (traits and performance). The substrate was composed of 1:3 mix of Iles Kerguelen sediments and sterilized sand, to ensure a colonization by microorganisms which are identical to those found in situ. ‘x’ in bold in the hexagonal pattern of plantation indicate target ramets.

Each pot was individually placed into a tray filled with water (12 cm height of water column; water nutrient content: N-NH<sub>4</sub><sup>+</sup> 8.0 µg/L, N-NO<sub>3</sub><sup>-</sup> 47.1 µg/L, P-PO<sub>4</sub><sup>3-</sup> 1.140 mg/L). Within each regulated room (one per tested temperature), pots were randomized every two weeks, and refilled with water once a week.

After 13 weeks of cultivation, experimental cultures were harvested. Target ramets of *L. australis* have produced new connected daughters of similar genotype (hereafter referred as 'clone') through clonal growth, allowing us to perform trait measurements controlling for genotypic effects. We randomly selected one of the three clones of *L. australis* in each pot, to assess the efficiency of the clonal growth, through measurements at the clone and at the ramet level. In addition, one newly produced and adult ramet within the clone was used for height measurements, and another one for leaf trait measurements. The remaining ramets of this clone, as well as the two other *L. australis* target clones were dedicated to the creation of litter bags for the second experiment.

#### *Effects of temperature and litter quality on litter decomposition and plant growth*

The dry aboveground biomass (*i.e.* the leaves, stems and clonal connections) of target clones of *L. australis* remaining from the first experiment, was used to create litter bags in this second experiment after being oven-dried at 65 °C for 48 h. We assumed that this litter would differ in quality among the nine treatments tested in the first experiment (temperature × plant-plant interactions), resulting in nine litter qualities. All the dry aboveground biomass originating from all the remaining *L. australis* ramets from the same treatment in the first experiment, was pooled and homogeneously mixed, before being dispatched into litter bags. Thus, all litter bags originating from the same treatment had the same litter quality and could be considered as replicates. Litterbags consisted in 5 mg +/- 10% of dry aboveground biomass, placed in

nylon bags with fine mesh to focus on microbial decomposition (6 cm x 4 cm). To determine the effects of temperature on litter decomposition, five replicates of litterbags with the same quality were placed under three temperatures (13°C, 18°C, 23°C – in one room per tested temperature) in 250 mL glass pots (9.5 cm diameter, 11 cm height) (Fig. 2 Part 2). This led to 27 treatments in total (9 litter qualities × 3 temperatures). The total experimental design consisted in 135 mesocosms in total (9 litter qualities × 3 temperatures × 5 replicates).

In the pots, we recreated, at small scale, conditions that are similar to pond ecosystems in the field. Pots were filled with 150 mL of ultra-pure sterilized water (to avoid microbial contamination and addition of exogenous nutrients) and with 100 mL of sedimentary substrate. This substrate was composed of 1:3 mix of Iles Kerguelen sediments and sterilized sand. Sediments were previously collected from the field at varying locations on the main island of Iles Kerguelen, to ensure a colonization by microorganisms which are identical to those found *in situ*. Sediments were brought from the field to the laboratory under 4°C to keep micro-organisms alive, and substrate was inoculated by the mixed sediments from all the locations, during one week to make sure sterilized sand was fully colonized by micro-organisms. In addition, in each pot, one week before litterbags were introduced, one ramet of *L. australis* was transplanted to further evaluate the crossed effects of temperature and litter decomposition on its growth and trait values (Fig. 2 Part 2). One genotype was assigned for each of the five replicates, *i.e.* 27 ramets originated from the same clone and standardized by their height, were dispatched between the 27 treatments to measure the plastic responses of *L. australis* ramet, as genotype reaction norms. Light conditions were set to a 12 h light/12 h dark regime.

This second experiment ended when all litterbags reached at least 50% of mass loss, *i.e.* after 56 days. Litterbags were collected, cleaned and freeze-drying for two

days before being weighted. Clones were also harvested and cleaned. One ramet per clone was dedicated to trait measurements at ramet level, with one fresh leave being frozen under 20 °C for further nutrient analysis and the remaining biomass of the ramet being freeze-drying for two days. The remaining biomass of the clones were oven-dried at 65 °C for 48 h for further measurements at the clonal fragment level.

We calculated the litter decomposition rate of all litter bags following an exponential decay model (Olson, 1963):

$$M_f = M_i * e^{-K*x}$$

where 'Mi' is the initial litter dry mass (5 mg +/- 10%), and 'Mf' is the remaining litter dry mass, after 'x' days. Thus, 'K' is the litter decomposition rate per day (.days<sup>-1</sup>) (Makkonen et al., 2012; Zhang et al., 2019):

$$K = -\frac{1}{x} \ln\left(\frac{M_f}{M_i}\right)$$

#### Trait measurements

At the end of the first and second experiments, we measured growth, leaf, and performances traits on *L. australis* plants at the clone and the ramet levels to (i) determine the ramet responses to [temperature × plant-plant interactions], and (ii) to assess the influence of potential modifications in the decomposition process on plant growth.

On each collected ramet, we measured height, Specific Leaf Area (SLA), Leaf Dry Matter Content (LDMC). In addition, only for the first experiment, we measured leaf carbon and nitrogen concentrations. These leaf traits were chosen to characterize ramet resource acquisition and conservation strategies since they are known to respond to temperature and plant-plant interactions (Cornelissen et al., 2003), and to be effect traits for litter decomposition (Santiago, 2007; Quested et al., 2007). SLA and LDMC were measured following Cornelissen et al. (2003) on one healthy and mature leaf that was randomly selected. Carbon and nitrogen concentrations were then measured on several leaves of the same ramet pooled together, to reach the

threshold mass needed for these analyses. 1 mg +/-10% of leaf dry biomass was weighed and encapsulated in tin capsules. Nitrogen and carbon concentrations were then measured using an elemental analyzer (Flash EA 1112, Thermo Scientific). In addition, the total dry mass of the ramet was measured (*i.e.* sum of the biomasses of stems, leaves, roots and one clonal internode), as a proxy of its performance.

On each collected clone, total dry mass and number of ramets were measured. Measurements of dry masses were performed after drying plant parts for 48 hours in oven at 65 °C or in freeze dryer for 48 hours. All plants were cleaned before any measurements.

#### Statistical analyses

We checked for correlations between all pairs of traits using Spearman rank correlation tests. We detected significant strong correlation (*i.e.* with Spearman's rho > 0.7, Dormann et al., 2013) between leaf N content and leaf C:N ratio only. We chose to keep leaf C:N ratio over leaf N content for further analyses, as leaf C:N ratio satisfies to the application conditions of performed tests.

First, we aimed to determine which morphological and performance traits respond to temperature × plant-plant interactions (fixed factors) based on a linear mixed-effect model procedure [glmer.nb function for the number of ramets, and lmer function for all other traits ("lme4" package, Bates, 2010)]. Models also included the clone genotype as random factor to detect trait plastic responses as genotype reaction norms. Trait data were normalized (log transformation) when needed. When the interaction between temperature and plant-plant interactions was non-significant, an additive model was fitted instead. When the effects of temperature and/or plant-plant interactions were significant, differences in trait means among treatments were determined using *post-hoc* tests based on the difflsmeans function ("lmerTest" package,

Kuznetsova et al., 2017) with adjusted p-values (Bonferroni correction).

Second, we aimed to assess the combined effects of temperature and litter quality on litter decomposition rate. We ordered the quality of the litters produced from the nine [temperature  $\times$  plant-plant interactions] treatments through leaf traits, which are known to influence litter quality (De Deyn et al., 2008; Makkonen et al., 2012). Leaf traits (leaf C content, leaf C:N ratio, SLA and LDMC) were then reduced to the first two axes of a PCA analysis, in which data were centered and standardized, to characterize the quality of each of the nine litters (Appendix 2). As all the dry aboveground biomass originating from the same [temperature  $\times$  plant-plant interactions] treatment was pooled and homogenized, we assumed the corresponding litter bags to have the same litter quality. Interactive effects of temperature (categorical factor) and litter quality (the first-two axes of the PCA, quantitative variables) on the litter decomposition rate  $K$  were tested. Trait data were previously normalized through square root transformation. A stepwise model selection based on the AIC criteria (dredge function, “MuMIn” package, Bartoń, 2013) was performed to select the most parsimonious model. Significance of model factors was determined using an ANCOVA test (type II).

Third, we aimed to determine whether morphological and performance traits respond to decomposition rate  $K$  (*i.e.* ecosystem process), and temperature. We thus fitted linear mixed-effect models with temperature (categorical variable) and decomposition rate (quantitative variable) as fixed interactive factors, and each of the six studied traits as response variable. Because one genotype was attributed to each replicate, models also included the clone genotype as random factor to detect trait plastic responses as genotype reaction norms. We used the `glmer.nb` function for the number of ramets, and the `lmer` function for all other traits (“lme4” package). Trait data were previously

normalized through log transformation. A stepwise model selection based on the AIC criteria (dredge function, “MuMIn” package) was performed to select the most parsimonious model. Significance of model factors was determined using an ANCOVA test (type II). When a statistically significant effect of temperature was detected, pairwise comparisons of trait means among temperatures were performed (`dunn_test` function, `statix` package) with adjusted p-values (Bonferroni correction).

All statistical analyses were carried out with R 4.0.3.

## Results

### *Traits and performance responses to combined temperature and plant-plant interactions*

On the one hand, three out of the four studied leaf traits responded to the interaction between temperature and plant-plant interactions *i.e.* leaf C:N ratio, SLA, and LDMC (Table 1, Fig. 3). First, in absence of any plant-plant interactions, along the tested gradient of temperatures, leaf C:N ratio remained constant, LDMC decreased, and SLA showed maximal mean value at 18°C. However, interactions modified this pattern of response in the three traits (Fig. 3). More specifically, under intraspecific *vs* interspecific interactions, SLA showed respectively no variation and an increase in response to increasing temperatures, while LDMC values displayed opposite response pattern. In addition, leaf C:N ratio values were significantly higher at 18°C with both intraspecific and interspecific neighbors. Second, at 13°C that is the optimal growth temperature, SLA showed higher mean value under interspecific interactions than without or under intraspecific interactions while LDMC values did not differ between interaction treatments. In addition, leaf C:N ratio values were overall higher when ramets grew under intraspecific interactions than without interaction, with intermediate values

under interspecific interactions. However, temperature modified these response patterns to plant-plant interactions, in particular for LDMC and leaf C:N ratio that displayed similar responses (Fig. 3). Indeed, at 18°C, their values increased under inter- and intraspecific interactions in comparison with the no interaction treatment, and at 23°C, their values were higher under intraspecific interactions than under interspecific interactions or without interaction. The two other leaf and growth traits (*i.e.* leaf C content and height) responded to plant-plant interactions only, regardless of temperature (Table 1). Ramets under intraspecific interactions were smaller than those cultivated without neighbors or with interspecific ones, while leaf C content was the lowest under interspecific interactions

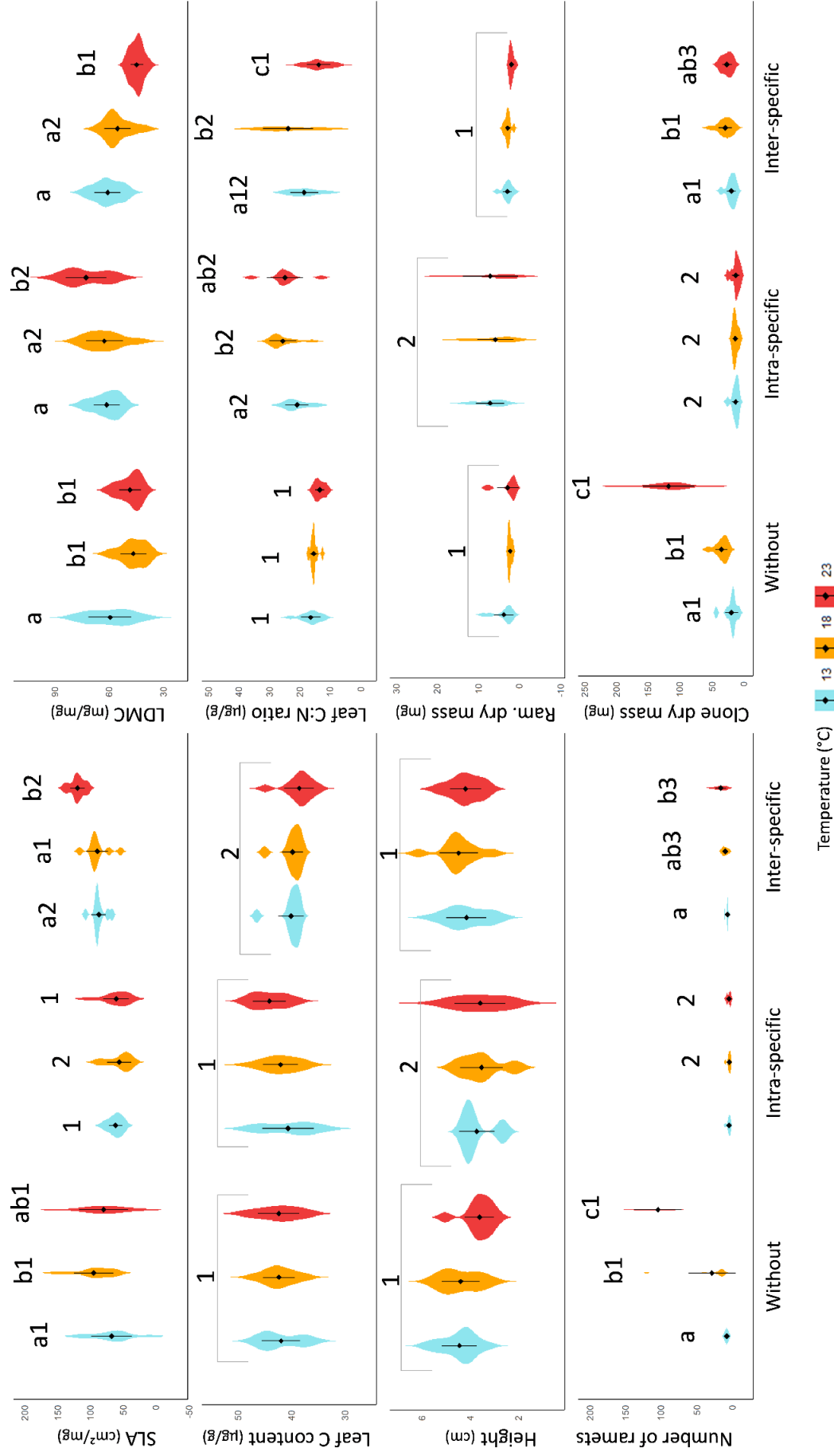
compared to under intraspecific interactions and without interaction.

On the other hand, the two performances traits measured at the clone level responded to the interaction between temperature and plant-plant interactions, whereas these only have an additive effect on ramet dry mass (with a much stronger effect of plant-plant interactions) (Table 1, Fig. 3). Indeed, ramet had significantly higher dry mass under intraspecific interactions compared to the two other interaction treatments. At clone level, number of ramets significantly increased along with rising temperatures except under intraspecific interactions. Moreover, at 13°C, number of ramets was similar between interactions treatments. At 18°C and 23°C

**Table 1.** Results of ANOVAs performed on mixed models with interactive fixed effects, that is the effect of temperature (three treatments) and plant-plant interactions (three treatments) on different traits (at ramet or clone level). In addition, models also included the clone genotype as random factor. Interaction term between both explanatory variables was deleted when non-significant, and models were fitted again with additive effect. Fstats in bold characters indicates a significant effect of the explanatory variable on the response variable. In addition, results of post-hoc tests are mentioned when one variable or additive effects were significant.

	Traits	Temperature (df=2)	Plant-plant interactions (df=2)	Temperature x plant-plant interactions (df=4)
Ramet leaf traits	SLA	<b>6.46*</b>	<b>47.81***</b>	<b>14.79**</b>
	LDMC	<b>7.22*</b>	<b>48.50***</b>	<b>35.67***</b>
	Leaf C content	0.90 <sup>ns</sup>	<b>14.04***</b>	x
	Leaf C:N ratio	<b>13.84***</b>	<b>51.80***</b>	<b>18.45**</b>
Ramet growth trait	Height	3.99 <sup>ns</sup>	<b>9.63**</b>	x
Ramet performance trait	Ramet dry mass	<b>7.33*</b>	<b>30.59***</b>	x
Clone performance trait	Number of ramets	<b>122.21***</b>	<b>219.96***</b>	<b>60.52***</b>
	Clone dry mass	<b>38.63**</b>	<b>140.21***</b>	<b>66.10*</b>

Notes: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ ; 'n.s.' not significant ( $p > 0.1$ ). 'x' the predictor did not influence the response variable and was removed from the tested model. Log transformation of the following variables: height, ramet dry mass and clone dry mass.



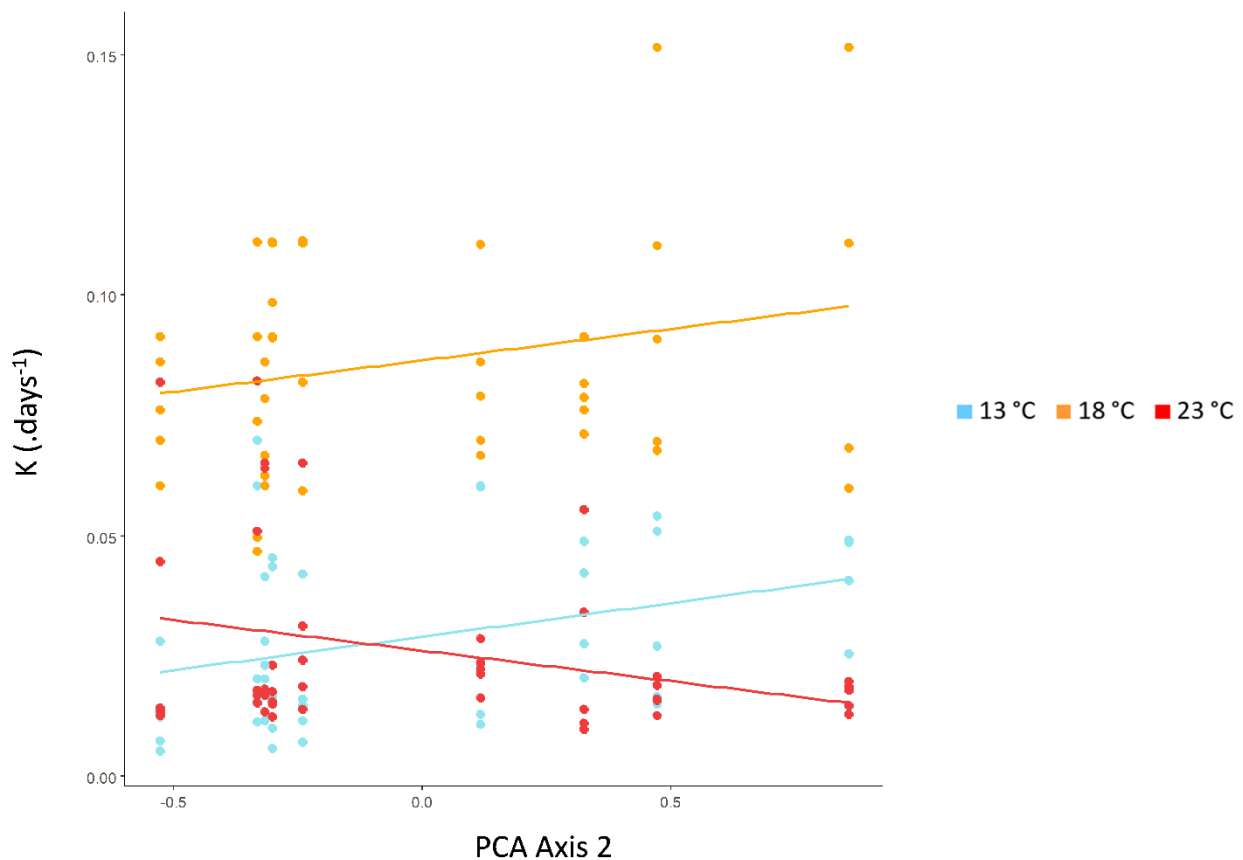
**Figure 3.** Violin plots showing the distributions of the values of the eight traits measured on *Limosella australis* individuals cultivated under the three tested temperatures (13°C, 18°C, 23°C) and the three treatments of plant-plant interactions. All traits were measured at ramet level, except for number of ramets and clone dry mass which were measured at clone level. 'a', 'b', 'c': results of pairwise comparisons of means among temperatures within each plant-plant interactions treatment. '1', '2', '3': pairwise comparisons of means among plant-plant interactions treatments within each temperature. When letters or numbers are absent: no significant difference in mean trait values. In black: mean  $\pm$  SD. 'Ram. dry mass': ramet dry mass.



however, it was the lowest under intraspecific interactions and the highest without interactions, with the interspecific interaction treatment displaying intermediate values. In the same way as number of ramets, clone dry mass significantly increased in absence of interactions along with the rising temperatures. Under intraspecific interactions clone dry mass remained constant regardless of temperature. At 13°C (optimal growth temperature), and at 18°C clone dry mass was the lowest under intraspecific interactions compared to the two other interactions treatments. At 23°C, clone dry mass was maximal without any interactions and minimal under intraspecific interactions, with an intermediate value under interspecific interactions.

*Evo to eco: Individual traits variations as a proxy of litter quality*

A Principal Component Analysis (PCA) was performed on leaf traits to reduce dimensions (Appendix 2), so that coordinates on PCA Axis 1 and 2 were used as a proxy of litter qualities. PCA Axis 1 (48.4%) was negatively related to SLA, and positively to LDMC and leaf C:N ratio. PCA Axis 2 (24.3%) was positively related to leaf C content. Thus, since LDMC and leaf carbon content are negatively correlated with litter decomposability in the literature and conversely for SLA and leaf nitrogen content, negative values on PCA Axes 1 and 2 were indicative of good litter quality, and conversely.



**Figure 4.** Decomposition rate (K) as functions of leaf C content (PCA Axis 2 values) at the three tested temperatures. The straight lines represent the linear model adjustment to the data (significant regressions).

*Decomposition rate (K) responded to temperature and leaf C content*

PCA Axis 1 was not kept as explanatory variable of decomposition rate K by the model selection procedure based on AIC criteria (neither alone nor in interaction with temperature). However, we found an interactive effect of temperature and PCA Axis 2 on decomposition rates K (ANOVA test,  $F_{df=2}=6.02$ , P-value=0.003). More specifically, at 13°C, K increased with values of PCA Axis 2 ( $t=0.01$ ), *i.e.* with increasing leaf C content. However, higher temperatures modified this response pattern as K decreased with higher leaf C content at 23°C (Fig. 4). Besides, K was overall significantly higher at 18°C than at 13°C and 23°C (ANOVA test,  $F_{df=2}=122.51$ , P-value<0.001).

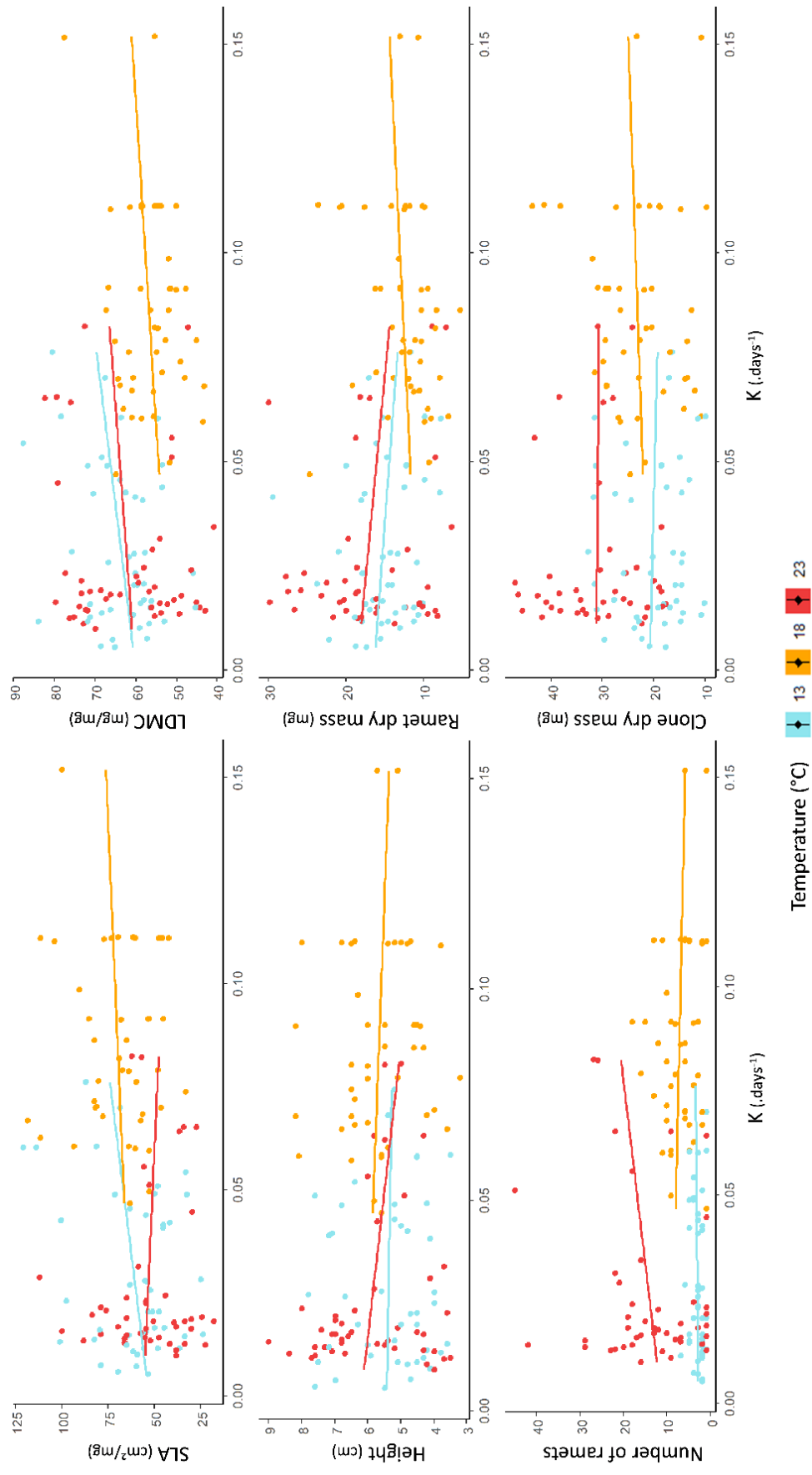
*Eco to evo: LDMC and performances responded to temperature and/or decomposition rate*

Three out of the four traits measured at ramet level (*i.e.* SLA, height, and ramet dry mass) did not respond to either decomposition rate K or temperature (Table 2). LDMC however, was influenced by K and temperature, but separately (no significant interaction between these two factors). LDMC significantly increased with decomposition rate ( $t= 1.77^*$ ), while its values were higher under 13°C and 23°C than 18°C (Fig. 5). In addition, performances at clone level (*i.e.* clone dry mass and number of ramets) were impacted by temperature: clones produced more ramets and with higher dry masses at 23°C compared to 13°C and 18°C (Table 2, Fig. 5).

**Table 2.** Trait responses to decomposition rate K × temperature. ANOVA tests were performed on the most probable mixed effects models determined based on the AIC selection method, and testing the interactive effect of temperature (three treatments) and decomposition rates on trait values (measured either at the ramet or clone level). In addition, models also included the clone genotype as random factor. Model predictors in bold characters had a significant effect on response variable values. Slope (t) of the explanatory variable K was added when significant. Pairwise comparisons among temperatures are indicated when temperature had significant effects on trait values.

		K (df=1)	Temperature (df=2)	K × Temperature (df=2)	Pairwise comparisons among temperatures
Ramet leaf traits	SLA	0.47 <sup>ns</sup>	5.46 <sup>ns</sup>	1.48 <sup>ns</sup>	
	LDMC	<b>3.89*</b> (t=1.77)	<b>14.13***</b>	0.24 <sup>ns</sup>	13/23°C > 18°C
Ramet growth trait	Height	x	x	x	
Ramet performance trait	Ramet dry mass	0.49 <sup>ns</sup>	3.79 <sup>ns</sup>	4.35 <sup>ns</sup>	
Clone performance traits	Number of ramets	0.35 <sup>ns</sup>	<b>102.24***</b>	2.13 <sup>ns</sup>	23°C > 18°C > 13°C
	Clone dry mass	0.18 <sup>ns</sup>	<b>6.25*</b>	3.07 <sup>ns</sup>	23°C > 13/18°C

Notes: \*  $p < 0.05$ ; \*\*\*  $p < 0.001$ ; 'n.s.' not significant ( $p > 0.05$ ). 'x' tested predictors did not influence the response variable and was removed during model selection. To normalize data: log transformation was performed on all traits, except for the number of ramets.



**Figure 5.** Studied traits as functions of decomposition rate ( $K$ ) at each tested temperature. All traits were measured at the ramet level, except for the number of ramets and the clone dry mass, which were measured at the clone level. Solid lines indicate the fitted linear models.

## Discussion

### *Plant response to increasing temperatures is modified by the community context*

Within their warming habitat, plant individuals are now exposed to both plant-plant interactions and thermal constraints, although their trait responses to these two factors remain studied separately in the literature. We then originally tested the functional responses of the macrophyte species *L. australis* to these two factors varying simultaneously. We evidenced responses of the resource-acquiring and conserving traits, subsequently affecting individual biomass production. Furthermore, plant individuals developed different strategies of resistance to temperature depending on plant-plant interactions.

Under mild thermal conditions (13°C), the no-interaction mean phenotype of *Limosella australis* corresponded to a short stature of ramet with high SLA, low LDMC, and intermediate values of leaf N content (as depicted by leaf C:N ratio). This no-interaction phenotype was altered by plant-plant interactions. Indeed, intraspecific interactions lead to even smaller ramet with lower leaf N content, whereas interspecific interactions produced ramet of higher SLA, and lower leaf C content. These no-competition and interactive mean phenotypes were modified under thermal stress. Indeed, we highlighted that temperature and plant-plant interactions had interactive effects on the three studied traits involved in the leaf economic spectrum (leaf C:N ratio informing on leaf N content, SLA, and LDMC) *i.e.* on the individual strategy of nutrient investment and dry mass in leaves (Wright et al., 2004). More precisely, overall trait values of SLA and/or LDMC increased or decreased with rising temperatures in the three plant-plant interactions treatments, suggesting a strategy of gradual response from 13°C to 23°C. However, leaf C:N ratio displayed either similar (at 18°C) or different (at 23°C) values under the two treatments with plant-plant interactions, highlighting that interactive

strategies differed among temperatures. In addition, as each temperature was conducted within the same chamber, we are aware that our replicas are pseudo-replicas. However, as it is typically done in studies on the effects of temperature, we are rather confident about the validity of our results.

Furthermore, phenotype variations in response to rising temperatures depended on whether neighbors were functionally similar or not. In absence of interactions, we respectively found an increase and a decrease in SLA and LDMC, in response to rising temperatures, suggesting a plastic switch towards a more acquisitive strategy (Bjorkman et al., 2018). Under intraspecific interactions however, SLA remained constant along the rising temperatures, while LDMC experienced an increase at 18°C, and leaf N values decreased from 13°C to 18°C (as depicted by an increase of leaf C:N values from 13°C to 18°C), which would correspond to a tolerance strategy adapted to unfavorable habitats (Keddy et al., 1998). In addition, negative interactions (competition) would be more intense among functionally similar neighbors (Stubbs and Bastow Wilson, 2004; Funk et al., 2008), supporting the need to invest in a tolerance strategy. Under interspecific interactions, trait variations in response to temperatures were close to those observed in absence of interaction, suggesting less intense competition based on better use of resources among functionally different species (Kraft et al., 2014). This overall suggests that the probability of meeting a functionally similar or a dissimilar competitor in the community is determinant for species resistance to rising temperatures of their habitat.

The evidenced plastic responses in phenotypes to plant-plant interactions × temperature, subsequently affected their performances. In absence of plant-plant interactions, higher temperatures stimulated ramet production of similar dry mass enabling the clone to rapidly colonize space (Fahrig et al., 1994; Stuefer et al., 2002). Nevertheless, this pattern of performance response to

temperature differed under interactions. First, intraspecific interactions canceled this beneficial effect of temperature on plant growth, as clone and ramet performances remained constant, regardless of temperature. Second, in interspecific interactions, clonal performance slightly increased with temperatures (due to an increase in clonal propagation), but to a lower extent. This result would indicate that the responses to temperature on the one hand, and to temperature  $\times$  plant-plant interactions on the other hand, were not adaptive. This indicates that plant-plant interactions constitute an additional selective pressure for plant in a context of climate change, and that our predictions of the fate of species in a community context that are only based on their temperature responses are biased.

To conclude, considering that clone performances were higher without than with interactions, we did not evidence facilitative interactions in our experimental systems, which could be explained by several hypotheses. First, 23°C may not be high enough to result in severe thermal stress, and thus to induce facilitation. In their habitat, *L. australis* individuals occasionally experience these temperatures which may have resulted in the selection of resistant genotypes. Second, facilitative mechanisms in response to rising temperature through the limitation of leaf transpiration, as commonly found in terrestrial plants (Gómez-Aparicio et al., 2005; Sales Lucas et al., 2022), cannot occur in aquatic systems. Third, we used the resulting performance as a measure of the competition/facilitation balance. It is likely that, in our experimental system, higher temperatures resulted in higher nutrient availability through increased substrate mineralization. As a consequence, high competition for resources can emerge, as already showed in productive habitats (Goldberg et al., 1999), exceeding the benefits of facilitation.

### *Litter quality drives decomposition rate depending on the temperature*

In this study, we considered the complexity of real ecosystems as suggested by De Meester et al. (2019), by integrating the influence of plant-plant interactions into individual leaves responses to increasing temperature. As expected, these leaf trait variations determined litter quality, with low leaf C:N ratio, low leaf C content, high SLA, and low LDMC resulting in good litter quality, and conversely.

These differences in litter qualities, especially regarding leaf C content, subsequently affected litter decomposition and thus nutrient cycling, in interaction with temperature, which is consistent with the stream experiment of (Lecerf and Chauvet, 2008). However, the role of leaf C content was here counter-intuitive, as higher values favored better decomposition at 13°C and 18°C. Similar results were however evidenced by Coûteaux et al. (1991) on chestnut leaves. Looking at the decomposition dynamics, they showed that litter with high nitrogen (and low carbon) content initially had a high decomposition rate but a low one by the end of the experiment in relationship with the decomposer community composition. In contrast, they suggested that litter with low N and high C content should have favored the development of organisms able to degrade resistant compounds during the late decomposition stages. At 23°C, temperature may have erased the importance of the decomposer community composition compared to litter quality in the decomposition process. Surprisingly, variations in SLA, LDMC, and leaf C:N ratio were not sufficient to impact decomposition rate, probably because *Limosella australis* litter remains of good quality at the intraspecific level. Indeed, macrophyte species are known to produce easily decomposable tissues with few lignin (Hanlon, 1982; Kögel-Knabner, 2002).

Nevertheless, temperature explained most of the variance in litter decomposition rate. This is consistent with several studies where environmental factors, such as mean annual temperature or mean annual rainfall, explained the highest proportion of variance in litter decomposition rates, in comparison with litter quality and soil organism activity, in both stream and terrestrial systems (Lavelle et al., 1993; Hättenschwiler et al., 2005; García-Palacios et al., 2016). Interestingly, litter decomposition was overall the most efficient at 18°C in comparison with 13°C and 23°C, suggesting that this process was stimulated with increasing temperatures from 13°C to 18°C, but got limited when temperatures became too warm (23°C). This confirmed our working assumption on microbial decomposer activity, and highlights that the relationships between temperature and litter decomposition follows a bell-curve with an optimum at 18°C, in our experimental system based on the Iles Kerguelen ponds. This apparent discrepancy between our results and the literature usually describing a positive linear relationship between litter decomposition rate and temperature (but see Bradford et al., 2017) could be explained by experimental designs, which generally assess temperature increase through a latitudinal or an altitudinal gradient *in situ*, testing temperatures not much above the optimal thermal range (Aerts, 2006; García-Palacios et al., 2013, 2016; Follstad Shah et al., 2017; Amani et al., 2019), or under controlled experiment with tested temperatures that are not high enough (Ferreira et al., 2015). In the particular case of decomposer communities adapted to cold temperatures, 23°C would have been sufficient to limit their activity. The size of the active microbial biomass would then here dictate the change in decomposition rate with changing temperature (Bradford et al., 2017). This observation calls into questions the fate of polar decomposer communities and the subsequent impact on

nutrient cycling with temperatures over 18°C, as these have already been recorded in different places of the sub-Antarctic region: at the Iles Kerguelen (Meteo France, Douce et al. *submitted*), and at Marion Island (Nyakatya and McGeoch, 2007).

To conclude, we evidenced the influence of changes in phenotypes on ecological properties (*i.e.* Evo-to-eco feedback), and we showed a direct impact of increasing temperatures on litter decomposition. Yet, climate change impacts other environmental factors that may alter litter decomposition in freshwaters, such as differences in water chemistry (Bruder et al., 2014). We then suggest to pursue this kind of experimental studies, to fully assess the impact of climate change on aquatic ecosystem functioning.

#### *Eco-to-eco feedback of temperature and litter decomposition on plant growth*

At the ecosystem level, we partially confirmed our third hypothesis, initially stating that decomposition efficiency (as measured by decomposition rate) combined to temperature would ultimately affect plant traits variations. Indeed, in our experimental system, no traits are impacted by their interaction. We highlighted instead that LDMC responds to their additive effects, confirming the existence of an eco-to-eco feedback of nutrient cycling on the functional traits of *L. australis*. Litter decomposition is an ecosystem process which mediates many ecosystem parameters such as carbon sequestration, as well as the amount of mineralized and bioavailable nutrients (Kaye and Hart, 1997; Regina, 2001; Schimel and Bennett, 2004; Aponte et al., 2012; Yang et al., 2022). We showed that litter decomposition was stimulated with increasing temperatures up to 18°C, and as warming stimulates microorganisms efficiency, it is likely that N mineralization is also accelerated (Rustad et al., 2001). This should especially be true in our system mimicking cold biomes where decomposition

is temperature limited (Hobbie et al., 2002; Robinson, 2002). This increase in N availability would positively impact plant nutrient uptake, resulting in the observed low LDMC values (Wardle et al., 2004; Freschet et al., 2013). These alterations of the leaf economic spectrum (Reich et al., 1997; Wright et al., 2004) characterize individuals with a nutrient acquisitive strategy, in line with similar studies of systems with high resources availability (Ordoñez et al., 2009; Stanisci et al., 2020). In the contrary, the higher values of LDMC recorded at 13°C and 23°C, *i.e.* when decomposition (and probably nutrient mineralization) are less efficient, show that *L. australis* individuals switch their nutrient allocations toward a conservative strategy. Considering that ramet dry mass does not change with neither temperature nor litter decomposition, the highlighted variations in ramet strategies, maintain its performance. At the clone level, temperature increase is even beneficial and stimulates ramet production, regardless of the litter decomposition process.

Studies considering the effect of variations in ecological processes on phenotype variations and subsequent evolution remain rare in the literature (but see Bull et al., 2006; Becks et al., 2012; Brunner et al., 2017), and have never been conducted on plants so far. Here, we originally highlighted that feedbacks between ecological and evolutionary dynamics can co-occur through plant driven processes within the aquatic ecosystem. If the observed LDMC variations are heritable, ecological properties should further select its most adapted values in response to thermal changes (De Meester et al., 2019), resulting in evolutionary changes of aquatic plant phenotypes.

## Conclusion

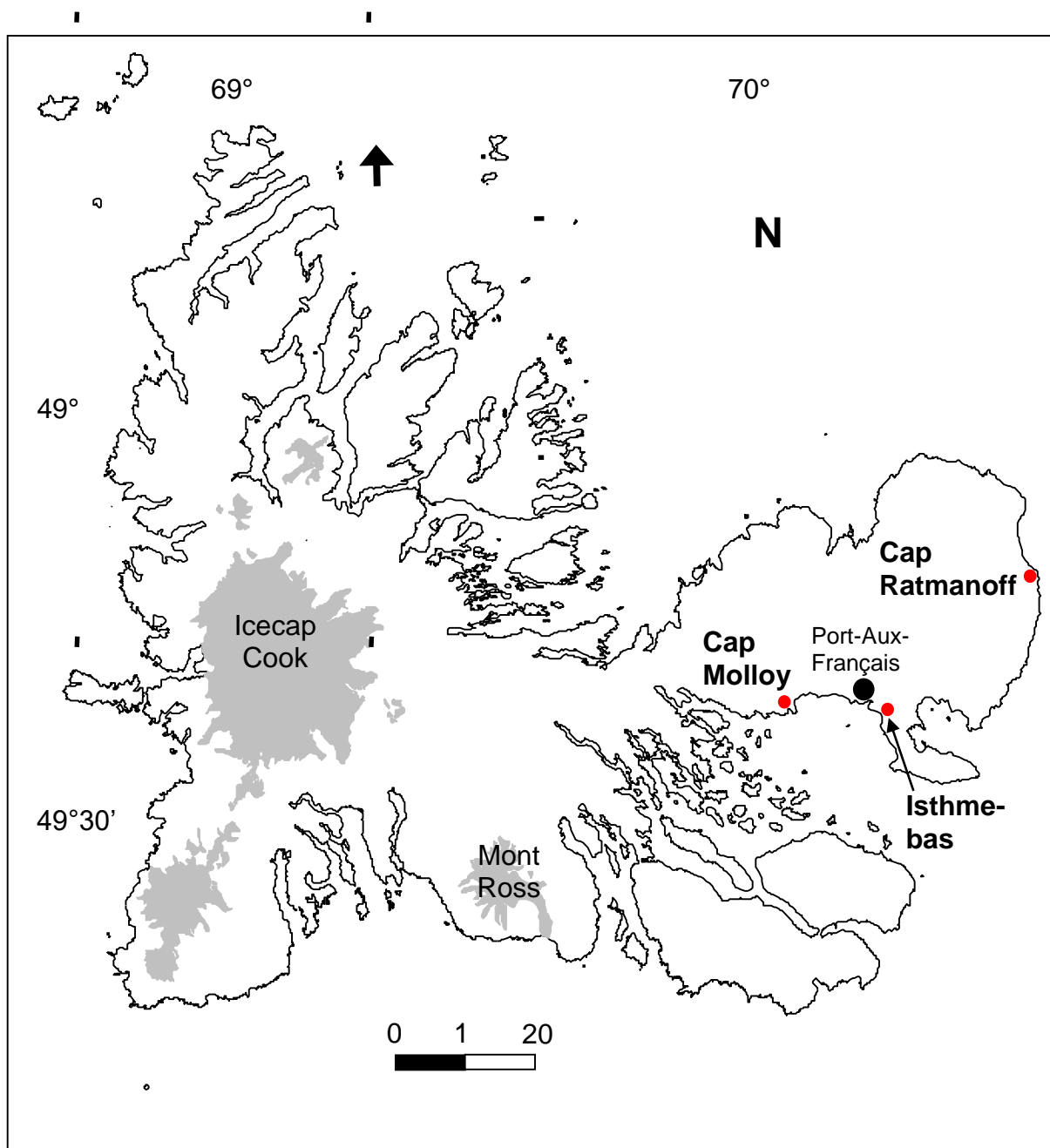
Through this study, we originally considered both the evo-to-eco and the eco-to-evo side of the Eco-Evo dynamics, together with the complexity of real systems by integrating within community interactions, to ultimately provide new evidence that ecological and

evolutionary dynamics can occur on similar timescales. Furthermore, we showed that temperature is directly but also indirectly (through litter quality and decomposition rate) involved in the Eco-Evo dynamics, bringing new insights on the underlying mechanisms of the effects of rising temperatures on plant biodiversity and aquatic ecosystems. In addition, we argue that to better evaluate thermal effects on litter decomposition, temperature variations should also be taken into account in mesocosm experiments. Indeed, previous studies indicated from model simulations that at a given mean temperature, these lead to higher decomposition rates than when temperature is kept constant (Tomczyk et al., 2020). Finally, although our study supports the emerging concept of eco-evolutionary dynamics, further researches are needed to better decipher impacts of ecological processes on evolutionary dynamics, especially on the long term (De Meester et al., 2019).

## Acknowledgements

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## Supplementary Information



**Appendix 1.** Locations (red points) of the three sampled sites on the French sub-Antarctic Iles Kerguelen ( $48^{\circ}30'–50^{\circ}S, 68^{\circ}27'–70^{\circ}35'E$ ). Black point: technical and scientific station.

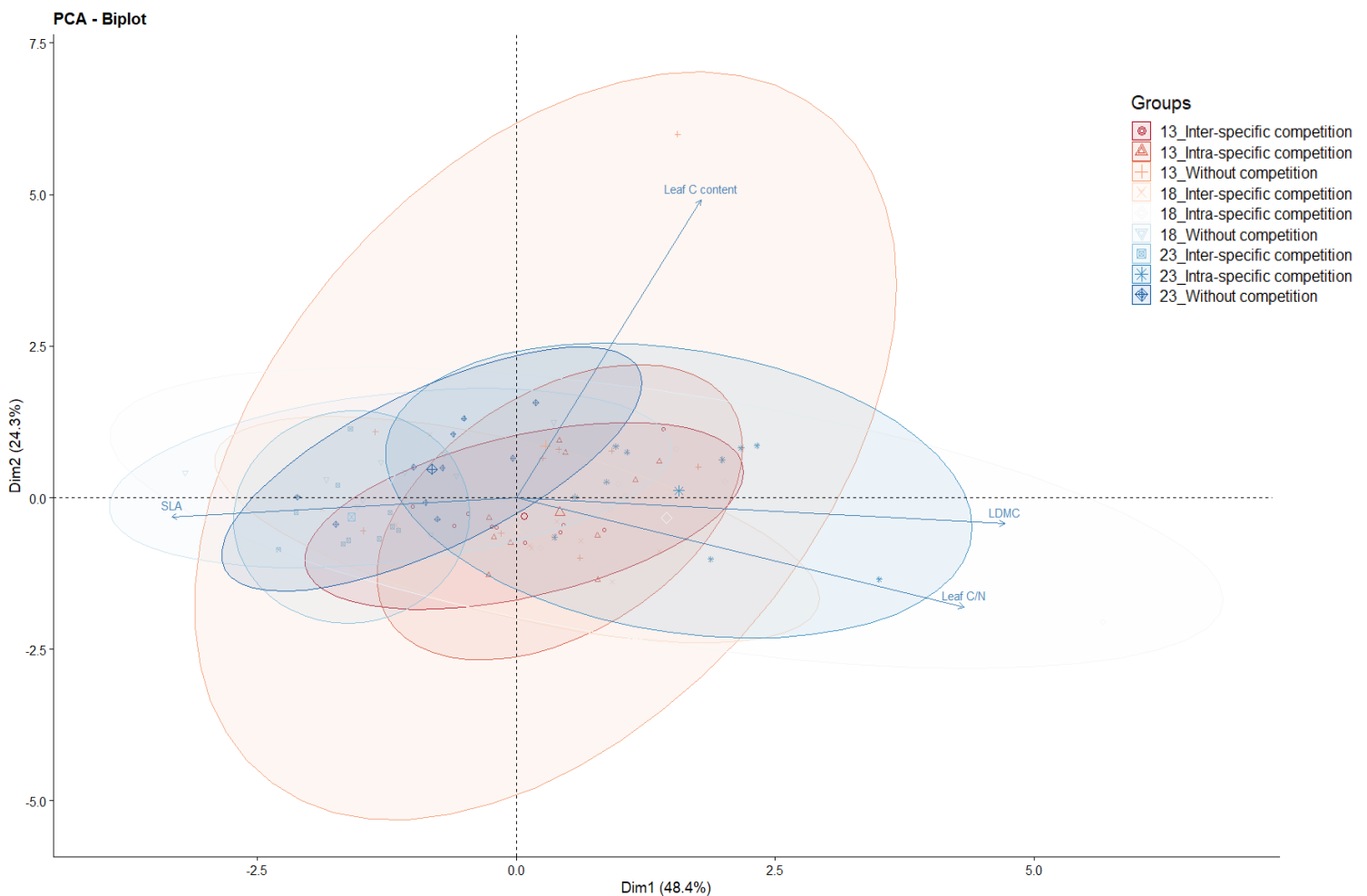


**Appendix 2.** a) Eigenvector scores for the first axis of a Principal Component Analysis (PCA) performed on leaf traits. The three highest eigenvector scores for each PCA axis are indicated in bold. Variance accounted for by the axes is indicated into brackets. PCA Axis 1 (48.4%) was negatively related to SLA, and positively related to LDMC and leaf C/N. b) PCA including the four leaf traits and one ellipsis per combination of [temperature x plant-plant interactions] treatment (nine ellipses in total). Ellipses centroids are indicated in bigger points, and their coordinates on PCA Axis 1 were used as proxy to the nine litter qualities.

a)

Leaf traits	PCA axis 1 (48.4%)	PCA axis 2 (24.3%)
Leaf C content	0.33	<b>0.92</b>
Leaf C/N	<b>0.80</b>	-0.05
SLA	<b>-0.62</b>	-0.08
LDMC	<b>0.88</b>	-0.33

b)



## DISCUSSION

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## 1. La température et la disponibilité en nutriments caractérisent l'habitat des macrophytes au sein des mares des Iles Kerguelen

Depuis quelques années, les mares d'eau douce suscitent un intérêt croissant (Oertli et al., 2010 ; Vad et al., 2017 ; Świerk & Krzyżaniak, 2019) grâce à la reconnaissance de leur contribution à la biodiversité d'un site (Oertli et al., 2002 ; Thiere et al., 2009 ; Oertli et al., 2010). Pourtant, ces systèmes restent encore peu étudiés, notamment en terme de sensibilité aux changements environnementaux, de structure, de fonctionnement, et de relations avec les systèmes terrestres environnants (Perotti et al., 2005). Jusqu'à présent, les études sur la végétation dans les mares ont surtout porté sur la composition floristique et la structure des communautés de macrophytes, sans lien avec les variations à la fois spatiales et temporelles des caractéristiques d'habitats (propriétés physiques et chimiques de l'eau et des sédiments) (Pienitz et al., 1997 ; Oertli et al., 2002 ; Della Bella et al., 2010 ; Vad et al., 2017). Ce manque de connaissances est encore plus important s'agissant des mares de la ceinture subantarctique et de la végétation qu'elles abritent, probablement en raison des difficultés logistiques pour échantillonner ces systèmes. Les dernières publications concernant la description abiotique des mares des Iles Kerguelen datent des années 1980 (Hureau, 1985 ; Smith, 1985), dans lesquelles celles-ci n'étaient pas réellement décrites comme des systèmes à part entière, mais plutôt comme des systèmes « côtiers » qui réunissaient sans distinction les systèmes terrestres et d'eau douce en bordure de littoral. Depuis, les changements climatiques rapides dans cette région (Chapuis et al., 2004 ; Frenot et al., 2006 ; Lebouvier et al., 2011) ont sûrement eu d'importantes répercussion sur la biologie de ces systèmes, dont les espèces sont adaptées à des températures froides et stables, soulignant la nécessité de mettre à jour les études. L'**article I** présenté dans cette thèse est le premier à décrire les variations spatio-temporelles de ces systèmes mares dans les Iles Kerguelen, en terme de caractéristiques abiotiques et de composition des communautés de macrophytes, et à déterminer les variables biotiques et abiotiques les plus structurantes pour ces communautés.

En particulier, nous avons montré une hétérogénéité intra-site des habitats, principalement expliquée par les valeurs moyennes et la variabilité de trois paramètres abiotiques : la hauteur de la colonne d'eau, la température de l'eau et la disponibilité en nutriments (**article I**). De plus, la structure des communautés de macrophytes diffère plus entre mares qu'entre sites (59.5% de la variation des compositions des mares sont expliqués par des différences inter-mares, contre 7.1% par des différences inter-sites), impliquant l'existence de paramètres locaux (à l'échelle des mares) qui contrôlent la structure de ces communautés. Ces

résultats font écho aux travaux de [Williams et al. \(2004\)](#), dans lesquels la diversité Beta mesurée était élevée entre des mares échantillonnées dans le sud de l'Angleterre. Plusieurs hypothèses non mutuellement exclusives ont été énoncées afin d'expliquer ces résultats.

Premièrement, [Williams et al. \(2004\)](#) ont évoqué un effet de la dispersion des individus ([Allen, 2007](#)) en lien avec la distance entre les mares ([Briers & Biggs, 2005](#)). En revanche, nous avons montré dans notre étude que la différenciation locale des communautés végétales n'est pas liée à cette distance. Ce résultat est confirmé par **l'article III** dans lequel nous avons montré que cette distance inter-mare n'avait aucun effet sur les paramètres biotiques mesurés (richesse spécifique, diversité fonctionnelle, patrons spatiaux). Ainsi, bien que les mécanismes de dispersion de ces espèces restent encore à approfondir, il est probable que la dispersion des graines entre mares se fasse par hydrochorie ([Hennion & Walton, 1997a](#)) ou à grande distance par zoochorie (par adhésion des graines aux pattes des animaux notamment). Elle ne serait donc pas limitée et ne correspondrait donc pas au moteur de la différenciation locale des communautés de macrophytes. Deuxièmement, au vu de la faible richesse spécifique dans nos systèmes et de sa stabilité temporelle (**article I**), il est peu probable que le turnover d'espèces explique les différences de composition de communautés entre mares, comme suggéré dans certains articles ([Briers & Warren, 2000](#) ; [Williams et al., 2004](#)). En revanche, nous avons mis en évidence de fortes variations de paramètres abiotiques entre mares, expliquant la variabilité locale des communautés végétales (autour de 27% de variation de composition des mares expliquée par ces paramètres). Dans notre étude, nous avons en particulier montré que les variations de températures journalières et de disponibilité en nutriments en lien avec la fréquentation de la faune locale, correspondent aux paramètres qui discriminent le plus les différents types d'habitat au sein des mares. Par ailleurs, nous avons noté que la composition des communautés diffère légèrement entre saisons et années, en lien avec des études ayant observé des variations inter-annuelles ([Wilcox & Simonin, 1987](#) ; [Körs et al.](#)) ou saisonnières ([Weiher & Keddy, 1995](#)) dans la distribution de macrophytes, en grande partie expliquées par les fluctuations de niveau d'eau. Toutefois, ces variations temporelles restent relativement négligeables face aux variations spatiales (intra-site) des communautés de macrophytes dans ces systèmes.

Pour conclure, l'hétérogénéité spatiale et temporelle des mares demeure un aspect essentiel à prendre en compte, tant pour notre compréhension de l'écologie fondamentale de ces systèmes que pour leur conservation. Les changements climatiques en cours dans la région

subantarctique pourraient impacter la biologie des mares, directement à travers la récurrence de températures extrêmes et les variations de précipitations (Chapuis et al., 2004 ; Frenot et al., 2006 ; Lebouvier et al., 2011), et indirectement *via* le déclin des populations des animaux marins qui maintiennent un apport nutritif (Hindell et al., 2017). Par ailleurs, les Iles du Subantarctique ne sont pas toutes impactées de la même manière par le changement climatique. Au sein des Iles Kerguelen et de l’Ile Marion, les températures moyennes annuelles augmentent, accompagnées d’une baisse du niveau annuel de précipitations (Lebouvier et al., 2011 ; McClellan et al., 2018). L’Ile Macquarie expérimente plutôt des saisons de plus en plus contrastées en terme de climat, avec des hivers plus humides et des étés plus chauds (Bergstrom et al., 2015). Aussi, bien que les espèces de macrophytes étudiées dans cette thèse soient présentes sur toutes ces îles (Iles du Prince Edward, Iles Heard et MacDonald, Iles Crozet, Ile Marion ...), avec néanmoins une suspicion d’endémisme de *Ranunculus moseleyi* aux Iles Kerguelen (Bergstrom & Selkirk, 2000 ; Chau et al., 2021), leurs réponses à ces changements climatiques pourraient s’avérer différentes, nécessitant des recherches plus approfondies à l’échelle de la région. En particulier, la conservation de ces espèces est un enjeu majeur puisqu’elles présentent une aire de répartition très limitée (Hennion & Walton, 1997b ; Van der Putten et al., 2010 ; Lehnebach et al., 2017 ; Chau et al., 2021). Ainsi, bien que deux espèces se soient avérées relativement tolérantes aux fortes variations de températures dans les mares (*J. scheuchzerioides* et *R. pseudotrullifolius*), les autres espèces apparaissent sensibles aux variations enregistrées (**article I**).

Par conséquent, les éléments théoriques issus des travaux de cette thèse pourraient être réinvestis dans le cadre de la gestion des milieux naturels des Iles Kerguelen, et contribuer ainsi au maintien de la biodiversité végétale originale et pristine de la Réserve Naturelle Nationale des Terres Australes Françaises, et plus largement d’autres régions froides du monde.

## 2. Mécanismes d'assemblage des communautés végétales dans les systèmes mares

A notre connaissance, les travaux sur les dynamiques temporelles des communautés de macrophytes étudient en grande majorité la dynamique des patrons observables à l'échelle des communautés, comme leur structure par exemple, sans prendre en compte l'aspect fonctionnel (Howard & Lee, 2003 ; Anderson, 2007 ; Hassler et al., 2010). Pourtant, les travaux s'appuyant sur une approche fonctionnelle permettent de définir les mécanismes sous-jacents à ces patrons (**article IV**). Elle permet également de prédire l'impact des paramètres abiotiques et biotiques de l'habitat sur le sens et l'intensité des interactions interspécifiques, et par conséquent sur la productivité et le devenir de la communauté végétale (**article III**). Dans ce contexte, les études menées sur le terrain et développées dans les **articles II, III et IV** se proposent de préciser les mécanismes en lien avec l'*habitat filtering* et les mécanismes de coexistence pouvant expliquer les variations de structure des communautés observés *in situ* dans les **articles I et III**.

### a. L'échelle des mares : la plus pertinente pour l'étude des assemblages au sein des communautés végétales aquatiques

La détermination des règles d'assemblage des communautés est largement dépendante de l'échelle spatiale considérée. S'il est communément suggéré que l'action des filtres abiotiques (*habitat filtering*) est observable à large échelle (régionale par exemple), les mécanismes de coexistence des espèces opèrent à des échelles plus locales (Bycroft et al., 1993 ; Stoll & Prati, 2001 ; Götzenberger et al., 2012). La partition de variance de traits se présente alors comme un outil pertinent pour inférer les mécanismes d'assemblage des communautés (Violle et al., 2007, 2012 ; McGill, 2008 ; Taudiere & Violle, 2016) et déterminer l'échelle écologique à laquelle ils opèrent : échelles temporelles, spatiales et/ou phylogénétiques. Pourtant, très peu de travaux ont étudié les variations de traits fonctionnels sur ces trois échelles simultanément ce qui limite les possibilités de comparer leurs effets relatifs (mais voir Luo et al., 2016 ; Henn et al., 2018 ; Liu et al., 2018). A travers une partition de variance sur un jeu de données comprenant plusieurs traits fonctionnels, nous avons montré l'action d'un filtre opérant à l'échelle temporelle (inter-années) et régionale (inter-sites) et qui a conduit à la réduction de la variabilité de l'ensemble des traits (probablement un filtrage abiotique) contrastant avec leur grande variabilité à l'échelle intra-site (**article II**). Cette dernière observation semble cohérente avec la forte variabilité de composition des communautés de macrophytes observées entre mares plutôt qu'entre sites

**(article I).** En effet, des transports de ramets sur de longues distances (entre sites) sont suspectés d'opérer grâce aux déplacements des oiseaux marins.

Par conséquent, nos travaux ont permis de montrer que l'échelle des mares est la plus pertinente pour inférer les mécanismes d'assemblage des communautés végétales aquatiques des Iles Kerguelen. C'est donc à cette échelle que nous avons étudié les mécanismes déterminant la structure spatiale des communautés de macrophytes **(article III)**. Aucune relation significative n'a été notée entre les patrons spatiaux et les interactions plantes-plantes, contrairement aux précédentes études (Lacoul & Freedman, 2006 ; Boschilia et al., 2008). Cette étude est la première à notre connaissance à trouver une absence de relation entre patrons spatiaux et interactions plantes-plantes en milieux aquatiques. En revanche, une approche basée sur un modèle d'équations structurelles, nous a permis de montrer que les paramètres abiotiques (en particulier la conductivité de l'eau) sont bien plus déterminants que les paramètres biotiques (diversité fonctionnelle de la communauté) pour la formation des patrons spatiaux des espèces au sein des mares.

Nous avons également montré que près de 75% des patrons spatiaux significatifs détectés à l'échelle des mares étaient des patrons de ségrégation, indiquant que les espèces se répartissent plutôt en patches monospécifiques **(article III)**, comme observé dans l'étude de Boschilia et al. (2008). Cela peut s'expliquer par plusieurs hypothèses non mutuellement exclusives, dont la faible richesse spécifique au sein des mares (impliquant une plus forte probabilité que deux espèces occupent deux micro-sites distincts), l'occupation de micro-sites favorables à la croissance des espèces, ou des phénomènes de compétition. Néanmoins, cette dernière hypothèse apparaît peu plausible, puisque nous n'avons relevé aucune modulation des patrons spatiaux par les interactions plantes-plantes.

#### **b. Les filtres abiotiques sont les facteurs les plus déterminants pour les assemblages des espèces au sein des communautés végétales aquatiques**

Une grande partie des études fonctionnelles qui portent sur les mécanismes d'assemblage des communautés végétales utilise des métriques de valeurs moyennes de traits fonctionnels, sans prendre en compte la dispersion des valeurs, limitant ainsi le pouvoir explicatif de ces études. En effet, les patrons de convergence/divergence de valeur de traits sont un puissant outil pour inférer les mécanismes d'assemblage au sein des communautés en réponse à des variations de

conditions environnementales (Cornwell & Ackerly, 2009 ; Herben & Goldberg, 2014 ; Kraft et al., 2015 ; Cadotte & Tucker, 2017). L'**article IV** est un des seuls à ce jour à étudier les patrons de dispersion de plusieurs traits fonctionnels sur une échelle temporelle et spatiale au sein des communautés en réponse à des variations d'habitats (mais voir Bjorkman et al., 2018). Pour cette étude, nous nous sommes appuyés sur une approche basée sur le calcul d'espaces multidimensionnels de traits (cinq au total) à l'échelle des communautés. Leurs variations informent en effet sur les patrons de convergence/divergence des valeurs de ces traits et renseignent donc sur les mécanismes d'assemblage des communautés étudiées (Mao et al., 2022).

En particulier, nous avons étudié les paramètres d'habitats des mares sur trois sites, et ce sur quatre années (**article IV**). Plusieurs facteurs abiotiques se sont avérés structurant pour les assemblages des communautés de macrophytes au cours du temps et entre les sites étudiés. La température, le niveau d'eau et la disponibilité en nutriments dans l'eau et les sédiments sont les filtres abiotiques qui, globalement, semblent diriger le plus les assemblages des communautés à l'échelle du site. De plus, nous avons également souligné l'importance du pH et du taux d'oxygène dans l'eau. Par conséquent, les résultats de cet article (**article IV**) complètent ceux de l'**article I**. En effet, les paramètres à l'origine des différences d'habitats entre les mares (**article I**) agissent finalement en tant que filtres abiotiques. L'approche par modèle d'équations structurelles (**article III**) nous a également permis de mettre en évidence une modulation des paramètres abiotiques entre eux. Notamment, de façon contre-intuitive, il apparaît que l'intensité lumineuse peut négativement impacter les performances d'une communauté *via* son effet positif sur la température de l'eau, renforçant les effets négatifs de cette température sur les communautés.

De la même façon, les paramètres abiotiques des habitats dans lesquels se trouvent les communautés de macrophytes modulent leurs paramètres biotiques. Nous avons ainsi montré une modulation des interactions plantes-plantes par la température et la disponibilité en nutriments (**article III**), un résultat bien connu de la littérature (Eränen & Kozlov, 2008 ; Biswas & Wagner, 2014 ; Schneider et al., 2015 ; Zhang et al., 2020). Les filtres abiotiques ne sont pas les seuls mécanismes à régir les assemblages des espèces au sein d'une communauté. Les interactions plantes-plantes inter- et intraspécifiques opèrent également sur les assemblages, amenant les espèces à adopter des mécanismes de réponse permettant leur coexistence (*i.e.* l'égalisation des fitness et la stabilisation des différences de niche, Chesson,



2000 ; Grime, 2006 ; Kraft et al., 2015). L'issue des interactions plantes-plantes est donc ici modifiée, définissant *in fine* les caractéristiques fonctionnelles de la communauté (Chesson, 2000). Toutefois, par phénomène de rétroaction, la composition fonctionnelle et la diversité au sein des communautés peuvent impacter les mécanismes de coexistence, et donc les interactions plantes-plantes (Suzuki et al., 2014 ; Valladares et al., 2015). En effet, nous avons montré que les caractéristiques fonctionnelles moyennes des individus voisins, ainsi que leurs différences fonctionnelles notamment en terme d'acquisition des ressources, affectent l'intensité voire la direction des interactions plantes-plantes *via* la modulation des mécanismes de coexistence (**article III**). En particulier, nos résultats ont révélé que les deux processus possibles de coexistence des espèces agissaient simultanément au sein des communautés végétales, en fonction de l'identité des espèces voisines. Par exemple, nous avons observé chez *R. biternatus*, une facilitation par un voisinage à forte diversité fonctionnelle aérienne, mettant en évidence des mécanismes de « limiting similarity » sur les ressources aériennes. De plus, *R. biternatus* était favorisée par un voisinage à faible diversité fonctionnelle racinaire, suggérant l'existence de hiérarchies compétitives liées aux ressources du sol. En outre, ces résultats indiquent que la direction et l'intensité des interactions, c'est-à-dire l'équilibre entre la concurrence et la facilitation dans un habitat soumis à des contraintes abiotiques, résultent des caractéristiques fonctionnelles des voisins liées à l'acquisition de ressources, pas seulement des caractéristiques fonctionnelles des cibles.

Pour conclure, les modulations réciproques entre les interactions plantes-plantes et la structure fonctionnelle des communautés, de même que les paramètres abiotiques, conduisent à des mécanismes d'assemblage complexes qui opèrent simultanément à l'échelle des communautés (Spasojevic & Suding, 2012 ; Copeland & Harrison, 2017). Ainsi, l'étude du modèle plutôt simple des mares des Iles Kerguelen nous a permis de bien appréhender et clarifier les mécanismes d'assemblage au sein de ces communautés, avant de pouvoir étudier des modèles plus complexes en terme de richesse spécifique. La détermination des stratégies des espèces en réponse aux variations de ces différents facteurs est également une étape essentielle pour la compréhension des dynamiques des communautés végétales, car elles déterminent les caractéristiques fonctionnelles des espèces, et sont donc à l'origine des variations de mécanismes d'assemblage et de structure de communautés observées dans l'**article I** et **IV**.

### c. Conséquences pour les performances des communautés végétales aquatiques

Les variations spatio-temporelles des facteurs biotiques et abiotiques déterminent *in fine* les performances des communautés, qui peuvent s'évaluer au travers de différentes métriques, comme la production de biomasse totale (productivité) ou le taux de recouvrement de la végétation.

Dans le cadre de l'**article III**, au travers d'une approche reposant sur un modèle d'équations structurelles, nous avons montré que l'influence de ces facteurs peut être directe ou s'opérer *via* la modulation d'autres paramètres biotiques ou abiotiques, soulignant l'importance de caractériser finement les paramètres environnementaux. En particulier, nous avons montré l'impact négatif indirect d'une forte profondeur et d'un fort taux de conductivité électrique de l'eau sur cette productivité, *via* leur action sur les interactions plantes-plantes, induisant en conséquences des variations de paramètres biotiques (diversité fonctionnelle, richesse spécifique et patrons spatiaux). Par exemple, une forte hauteur de colonne d'eau amène les espèces à présenter des caractéristiques fonctionnelles similaires pour faire face à un manque de luminosité (Fu et al., 2018), conduisant à une exclusion compétitive des individus les moins adaptés, et donc à une communauté moins performante par manque de complémentarité fonctionnelle. Par ailleurs, nous avons montré que le taux de couverture des mares par la végétation (**article I**) varie en fonction de la distance à la mer, suggérant l'importance de la fréquentation par les animaux marins et de leurs apports en nutriments pour la performance de la communauté de macrophytes.

Ainsi, ces deux articles (**article I et III**) s'inscrivent dans la lignée de précédentes études qui ont montré les effets directs de certaines variables abiotiques (morphologie du système aquatique, physico-chimie des sédiments et de l'eau) sur la physiologie des macrophytes, et donc sur leur biomasse (Wrona et al., 2006 ; MacKay et al., 2009 ; Dhir, 2015 ; Hossain et al., 2017 ; Velthuis et al., 2018 ; Zhang et al., 2020). De la même façon, l'**article III** soutient les travaux antérieurs sur l'effet indirect des conditions abiotiques sur les biomasses des communautés à travers leurs impacts sur les interactions plantes-plantes (travaux relevant de la Stress Gradient Hypothesis par exemple).

Pour conclure, ces variations de performance des communautés de macrophytes pourraient être liées à des variations de stratégies de réponse des espèces aux filtres abiotiques et biotiques de leur habitat et au caractère adaptatif de ces stratégies.

### 3. Réponses fonctionnelles des espèces de plantes aquatiques au stress thermique combiné aux interactions biotiques

Afin de déterminer les mécanismes sous-jacents aux patrons de réponses des communautés aux filtres biotiques et abiotiques observés sur le terrain, l'approche fonctionnelle a été particulièrement intéressante. Nous avons montré que différentes communautés développent des stratégies similaires en réponse à des conditions données de température et de disponibilité en nutriments (**article IV**). En parallèle, nos expérimentations en conditions contrôlées nous ont permis de mettre en évidence les réponses à l'échelle spécifique. En particulier, nous avons étudié les stratégies fonctionnelles mises en place par les espèces en réponse à un des facteurs abiotiques les plus structurants pour les communautés de macrophytes au sein des mares (la température de l'eau, **articles II, III et IV**), dans un contexte d'interactions plantes-plantes. En effet, à notre connaissance, aucune étude n'a étudié les effets interactifs de ces deux facteurs, bien que les espèces végétales y soient soumises simultanément *in natura*.

#### a. Stratégies de réponses des espèces de macrophytes des Iles Kerguelen

Les réponses fonctionnelles de quatre espèces (*L. australis*, *C. antarctica*, *R. moseleyi* et *R. pseudotrullifolius*) ont été testées face une augmentation de la température en situation d'interactions plantes-plantes, en conditions contrôlées (**articles V et VI**). En particulier, la réponse fonctionnelle des individus de *L. australis* a été testée face à un gradient thermique de 13 °C à 23 °C uniquement sur des traits aériens (**article VI**), tandis que celle des individus de *C. antarctica*, *R. moseleyi* et *R. pseudotrullifolius* a été testée sur un gradient de 8 °C à 18 °C sur plusieurs catégories de traits (aériens, clonaux et racinaires chez *C. antarctica*, aériens et racinaires chez les deux espèces de Renonculacées) (**article V**). De façon intéressante, nous avons montré que les valeurs moyennes de trois traits foliaires, chez *L. australis*, répondent aux effets interactifs de la température et des interactions plantes-plantes (**article VI**). En revanche cet effet interactif n'a pas pu être mis en évidence chez les trois autres espèces étudiées (**article V**), indiquant l'absence d'une mise en place d'une stratégie intermédiaire entre aptitude compétitive et résistance à la contrainte thermique chez ces espèces. De plus, cela nous indique que les réponses sont finalement espèces dépendantes.

Plus précisément, chez *L. australis*, nous avons mis en évidence une plasticité foliaire en réponse à la hausse des températures, qui s'est avérée dépendre de la similarité fonctionnelle

entre l'individu cible et les individus voisins (**article VI**). Sans interaction plantes-plantes, les modules témoins présentent des valeurs moyennes de SLA plus fortes en réponse à la hausse des températures (23 °C), traduisant une stratégie d'acquisition des ressources. Dans le cas d'interactions intraspécifiques, nous avons noté une forte intensité de compétition entre voisins fonctionnellement semblables (Stubbs & Bastow Wilson, 2004 ; Funk et al., 2008), conduisant les individus à investir dans une stratégie de tolérance basée sur la conservation des ressources (*i.e.* augmentation des valeurs moyennes de LDMC de 18 °C à 23 °C, et baisse des valeurs moyennes d'azote foliaire de 13 °C à 18 °C). En revanche, dans les mélanges interspécifiques, les variations de traits fonctionnels en réponse aux températures étaient proches de celles observées en l'absence d'interaction, ce qui laisse supposer une compétition moins intense qu'en monocultures, basée sur une meilleure utilisation des ressources chez des espèces fonctionnellement différentes (Kraft et al., 2014).

Chez *C. antarctica*, les modules ont mis en place une réponse plastique au niveau racinaire et clonal, plutôt qu'une plasticité aérienne (**article V**). En effet, nous avons observé respectivement une augmentation et une diminution de la mise en réserve au sein des racines et des connexions clonales, contrairement à nos attendus. Cette augmentation d'allocation des ressources à la mise en réserve dans les racines peut indiquer une stratégie de tolérance en réponse à un renforcement des contraintes thermiques (Grime, 2006), ou à l'inverse, un bénéfice apporté par des températures plus chaudes sur le métabolisme des modules. Par ailleurs, *C. antarctica* est une espèce qui se présente sous forme de canopée flottante, et se distingue donc du port en rosette des autres espèces. Ainsi, il est possible qu'elle n'ait pas le besoin d'investir dans des stratégies d'aptitudes compétitives, c'est-à-dire dans l'acquisition de ressources.

Chez *R. moseleyi* et *R. pseudotrullifolius*, deux espèces phylogénétiquement proches, les modules présentent des valeurs moyennes de SLA plus fortes en réponse à la hausse des températures (13 °C pour *R. moseleyi* et 18 °C pour *R. pseudotrullifolius*), accompagnée d'une hauteur moyenne plus importante chez *R. moseleyi* (**article V**). Aussi, il semblerait que ces deux espèces investissent dans une plasticité aérienne, avec une stratégie d'acquisition de ressources face à l'augmentation des températures, ce qui semble cohérent avec de précédentes études observant une croissance plus importante sous des températures plus chaudes (Poorter et al., 2009 ; Bjorkman et al., 2018). Aucun investissement dans les fonctions racinaires n'a par ailleurs été détecté (les réponses des traits clonaux n'ont pas pu être testées sur ces espèces). De plus, des modifications des co-variations entre plusieurs traits en réponse à la température et

aux interactions plantes-plantes ont été mises en évidence chez ces deux espèces. Cette stratégie permet de coordonner différentes fonctions pour maximiser la performance des individus avec un minimum d'investissement possible (Murren, 2002 ; De Kroon et al., 2005). En particulier, nous avons montré que les co-variations entre SLA et LDMC, et entre longueur des racines et hauteur différaient en terme d'intensité et/ou de direction chez les deux espèces de Renonculacées en fonction de la température et du type d'interactions. Par conséquent, nous avons souligné que le signe et l'intensité des co-variations des traits fonctionnels sont susceptibles de changer en réponse aux conditions environnementales variables, en particulier celles liées aux changements climatiques (Wright et al., 2004, 2005; Sgrò & Hoffmann, 2004; Pellissier et al., 2018; Maccagni & Willi, 2022). Ainsi, la plasticité phénotypique offrirait aux espèces la possibilité d'ajuster leur réponse à des variations environnementales au moyen des co-variations entre traits.

Pour conclure, ces études menées en conditions contrôlées soulignent les effets simultanés voire interactifs des interactions plantes-plantes et de la température sur les macrophytes, en particulier chez *L. australis*, démontrant l'importance de la prise en compte des facteurs biotiques dans les réponses fonctionnelles des plantes aux changements climatiques. De façon similaire, les mesures de traits fonctionnels réalisées *in situ* indiquent une modulation des valeurs moyennes de certains traits par des variables biotiques. Par exemple, la hauteur moyenne des individus (toutes espèces confondues) à l'échelle du site est modulée par la diversité de la communauté de macrophyte (**article IV**), tandis qu'à une spatiale échelle plus fine (intra-mare), les valeurs moyennes des traits clonaux et racinaires répondent à sa composition (**article II**). Il semble alors que la probabilité de rencontrer un concurrent fonctionnellement semblable ou différent dans la communauté soit déterminante pour la résistance des espèces à la hausse des températures de leur habitat. Nos résultats indiquent donc que la prise en compte des interactions biotiques, qui renforcent les pressions de sélection exercées sur les plantes aquatiques, permettrait d'affiner les modèles de prédictions des conséquences des changements climatiques sur la coexistence des espèces de macrophytes.

### b. Conséquences des variations phénotypiques sur la performance des espèces de macrophytes

Nous avons étudié les conséquences des variations phénotypiques mises en évidence, sur la performance des espèces de macrophytes. A l'échelle des communautés, nous avons montré

des modulations entre plusieurs traits fonctionnels et leurs conséquences sur la production de biomasse (**article II**). Les traits de croissance (hauteur) et de stockage de réserve (masse spécifique des racines et des entrenœuds) sont les traits qui favorisent le plus la performance des communautés, à l'inverse des traits architecturaux. Les traits clonaux affectent plus directement et plus intensément la performance des communautés qu'attendu, soulignant l'importance de la clonalité chez ces espèces de macrophytes pour faire face à des variations environnementales. Enfin, une hausse et une baisse des valeurs moyennes de SLA et de longueur des racines respectivement, affectent négativement la performance des communautés (**article II**), comme observé en cas de hausse des températures dans la gamme des valeurs mesurées sur le terrain (5.31 °C - 7.07 °C, **article II**).

Pour affiner notre compréhension des variations observées de performance des communautés, les expérimentations en conditions contrôlées ont permis de mettre en évidence les conséquences des variations phénotypiques sur les performances de quatre espèces en situation de températures élevées (18 °C ou 23 °C selon l'espèce). Chez *L. australis*, les clones semblent bénéficier de la hausse des températures (23 °C), étant donnée l'augmentation de leur performance (*i.e.* biomasse) en absence d'interaction (**article VI**). Néanmoins, les interactions plantes-plantes ont modifié les performances de cette espèce face à l'élévation des températures (**article VI**). En effet, les interactions inter- mais surtout intraspécifiques ont atténué le bénéfice procuré par la hausse des températures sur la croissance clonale et la performance des clones, suggérant des effets compétitifs. Il serait intéressant de tester ce même gradient de température (13 °C – 23 °C) chez les autres espèces de macrophytes des Iles Kerguelen, afin de pouvoir réellement comparer les réponses. Chez *C. antarctica* et *R. pseudotrullifolius*, les réponses ont été testées jusqu'à 18 °C. La plasticité des traits morphologiques permet visiblement aux individus de produire une biomasse similaire (et donc de maintenir leurs performances) sous de hautes températures (**article V**), soutenant ainsi la tolérance des clones, et ce indépendamment des interactions plantes-plantes (Pilon & Santamaría, 2002 ; Nicotra et al., 2010). Par conséquent, il semblerait que 18 °C (*C. antarctica* et *R. pseudotrullifolius*) et 23 °C (*L. australis*) n'atteignent pas les limites hautes de tolérance chez ces trois espèces. Les plants et les graines utilisées pour ces expérimentations ont au départ été collectés sur le terrain et multipliés végétativement en conditions contrôlées. *In situ*, des températures de 23 °C ont déjà été enregistrées. Il est donc possible qu'une sélection des génotypes résistants à ces températures ait déjà eu lieu (phénomène d'adaptation), expliquant que 18 °C ou 23 °C n'atteignent pas les limites hautes de tolérance de ces espèces. En revanche, chez *R. moseleyi*,

le fort taux de mortalité observé à 18 °C pourrait indiquer un dépassement des valeurs limites de tolérance thermique.

Les données manquantes sur les réponses de *J. scheuchzerioides* et de *R. biternatus*, deux espèces parmi les plus abondantes *in situ*, pourraient apporter des informations cruciales. Des études en conditions contrôlées sont prévues pour affiner nos connaissances des niches fondamentales et réalisées des six espèces de macrophytes des mares des Iles Kerguelen. Cependant, la baisse de performance des communautés végétales, observée dans les mares en réponse à des températures moyennes élevées (pourtant bien plus faibles que celles testées en conditions contrôlées) est à replacer dans la réalité plus complexe des conditions *in situ*. En effet, de multiples variables biotiques et abiotiques sont interconnectées et se modulent, et peuvent ensemble expliquer la baisse de performance des communautés. De plus, les températures peuvent varier sur de grandes amplitudes *in situ*, avec des températures au-delà de 23 °C relevées dans les mares les moins profondes, pouvant ainsi drastiquement augmenter les contraintes thermiques et dépasser les seuils de tolérance des macrophytes.

De plus, il serait intéressant d'étudier les conséquences des variations phénotypiques sur d'autres variables de performance (taux de survie, succès de la reproduction sexuée...) pour véritablement évaluer les conséquences des variations phénotypiques mises en évidence, sur les valeurs sélectives des individus.

### c. Perspectives

Les variations de plusieurs traits aériens et clonaux ont été expliquées par les variations de disponibilité en nutriments à l'échelle des sites (**article IV**) et des mares *in situ* (**article II**). Aussi, cela souligne l'importance de mener des expérimentations sur les effets de la disponibilité en nutriments sur les variations de valeurs des traits fonctionnels, notamment afin d'identifier les préférendums des six espèces de macrophytes étudiées, en terme de quantité mais aussi de formes disponibles de nutriments. En effet, manchots et éléphants de mer, les deux espèces marines qui enrichissent le plus les mares par leurs déjections, apportent différentes formes d'azotes (Smith, 1985) qui pourraient favoriser certaines espèces de macrophytes au détriment d'autres.



Pour approfondir notre compréhension des mécanismes de réponse des espèces étudiées aux interactions plantes-plantes × température, des analyses métabolomiques sont prévues. En effet, l'expression du métabolome se situe à l'interface entre la perception des signaux environnementaux et leur traduction au niveau des traits fonctionnels, jouant ainsi un rôle majeur dans les réponses aux contraintes environnementales ([Smirnoff, 1995](#) ; [Croteau et al., 2000](#) ; [Wahid & Ghazanfar, 2006](#) ; [Groppa & Benavides, 2007](#) ; [Wink, 2013](#)). Dans cette optique, dans le cadre des suivis *in situ* (**Articles II et IV**) et de l'expérimentation faisant l'objet de l'**article V**, les parties aériennes, racinaires et clonales (connexions) ont été échantillonnées, et conservées afin d'être analysées. Les résultats issus de ces futures analyses devraient nous permettre de produire de nouvelles connaissances sur les mécanismes de réponse des espèces végétales aux contraintes multiples de leur habitat. En effet, à ce jour, les études métabolomiques n'ont que très rarement été menées en réponses à des interactions biotiques (mais voir [Hennion et al., 2016](#)) et jamais dans un contexte simultané de contraintes thermiques.

#### 4. Effets sur le fonctionnement des systèmes mares

##### a. Mise en évidence d'une dynamique Eco-Evo au sein d'un écosystème aquatique

Le champ disciplinaire des boucles éco-évolutives s'inscrit parfaitement dans la compréhension des réponses des communautés et du fonctionnement des écosystèmes face aux changements environnementaux rapides telle que l'élévation des températures (De Meester et al., 2011 ; Urban et al., 2012 ; Merilä & Hendry, 2014). En effet, les réponses des espèces peuvent impacter les processus opérant à des échelles plus larges, notamment les fonctions écosystémiques (effet « bottom-up ») (Suding et al., 2008). C'est alors la composante « Evo vers Eco » des boucles éco-évolutives. En retour, les modifications du fonctionnement de l'écosystème peuvent impacter des échelles d'intégration beaucoup plus fines comme celles des espèces ou des communautés (effet « top-down », **article VI**), définissant la composante « Eco vers Evo » des boucles éco-évolutives. Réaliser ces changements d'échelle est d'un intérêt majeur dans un contexte de changements climatiques, puisqu'ils permettent d'étudier les effets directs et indirects des changements environnementaux sur les écosystèmes et les communautés qu'ils abritent. Les traits fonctionnels permettent de réaliser les changements d'échelle nécessaires dans cette approche et sont donc pertinents pour étudier les phénomènes bottom-up et top-down.

L'**article VI** fait l'objet d'une étude sur les boucles éco-évolutives opérant au sein des écosystèmes aquatiques, dans un contexte de communautés. Cette étude a été menée en conditions contrôlées, *via* l'utilisation de mésocosmes, afin de se rapprocher au mieux des conditions des mares *in situ*. Premièrement, cette étude participe à la compréhension des relations entre les communautés végétales et les fonctions écosystémiques au sein des zones humides, qui reçoivent peu d'attention malgré leurs caractéristiques uniques et les fortes pressions anthropiques qui pèsent sur ces systèmes (Bardecki, 1991 ; Khelifa et al., 2022). Deuxièmement, peu de recherches sur les dynamiques Eco-Evo prennent en compte la réalité complexe au sein d'une communauté (Barraclough, 2015 ; De Meester et al., 2019). Il a pourtant été suggéré que la prise en compte des coévolutions entre espèces permettrait d'améliorer la compréhension des boucles éco-évolutives. En effet, les phénotypes de chaque espèce peuvent non seulement influencer la dynamique de sa population, mais aussi impacter celle des autres espèces au sein de la communauté (McPeck, 2017). Ces changements déterminent ensemble les

caractéristiques de la communauté et les conséquences sur l'écosystème (De Meester et al., 2019). Aussi, l'**article VI** permet d'apporter des premières réponses sur la modulation des dynamiques Eco-Evo par les interactions plantes-plantes. Troisièmement, ces travaux sont les premiers, à notre connaissance, à étudier la boucle éco-évolutive complète (c'est-à-dire les composantes simultanées « Eco vers Evo » et « Evo vers Eco ») au sein d'une communauté végétale (De Meester et al., 2019).

#### b. Les réponses des macrophytes à la température × interactions plantes-plantes déterminent le fonctionnement de l'écosystème mare

Dans l'**article V**, nous avons mis en évidence des variations de qualité des feuilles (SLA) en réponse au gradient thermique testé chez *R. moseleyi* et *R. pseudotrullifolius*. En particulier, nous avons montré que les modules présentent en moyenne, des valeurs de SLA plus fortes à 13 °C chez *R. moseleyi* et à 18 °C chez *R. pseudotrullifolius*, en comparaison avec 8 °C. De la même façon, *in situ*, nous avons constaté de plus fortes valeurs de SLA chez les communautés de macrophytes des mares les plus chaudes. Or, les résultats de l'**article VI** nous indiquent que la SLA participe à définir la qualité des litières : des feuilles avec de fortes SLA conduisent après leur sénescence, à une litière de meilleure qualité. Par conséquent, nos résultats semblent indiquer que la qualité des litières augmenterait à l'échelle des communautés de macrophytes, en réponse à une augmentation des températures. Néanmoins, cette hypothèse reste à vérifier puisque les variations des taux de carbone et azote foliaires, qui participent également à la qualité de la litière, n'ont été mises en évidence que chez *Limosella australis*, ne nous permettant pas d'extrapoler quant aux potentiels effets des réponses fonctionnelles des cinq autres espèces sur les taux de décomposition des litières, et donc sur le fonctionnement de l'écosystème mare.

Plus particulièrement, dans l'**article VI**, nous avons montré que les variations de traits foliaires (*i.e.* teneur en carbone foliaire) modifient les processus de décomposition des litières résultantes, composante « Evo vers Eco » de la boucle éco-évolutive. En effet, les valeurs de teneur en carbone foliaire affectent la qualité de litière, et donc indirectement sa décomposition. Les interactions plantes-plantes ont conduit à des modifications de ces valeurs de teneur en carbone foliaire (avec notamment des taux de carbone foliaires plus faibles en interactions interspécifiques), et donc *in fine*, de la décomposition de la litière et de tous les processus

écosystémiques associés. De plus, la température est venue moduler les effets de la teneur en carbone foliaire, avec une meilleure décomposition sous 18 °C, en comparaison des températures 13 °C et 23 °C. En retour, ces variations de décomposition ont impacté les valeurs moyennes de LDMC chez les individus de *L. australis*, caractérisant la dynamique « Eco vers Evo » si et seulement si ces variations de LDMC ont une base génétique et sont donc héréditaires. Par conséquent, nous avons montré que les dynamiques « Eco vers Evo » et « Evo vers Eco » opéraient simultanément, et spécialement au sein d'une communauté végétale. Nous prévoyons de compléter notre étude par la mise en évidence des effets des variations des taux de décomposition sur les nutriments foliaires. Par ailleurs, en complément de cette étude en conditions contrôlées, il serait intéressant de mener une expérimentation *in situ* avec un traçage isotopique pour reconstituer les cycles biogéochimiques et le fonctionnement écosystémique associé dans un contexte naturel.

Etant à la base de toute chaîne trophique, la compréhension des phénomènes de rétroaction entre processus évolutifs et écologiques sous un climat changeant doit attirer d'avantage d'attention. En effet, la température a impacté différents processus : que ce soit la décomposition de la litière, ou les réponses phénotypiques des individus de *L. australis*. Ainsi, la température joue un rôle important dans les processus écosystémiques des zones humides (Bridgham et al., 1995 ; Lafleur et al., 2005 ; Chivers et al., 2009), non seulement en modifiant directement les paramètres biogéochimiques des systèmes (Kløve et al., 2010 ; Song et al., 2013), mais aussi en modifiant les valeurs de traits fonctionnels des macrophytes. Par conséquent, il serait particulièrement intéressant d'étendre cette étude à d'autres types de communautés végétales, qu'elles soient terrestres ou aquatiques, notamment sur des communautés en régions polaires particulièrement sensibles au changement climatique.

### c. Perspectives

Bien que les macrophytes soient des espèces cruciales dans le fonctionnement d'un écosystème aquatique, les communautés microbiennes joueraient également un rôle important (Graham et al., 2016 ; Balsler et al., 2022). Pourtant, aucune étude à ce jour n'a caractérisé ces communautés dans les régions subantarctiques, en particulier dans un contexte de changements climatiques, alors que ces communautés sont adaptées à des conditions fraîches et sont à la base de nombreux processus écosystémiques. Des travaux sur leurs sensibilités aux modifications climatiques permettraient d'affiner notre étude, et donc les connaissances sur les perturbations du

fonctionnement de ces écosystèmes particuliers. D'après nos résultats, nous avons supposé que 23 °C se rapprochait des limites hautes de tolérance thermique pour les communautés microbiennes des Iles Kerguelen, de par la baisse d'efficacité de la décomposition de la litière observée de 18 °C à 23 °C (**article VI**). Toutefois, bien que peu nombreux, de récents travaux ont montré un fort potentiel d'évolution rapide des communautés microbiennes en réponse à la hausse des températures, surtout au sein de systèmes froids ([Cherabier & Ferrière, 2022](#) ; [Abs et al., 2022](#)). En particulier, il a été montré que certains micro-organismes décomposeurs tirent des bénéfices de l'élévation des températures, permettant d'augmenter la production d'enzymes, et par conséquent, d'accélérer les taux de décomposition, en particulier dans les régions froides ([Cherabier & Ferrière, 2022](#) ; [Abs et al., 2022](#)). Aussi, la prise en compte simultanée des deux communautés, microbienne et végétale, dans les dynamiques éco-évolutives, permettrait de prendre en compte les possibles co-évolutions entre plantes et microorganismes décomposeurs dans les réponses des écosystèmes mares face aux changements climatiques. Une hypothèse serait qu'une meilleure qualité de litière, résultant de la hausse des températures (**article VI**), amènerait à un relâchement des contraintes pour les communautés microbiennes, rendant ces communautés moins déterminantes pour les processus de décompositions, et donc le fonctionnement de l'écosystème mare.

Lors de notre expérimentation de décomposition de litières de différentes qualités et sous différentes températures, en complément des mesures décrites dans l'**article VI**, nous avons effectué un suivi des flux de carbone et d'azote entre les différents compartiments de notre système expérimental par traçage isotopique. Les résultats issus de ces mesures feront l'objet d'un prochain article. L'objectif est de reconstruire les cycles de la matière qui se déroulent au sein des mares dans un contexte de changement climatique en quantifiant les transferts de C et N depuis la litière vers les plantes, les sédiments, l'eau et l'atmosphère. En effet, l'accélération des flux de nutriments au sein des cycles biogéochimiques en réponse à une augmentation des températures peut favoriser les transferts de C, N et P depuis le compartiment litière vers les sédiments et la colonne d'eau, et donc accélérer le relargage de gaz à effets de serre directement à travers une meilleure efficacité des micro-organismes décomposeurs, ou indirectement à travers l'impact sur la composition fonctionnelle de la communauté ([Peñuelas et al., 2013](#)). Nous avons également quantifié la production de deux gaz effet de serre (CO<sub>2</sub> et CH<sub>4</sub>) relâchés dans l'atmosphère, tous les 15 jours, pendant la durée de l'expérimentation. Cette étude serait alors l'une des premières à reconstruire les flux de nutriments au sein d'écosystèmes aquatiques de type « mare ».

## Conclusion

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Dans cette thèse, nous avons montré l'importance des facteurs abiotiques, tels que la température et la disponibilité en nutriments, mais aussi des facteurs biotiques, comme les interactions plantes-plantes, dans plusieurs processus opérant à différents niveaux d'organisation biologique, notamment les mécanismes d'assemblage des communautés végétales aquatiques et les processus écosystémiques associés. De plus, nous avons mis en évidence l'existence de modulations complexes entre ces facteurs, grâce à la simplicité du modèle des mares des Iles Kerguelen. Par ailleurs, les données collectées *in situ* pendant quatre années, ont déjà permis de montrer l'impact négatif des changements climatiques sur les systèmes mares. Ces résultats ouvrent alors de nombreuses perspectives d'études sur les dynamiques futures des systèmes aquatiques de la région Subantarctique et d'autres régions froides du monde, sensibles à une augmentation des températures, même modérée. De même, ces travaux pourraient être étendus sur des systèmes plus grands et anthropisés (lacs), dont le fonctionnement et la sensibilité aux changements thermiques sont probablement différents de par leur taille et leur exposition probable à des contraintes additionnelles d'origine humaine (Carpenter et al., 2005).

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