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arthropods and vegetation as ecological bioindicators
over time in the archipelago of Saint-Pierre & Miquelon
(France)**

Axel Hacala

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L'UNIVERSITE DE RENNES

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par **Axel HACALA**

Conservation et dynamiques des tourbières subarctiques : les arthropodes et la végétation comme bioindicateurs à travers le temps sur l'archipel de Saint-Pierre et Miquelon

Thèse présentée et soutenue à Rennes, le 28 mars 2024

Unité de recherche : ECOBIO, UMR 6553 CNRS - UR

Composition du Jury :

Présidente :

Gabrielle Thiébaud, Professeure, Université de Rennes, Laboratoire ECOBIO, UMR 6553

Rapporteurs avant soutenance :

Emilie Gauthier, Professeure, Université de Franche-Comté, Laboratoire Chrono-environnement, UMR 6249

Peter Convey, Professeur à la British Antarctic Survey

Examineurs :

Joël Bêty, Professeur, Université du Québec à Rimouski

Sébastien Gallet, Maître de conférences HDR, Université de Brest, Laboratoire Géoarchitecture

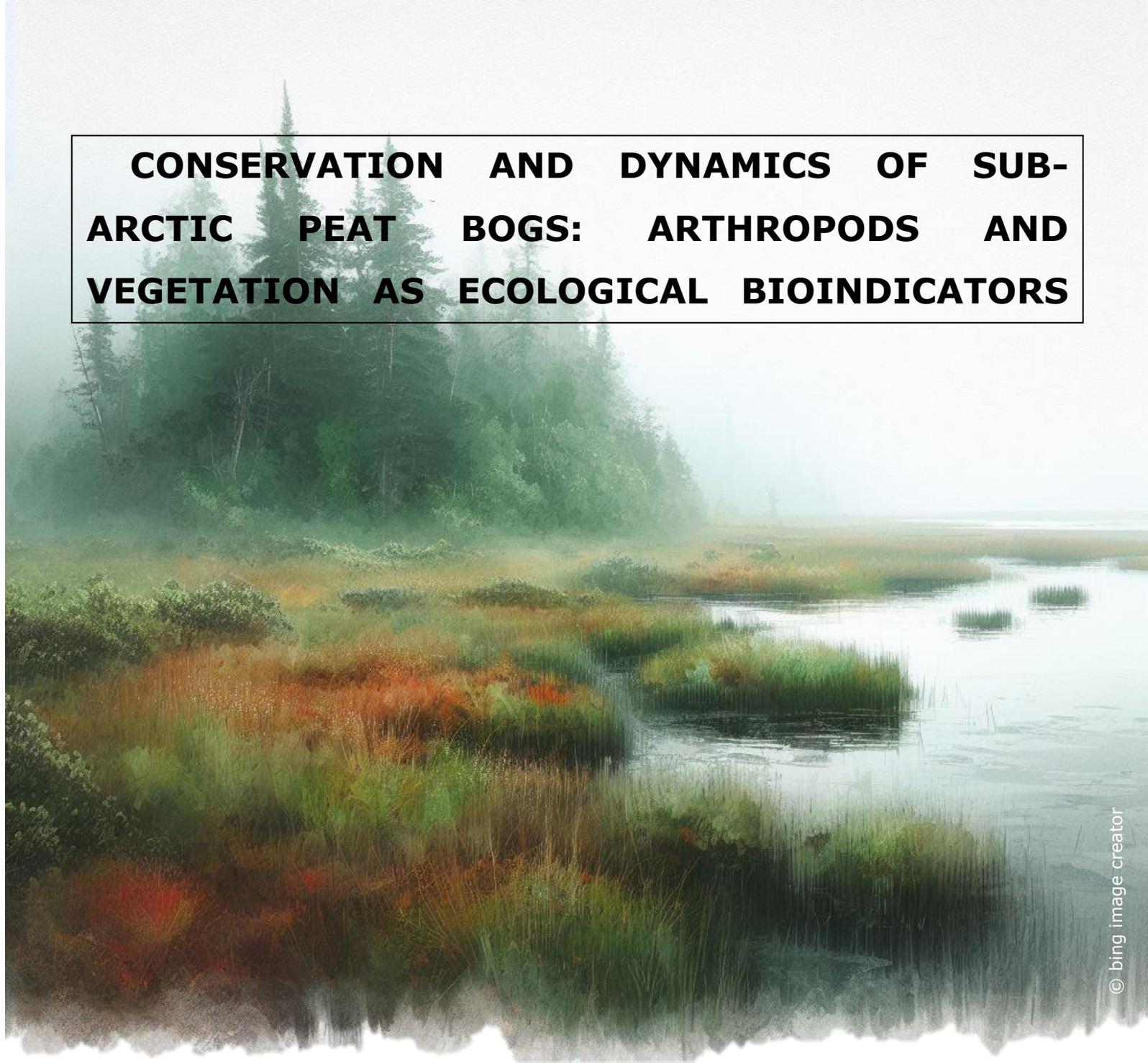
Directrice et directeurs de thèse :

Directeur : Dominique Marguerie, Directeur de recherche, Université de Rennes, Laboratoire ECOBIO, UMR 6553

Co-Directrice : Allison Bain, Professeure, Université Laval, Laboratoire d'archéologie environnementale

Co-Encadrant : Julien Pétilon, Professeur, Université de Rennes, Laboratoire ECOBIO, UMR 6553

CONSERVATION AND DYNAMICS OF SUB-ARCTIC PEAT BOGS: ARTHROPODS AND VEGETATION AS ECOLOGICAL BIOINDICATORS



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“The philosophical study of nature endeavors, in the vicissitudes of phenomena, to connect the present with the past.”

— Alexander Von Humboldt



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TABLE OF CONTENTS

List of figures.....	I
List of tables.....	VII
Résumé en français	IX
I. Introduction	1
A. Thesis objectives	3
B. Theoretical framework.....	5
1. Ecological indicators.....	5
2. Peat bogs, a peculiar habitat.....	10
3. Multiplicity of model: complementarity through time and space	15
4. Ecology, climatology and History: Studying a North American French archipelago	24
II. Material and methods: Thesis course and actions justifications.	31
A. The 2021 season on Saint-Pierre & Miquelon (FRANCE)	34
B. The 2022 campaign of Nain archipelago (Labrador, Canada)	41
C. Sample treatment.....	41
D. Study sites	42
1. Saint-Pierre site, ZS.....	42
2. Miquelon and Langlade sites, ZM and ZL.....	43
E. Methods performed by colleagues	43
F. Thesis manuscript outline	43
III. Neoecology	45
Spider and Vascular Plant Assemblages in Subarctic Peat Bogs are Complementary Ecological Indicators of Variation in Local and Landscape Factors.....	47
Highlights	47
Résumé	48
Abstract.....	49

1. Introduction.....	50
2. Material and methods.....	53
3. Results.....	57
4. Discussion	67
Acknowledgements	73
Funding	73
IV. Paleoecology	75
A. Oribatid mites as bioindicator of past climates: an exploratory approach using climate reconstruction method and a case study from St. Pierre and Miquelon, France.	77
Résumé	77
Abstract.....	78
1. Introduction.....	79
2. Material and methods.....	81
3. Results.....	85
4. Discussion	93
Acknowledgements	96
Funding	96
B. Atlantic subarctic peat bogs ecology through a two millennia dynamic, a transdisciplinary multi-taxon approach.	97
Résumé :	97
Abstract:	98
1. Introduction.....	99
2. Material and methods.....	101
3. Results.....	107
4. Discussion	128
5. Conclusions	136
Acknowledgements	137
Funding	137

V. General discussion	139
A. Objectives recall	141
1. Synthesis of the results and conclusions	141
B. Peat bog, a complex habitat	143
1. Peat bog, resistant yet sensitive	143
C. Bioindication, a powerful tool that still can grow through theory and usage 146	
1. What we learnt about the indicators	146
2. Which indicator to pursue next?	148
D. From pluridisciplinarity to multidisciplinarity: reunite past and present peat-bog diversities, crossing paleoecology and neoecology to resolve ecological dynamics	149
1. Defining the gap between what is done and what could be aimed for ..	149
2. How could this goal be achieved?	150
Bibliography	151
Appendix 1: Species lists	199
Appendix 2: projected weight of traits and variables from the RLQ analysis	205
Appendix 3: Climate reconstruction curves	207
Appendix 4: Curriculum Vitae	215

LIST OF FIGURES

- Figure 1 Adapted from Rydin et al. 2013: the classification of different peat bog depending on wetness, hydrological regime, level of tree cover and nutrient regimes.12
- Figure 2 Example of carnivorous plants in Saint-Pierre & Miquelon's bog. *Sarracenia purpurea* (1) from Langlade and *Drosera rotundifolia* (2) from Miquelon. (Photographers: Pascaline Caudal & Dominique Marguerie respectively)..14
- Figure 3 *Dolomedes striatus* female with cocoon, observed walking on water in a bog. Miquelon, chemin des boeufs, 2021. Photographer: Axel Hacala.16
- Figure 4 Example of Spider's sub-fossil from Scott (2003) that were identifiable. 8: Lycosidae cephalothorax; 9: Salticidae cephalothorax, possibly *Neon reticulatus*; 10: Male palp similar to *Trochosa terricola*; 11: Male palp similar to *Alopecosa pulverulenta*; 12: Palpal tibia from *Erigone atra*; 13: Epigynum from *Pardosa pullata*.17
- Figure 5 Example of a pteromorph, highlighted in darker grey, on a *Galumna perakensis*. Dorsale (left) and ventral (right) views. Only one pteromorph is represented per individuals but is usually symmetrical. Scale bar 100 μ m. Figure adapted from Ermilov & Kalúz (2019).18
- Figure 6 Example of oribatid mites sub-fossils from Erickson et al. (2003). A: *Limnozetes onondaga*; B: *Xylobates lophotrichus*; C: undetermined ceratozetoid; D: *Carabodes radiatus*; E: Oripoda sp.; F: *Naiazetes reevesi*; G: *Pelopsis bifurcatus*; H: *Suctobelbella* sp.; I: *Peloptulus* sp; J: *Tectocephus velatus*.20
- Figure 7 Morueta-Holme et al. (2015) adaptation of Humboldt "Tableau de la nature" to display the altitudinal variations of vegetations belts over 2010 years.21
- Figure 8 Example of macrofossils both, leaves and seeds, from an analysis performed by the Centre d'étude nordique (Québec, Canada) on samples from the peat core of Saint-Pierre (ZS1). Image from a report by Marie-Eve St-Pierre and Najat Bhiry.23
- Figure 9 The great double tombolo that links the islands of Miquelon and Langlade. Photo taken from Langlade facing north to Miquelon. (Photographer: Patrick Hacala)24

Figure 10 Erratic block in Saint-Pierre.25

Figure 11 Map of shipwreck on the Saint-Pierre & Miquelon archipelago between 1816 to 1959. Published in 1959 by the Ministère des travaux publics et des transports, Institut géographique national.26

Figure 12 Example of *Abies balsamea* in a boreal forest of Saint-Pierre Island in winter.27

Figure 13 *Rhododendron groenlandicum*, in flower. (Photographer: Patrick Hacala)28

Figure 14 Map of the two areas sampled. Up north the archipelago of Nain and down south the archipelago of Saint-Pierre & Miquelon.33

Figure 15 Schematization of one sampling units. Each yellow circle is the capture area on pitfalls traps placed at its center. The inner circle of 10m side represented the minimum distance between the pitfalls to avoid pseudoreplication while the outer square is the limit of the sampling unit, where the D-Vac aspirations are randomly distributed.34

Figure 16 Example of pedological exploration on ZM. (Photographer: Tristan Briand)35

Figure 17 Saint-Pierre site (ZS) sampling spatialization. The pitfall traps being represented with red dots.36

Figure 18 Miquelon site (ZM) sampling spatialization. The pitfall traps being represented with pink dots.37

Figure 19 Langlade site (ZS) sampling spatialization. The pitfall traps being represented with red dots.37

Figure 20 Example of temperature and hygrometry loggers on ZS3 sub-site. (Photographer: Pascaline Caudal).38

Figure 21 Example of micro-topography assessment based on drone imagery. The raster of topographical variation of a sub-site (right) and the 5m buffer around each pitfall traps (red dot) on ZS1 (left).39

Figure 22 Example of landscape habitat assessment with the example of ZM. Brown: Peat bogs; Light green: sub-arctic heathlands; Dark green: *Larix laricina* woods; Red: *Abies balsamea* woods; Pink: pools; Light yellow: ponds; Dark yellow: rivers; Red dots: pitfall traps.39

Figure 23 Illustration of peat coring with the extraction of the DNA cores in ZS1. The core extraction (left) and the wrapping of the sampled core (right). (Photographer: Sylvie Allen-Mahé).....40

Figure 24 Anse à Henry bonus site. (Photographer: Dominique Marguerie).....40

Figure 25 : ZS1 subsites. (Photographer: Patrick Hacala).....42

Figure 26 Miquelon sites from the south. (Photographer: Tristan Briand)44

Figure 27: Example of peat bogs surrounding the Langlade sites. (Photographer: Pascaline Caudal).....44

Figure 28 Map of St. Pierre & Miquelon. The red dots indicate the three study sites.53

Figure 29 Spider (A) and vegetation (B) alpha taxonomic diversity against sample coverage comparison between sites: S= St. Pierre; L= Langlade; M= Miquelon. The interval of confidences of each curve is based on a bootstrap following Chao et al. (2021).58

Figure 30 Spider (A) and vegetation (B) functional diversity against sample coverage comparison between sites: S= St.Pierre; L= Langlade; M= Miquelon. Functional diversity AUC corresponding to the area under the curve for the functional distinctiveness profile based on functional diversity calculation from Chao et al. (2021). The interval of confidences of each curve is based on a bootstrap following Chao et al. (2021).58

Figure 31 Spider (A & C) and vegetation (B & D) beta taxonomic (A & B) and functional (C & D) diversity against sample coverage comparison between sites: S= St. Pierre; L= Langlade; M= Miquelon. Functional diversity AUC corresponding to the area under the curve for the functional distinctiveness profile based on functional diversity calculation from Chao et al. (2021). Confidence interval of each curve is based on a bootstrap following Chao et al. (2021).59

Figure 32 4 RLQ projection of spider assemblages. Sites L= Langlade; M= Miquelon; ZS1, ZS2 & ZS3 = the three sub sites of St. Pierre.....61

Figure 33 The projected weight of each traits of spider’s assemblages link to the first (A) and second (B) axis and the projected weight of each environmental variable link to spider’s assemblages on the first (C) and second (D) axis. The dashed line was added to help visualize the 0.....61

- Figure 34 RLQ projection of vascular plant assemblages. Sites L= Langlade; M= Miquelon; ZS1, ZS2 & ZS3 = the three sub sites of St. Pierre.63
- Figure 35 The projected weight of each trait of vascular plants assemblages links to the first (A) and second (B) axis and the projected weight of each environmental variable links to vascular plants assemblages on the first (C) and second (D) axis. The dashed line was added to help visualizing the zero.63
- Figure 36 The relative variance explained by environmental variables in alpha diversity models for: (A) Spider taxonomic diversity; (B) Spider functional diversity; (C) Vascular plant taxonomic diversity; (D) Vascular plant functional diversity.65
- Figure 37 St. Pierre case study sites with example (left) of the landscape surrounding the sites (Photographer: Pascaline Caudal) and (right) the peat bog where the peat core was sampled (Photographer: Patrick Hacala).82
- Figure 38 Oribatid mites abundance through the peat core. In yellow the xerophilic species, in blue the aquatic, semi-aquatic and hygrophilous species, in orange, the mesophilic species, in green the species associated with forests and in grey the species without an associated ecology. The CONISS dendrogram is represented on the right of the diagram.83
- Figure 39 List and occurrences of species that were removed for the reconstruction. In blue the number of sites from which the species was removed, in orange the number of sites in which the species was kept.86
- Figure 40 Worldwide repartition of *Pergalumna nervosa* projected a maximum temperature raster.86
- Figure 41 Climatic reconstructions based on oribatid mite's assemblages for each month. In green the known temperature of the studied site, the upper and lower line being maximum and minimum temperatures while the middle line being the median temperature. In red, the reconstructed intervals of maximum temperature. In purple, the intervals of reconstructed median temperature. In blue, the intervals of reconstructed minimal temperatures. A: an example of poor temperature reconstruction with the Prus1 site; B: an example of intermediate temperature reconstruction with the Prus7 site; C: an example of improved temperature reconstruction with the Pcan1 site; C:

an example of miscellaneous temperature reconstruction with the site of Pcan5.	87
Figure 42 Fitted Gamma regression models showing the effect of explanatory variables on the delta between reconstructed and observed mean temperatures for the number of points (left) and the number of species (right).	89
Figure 43 Fitted Gamma regression models showing the effect of explanatory variables on the delta between reconstructed and observed maximum temperatures for the number of points (left) and the number of species (right).	89
Figure 44 Fitted Gamma regression models showing the effect of explanatory variables on the delta between reconstructed and observed minimum temperatures for the number of points (left) and the number of species (right).	90
Figure 45 Temperature reconstruction based on the oribatid assemblages for each month and for each time zone. In red the interval of maximum temperatures, in purple the interval of mean temperature and in bleu the interval of minimum temperatures.	92
Figure 46 Temperature reconstruction based on the vegetation assemblages for each month and for each time zone. In red the interval of maximum temperatures, in purple the interval of mean temperature and in bleu the interval of minimum temperatures.	92
Figure 47 Map of the Saint-Pierre & Miquelon archipelago with, on the right, the Burrin peninsula of the Newfoundland territory. The red dot being the sampling site on the Saint-Pierre Island.	102
Figure 48 Age-depth curve of the ZS1 core, ChronoModel 3.2.3.	104
Figure 49 Oribatid mites diagram.	108
Figure 50 Vegetation macrofossils diagram.	115
Figure 51 Vegetale matrix diagram.	116
Figure 52 Pollen diagram.	122
Figure 53 Synthesis of interpretations.	129

LIST OF TABLES

Table 1 Variance partitions between landscape and local variables for community and beta diversity following Borcard <i>et al.</i> (2018). Statistical significance threshold of each partition was set for $p < 0.05$ *; 0.01**; 0.001 ***. NA value corresponds to models that failed to converge	66
Table 2 Example of macrofossils both, leaves and seeds, from an analysis performed by the Centre d'étude nordique (Québec, Canada) on samples from the peat core of Saint-Pierre (ZS1).	84
Table 3 Spatial Autocorrelation test values. For every month, the autocorrelation between the reconstruction errors and the site locations were tested for the errors of mean, maximum and minimum temperatures.	88
Table 4 Species by time zone for oribatid mites and vegetation. The richness and number of points associated to the assemblages of each time zone is specified.....	91
Table 5 Radiocarbon dates and calibrated age of the ZS1 core, Saint-Pierre....	103

RESUME EN FRANÇAIS

I. INTRODUCTION

A. Cadre théorique

1. LES BIOINDICATEURS

La science de l'écologie étudie les interactions entre les espèces et entre celles-ci et leur environnement, conduisant à une très grande complexité. La biodiversité, dont la richesse comprend plus de 1,5 million d'espèces connues, est urgente à surveiller et à protéger dans la période actuelle marquée par les impacts humains, souvent qualifiée d'«Anthropocène». Dans ce contexte, les outils pour évaluer la biodiversité et les processus écologiques deviennent de plus en plus nécessaires.

Pour répondre à ces défis, le concept de bioindicateurs est apparu dès le début du XXe siècle et a gagné en popularité depuis. Les bioindicateurs offrent des avantages en termes d'efficacité par rapport à leurs coûts, et leur utilisation est justifiée par leur capacité à fournir des informations précieuses sur les écosystèmes complexes. Ces indicateurs biologiques sont utilisés pour obtenir des informations sur les écosystèmes qu'ils habitent et peuvent être divisés en plusieurs catégories selon les objectifs de conservation : indicateurs de biodiversité, indicateurs environnementaux et indicateurs écologiques.

Les indicateurs de biodiversité permettent de recueillir des informations sur les éléments de la diversité des habitats étudiés, ce qui peut aider à identifier les zones prioritaires pour la conservation. Les arthropodes peuvent être de bons indicateurs de biodiversité sur de larges espaces comme l'ont montré de nombreuses études.

Les indicateurs environnementaux sont des espèces qui réagissent aux variations de leur environnement et sont utilisés pour les détecter. Ils peuvent être des sentinelles, des détecteurs, des exploitants, des accumulateurs ou des organismes de test en laboratoire. Ces indicateurs sont utiles pour évaluer les concentrations de polluants dans l'environnement et peuvent être utilisés dans des études sur les pesticides, par exemple.

Enfin, les indicateurs écologiques, visent à comprendre les impacts anthropiques sur les biocénoses. Ils fournissent des informations sur l'environnement et sur les espèces étudiées. Ils peuvent également être utilisés pour évaluer les dynamiques de restauration des habitats dégradés.

Ainsi, les bioindicateurs sont des outils précieux pour surveiller et protéger l'environnement, en fournissant des informations sur la biodiversité, les perturbations environnementales et les impacts anthropiques. Ils permettent une évaluation efficace des écosystèmes et peuvent guider les décisions de conservation et de gestion des ressources naturelles.

2. LES TOURBIÈRES

Les tourbières sont des habitats définis principalement par la présence de tourbe, avec un seuil minimum de 30 à 40 cm d'accumulation de tourbe pour être considérées comme telles, exception faite de certaines tourbières arctiques où les conditions rigoureuses entraînent une accumulation extrêmement lente de la matière organique. La tourbe est principalement composée de végétaux tels que la mousse, les carex et les roseaux, qui s'accumulent en raison des conditions de dépôt qui inhibent la décomposition. Les tourbières se caractérisent par une hydrologie élevée, ce qui limite la dégradation et favorise l'accumulation de la tourbe dans des conditions humides et anoxiques. Ces habitats sont principalement présents dans les climats arctiques, subarctique et boréal, où les précipitations fréquentes alimentent l'hydrologie des tourbières et le climat froid limite l'évaporation.

Les tourbières sont parmi les habitats les plus menacés de la planète, couvrant environ 4 millions de km² à travers le Monde. Elles subissent actuellement les menaces de la destruction due à l'agriculture, à l'urbanisation croissante, ainsi qu'à l'extraction de la tourbe. Les tourbières fournissent de nombreux services écosystémiques, tels que la production de fruits, l'habitat pour la faune sauvage et les poissons, ainsi que des services régulateurs tels que la bioremédiation, la dilution et la séquestration des eaux usées. De plus, les tourbières abritent une biodiversité unique, avec des espèces adaptées à leurs conditions extrêmes. La conservation des tourbières est donc une priorité en raison de leur état de

conservation mondial préoccupant et de leur importance pour la préservation de la biodiversité.

Il existe différents types de tourbières, classés en fonction de leur richesse et de leur alimentation en eau, allant des tourbières « pauvres » aux tourbières « riches », en passant par les tourbières ombrotrophes et minérotrophes. Chaque type de tourbière présente des adaptations uniques à ses conditions environnementales spécifiques, avec des espèces végétales et animales spécialisées. La biodiversité des tourbières est donc composée d'espèces adaptées à des stratégies de vie lente et de grande longévité, ainsi que d'espèces généralistes hautement polyvalentes. La conservation des tourbières implique la protection de ces habitats uniques et de la diversité biologique qu'ils abritent, face aux pressions croissantes exercées par les activités humaines.

3. LES MODELES D'ETUDES

3.1. Les arthropodes

Les arthropodes, en raison de leur immense diversité, représentent le taxon avec le plus d'espèces en environnements terrestres, et leur rôle fonctionnel joue un rôle significatif en écologie. Les arthropodes ont une histoire substantielle d'utilisation en bioindication, principalement dans les environnements aquatiques et de plus en plus dans les environnements terrestres depuis la fin du 20^e siècle. Leur grande diversité a été un critère considéré par plusieurs auteurs dans leur choix de modèles d'étude pour la bioindication. Parmi ces critères, figure leur capacité à répondre rapidement aux perturbations en raison de leur petite taille, de leurs temps de génération très courts et de leur abondance. De plus, leur grande diversité fonctionnelle permet des analyses à partir de perspectives d'étude pertinentes, tenant compte de la variété des réponses aux perturbations que les arthropodes offrent en tant que communautés fonctionnelles.

3.2. Les araignées

Les araignées, avec plus de 50 000 espèces connues, constituent le groupe d'animaux presque exclusivement composé de prédateurs le plus diversifié connu. Les araignées sont principalement considérées comme des prédateurs, mais il

existe quelques exceptions, comme *Bagheera kiplingi*, une araignée sauteuse qui peut changer son régime alimentaire pour se nourrir de pousses d'hibiscus à hauteur de 90% de son régime en fonction de la pression concurrentielle dans son habitat. Ces exceptions mettent en évidence la vaste diversité des araignées. Cette diversité s'exprime sur tous les continents et dans tous les habitats. Parmi le spectre de la diversité des araignées, les guildes sont particulièrement riches. Les araignées sont principalement considérées comme des prédateurs, et donc les guildes au sein des araignées permettent de distinguer les différentes façons de chasser. Dans le contexte des tourbières nord-américaines, les araignées sont parmi les taxons ayant le plus grand nombre et la plus grande proportion d'espèces spécialisées. Cette spécialisation et cette diversité font d'elles d'excellents bioindicateurs.

3.3. Les acariens oribates

Les acariens oribates représentent un riche sous-ordre d'acariens avec plus de 13 000 espèces. Ils sont parmi les premiers animaux à avoir vécu sur Terre, avec des exemples de fossiles datant du Dévonien. Ces arthropodes habitant le sol présentent une diversité de guildes alimentaires comprenant des décomposeurs primaires et secondaires, qui peuvent être mycophages, phytophages et prédateurs. Ils sont les arthropodes les plus nombreux dans la plupart des environnements, avec des densités pouvant atteindre 425×10^3 ind/m². Ils présentent une écologie singulière avec un développement, une reproduction et une assimilation des ressources lentes, ce qui les conduit à être considérés comme des espèces à stratégie K. La grande diversité des mécanismes de défense présents chez les acariens oribates renforce la définition d'une stratégie K. Parmi les mécanismes de défense chimiques trouvés chez les acariens oribates, il y a les cérocucules produites sur leurs carapaces qui préviennent la prédation par la protection et le camouflage mais réduisent également la transpiration et la protection contre les infections. Enfin, les glandes opisthonotales peuvent être trouvées sous une variété de formes et produisent une diversité de substances. Ces substances ont un rôle répulsif contre les gros prédateurs comme les coléoptères mais moins contre les plus petits prédateurs comme les acariens gamasides.

Dans le registre paléoécologique, les acariens oribates sont rarement utilisés. Cependant, ils sont trouvés en quantités abondantes dans les contextes paléoécologiques et sont suffisamment bien conservés pour que plus de 80 % d'entre eux puissent être identifiés au niveau de l'espèce. Cette bonne identification peut être attribuée à leur bon état de conservation car souvent, seules les parties distales de leur corps comme les pattes sont absentes. Lorsque l'identification n'est pas possible à un niveau taxonomique aussi fin, l'identification générique peut encore fournir des informations car elle peut être associée à des biofaciès.

3.4. La végétation

La végétation est largement utilisée comme indicateur écologique des modèles environnementaux, car la plupart des habitats étudiés ont été conceptualisés à travers leur végétation. De plus, les restes de végétation passés ont été largement utilisés en paléoécologie. La végétation en paléoécologie est principalement connue grâce à l'analyse du pollen. Le pollen, le gamète mâle reproducteur des végétaux supérieurs, est répandu dans l'environnement, soit par voie aérienne, aquatique ou transporté par la faune. Les caractéristiques biologiques du pollen le rendent hautement résistant et sa diversité de formes et de micro-structures sur leur enveloppe externe les rendent identifiables même après de longues périodes allant pour le maximum connu jusqu'à 250 millions d'années.

Les restes macroscopiques de végétation comprennent des tiges, des feuilles ou des parties reproductrices comme les graines. Contrairement au pollen qui donne des informations sur les communautés tout autour du point d'échantillonnage localement et régionalement, les restes macroscopiques mettent en évidence des schémas plus locaux. Les restes macroscopiques ont l'avantage d'offrir une bonne résolution taxonomique et ont été utilisés pour comprendre l'environnement et le climat des habitats passés en paléoécologie et pour suivre les activités anthropiques en archéologie.

4. CONTEXTE GEOLOGIQUE CLIMATIQUE ET ENVIRONNEMENTAL

L'archipel de Saint-Pierre et Miquelon est situé au large de la côte est du Canada, à 17 km des côtes de la péninsule de Burin, au sud de l'île de Terre-Neuve. Il est composé de trois îles principales, Saint-Pierre, Miquelon et Langlade. Les deux dernières îles sont reliées par un tombolo sableux depuis le XVIIIe siècle. Sur le plan géologique, l'archipel appartient au Bouclier canadien, plus précisément à la province de Greenville, caractérisé par des roches de l'orogénèse précambrienne la plus récente.

La température moyenne de l'archipel est de 5,5 °C, avec un maximum en août de 15,7 °C et un minimum en janvier de -2,97 °C. Malgré sa position à une latitude méridionale, l'archipel est décrit comme une enclave subarctique, héritant ses conditions froides du courant du Labrador descendant du cercle arctique. Une autre caractéristique principale de l'archipel est l'hygrométrie élevée de ses climats, liée à la grande quantité de brouillard. Le Grand Banc de Terre-Neuve, où se trouve l'archipel, est l'un des deux endroits les plus brumeux du Monde, caractérisé par la rencontre des eaux froides du courant du Labrador et des eaux plus chaudes du Gulf Stream.

Les principaux habitats de l'archipel sont la forêt boréale, les tourbières, la toundra et les landes subarctiques. La forêt boréale est dominée par *Abies balsamea*, avec d'autres essences résineuses telles que *Picea mariana* et *P. glauca*, ainsi que *Larix laricina* dans les zones humides. Parmi les arbres feuillus, certains *Betula papyrifera* peuvent être notés, ainsi que d'autres espèces, souvent à proximité des cours d'eau, mais minoritaires. Dans des paysages plus ouverts, souvent près de la forêt résineuse et dans les zones perturbées, une autre *Betulaceae*, *Alnus crispa*, est très fréquent. Les tourbières de l'archipel sont soit des bas-marais minérotrophes, soit des tourbières ombrotrophes dominantes, couvrant une grande surface de l'archipel, principalement à Miquelon et Langlade. Les habitats de toundra sont caractérisés par des *Ericaceae* comme *Empetrum eamesii* et de petites fleurs arctiques comme *Diapensia lapponica*.

Les landes subarctiques sont des habitats arbustifs dominés par des espèces d'*Ericaceae*, principalement *Rhododendron groenlandicum* dans l'archipel, une espèce connue pour être très compétitive et dominante dans les habitats pauvres où elle prospère grâce à des réseaux mycorhiziens.

Il existe une longue histoire des occupations autochtones sur l'archipel, s'étalant de 5000 BP à 325 BP. La première colonisation européenne a été établie en 1604. Les deux cents années suivantes ont été très tumultueuses, car la France et l'Angleterre se sont disputées la colonie.

Le climat de la région au cours des deux derniers millénaires est connu pour sa diversité. Cette variabilité s'exprime à diverses échelles alors que la région connaît divers événements climatiques. L'Anomalie climatique médiévale était une période chaude notée en Europe entre les 9^e et 14^e siècles. Le Petit Âge Glaciaire était une période plus froide à la fin de l'Holocène entre le 14 et 19^e siècles vécus dans l'hémisphère nord. Enfin, le réchauffement anthropique récent est tangible localement, menaçant l'archipel en raison de son emplacement océanique et de sa sensibilité aux variations du niveau de la mer ainsi qu'à l'érosion côtière.

B. Les objectifs de la thèse

Ce projet de recherche vise à comprendre les dynamiques des tourbières subarctiques à travers le prisme de la bioindication. Cet objectif peut prendre plusieurs formes, à l'image de la complexité des habitats de tourbières eux-mêmes. Les tourbières sont des habitats caractérisés par leurs conditions abiotiques souvent contrastées par rapport aux habitats adjacents et par leur processus de formation. Le premier point les rend intéressantes pour les études écologiques et les considérations de conservation. Le deuxième point, leur formation, fait des tourbières un livre d'histoire naturelle, accumulant lentement de la matière organique et minérale et préservant de nombreux vestiges biologiques qui racontent les histoires de l'environnement dans et autour des tourbières. Cette dernière caractéristique fait des tourbières un habitat privilégié pour les études paléoécologiques.

La pleine complexité des tourbières peut être étudiée par une large gamme de domaines, y compris la biologie, l'écologie, la paléoécologie, l'hydrologie, la chimie, la climatologie et plus encore, tous interagissant à différentes échelles spatio-temporelles. S'attaquer directement à cette complexité dépasse la portée d'un seul projet. Ce projet spécifique vise à comprendre les dynamiques des tourbières à différentes échelles de temps, en se basant sur le concept de bioindicateurs pour

déduire des informations environnementales des écologies observées chez les taxons étudiés dans leurs environnements.

Ce projet sera divisé en trois approches différentes utilisant la bioindication afin d'améliorer la compréhension des tourbières. Le premier chapitre est une étude des assemblages actuels d'arthropodes et de végétation dans une tourbières subarctiques, étudiés à travers plusieurs métriques de diversité et comparés entre eux et ce à travers différents paysages de tourbières. Ces comparaisons visent à éclairer les relations entre les taxons, les métriques et les paramètres environnementaux à différentes échelles, mettant en évidence leur complémentarité et leurs sensibilités respectives. L'objectif global de ce chapitre est à la fois d'augmenter les connaissances sur les réponses des tourbières aux paramètres environnementaux et sur les taxons utilisés comme indicateurs eux-mêmes, tout en améliorant simultanément nos connaissances et nos outils d'évaluation.

Les deuxième et troisièmes objectifs relève de la paléoécologie, car ils étudient les tourbières via les restes trouvés dans les carottes. Cette approche vise à comprendre la dynamique des tourbières au cours des deux derniers millénaires. Cette partie paléoécologique de l'étude est divisée en deux chapitres avec des objectifs distincts. Le premier vise à découvrir et à comprendre le potentiel des acariens oribates en tant qu'indicateurs des climats passés à travers des méthodes de reconstruction climatique. Les acariens oribates sont un groupe peu étudié dans le domaine de la paléoécologie, malgré leur fort potentiel, et n'ont jamais été utilisés comme taxons modèles pour la reconstruction climatique. Comme ce taxon est largement présent dans les enregistrements subfossiles et est souvent identifiable au niveau de l'espèce, il est pertinent de tester comment il peut être utilisé à des fins paléoécologiques.

Le deuxième objectif paléoécologique vise à comprendre les dynamiques des tourbières au fil du temps grâce à la comparaison de plusieurs bioindicateurs, comprenant à la fois des arthropodes et de la végétation avec différentes sensibilités et échelles de réponse. En miroir avec le premier chapitre, il repose sur une comparaison des arthropodes et de la végétation en tant que bioindicateurs de signaux environnementaux. Cependant, contrairement au premier chapitre, les données paléoécologiques sont analysées de manière plus qualitative, car les signaux du passé nécessitent des précautions spécifiques et

rigoureuses dans leur interprétation. L'objectif est de comprendre l'histoire naturelle de la tourbière via l'histoire environnementale et en relation avec le climat de l'archipel. Deuxièmement, grâce à la comparaison des taxons indicateurs, cette étude éclairera leurs sensibilités spécifiques, mettant en évidence où ils se renforcent ou se complètent mutuellement et, ce faisant, démêlera l'histoire écologique de la tourbière étudiée.

Ensemble, ces objectifs capturent différents aspects de l'histoire des tourbières jusqu'à nos jours, améliorant les connaissances sur les habitats et sur la manière de les comprendre.

II. MATRIELS ET METHODES GLOBALE DU PROJET

Pour répondre aux questions de ce projet, deux campagnes sur le terrain ont été organisées. Une dans l'archipel de Saint-Pierre & Miquelon en 2021 et une dans l'archipel de Nain, au Labrador, en 2022. Les objectifs de la première campagne comprenaient l'évaluation de la biodiversité actuelle des arthropodes et de la végétation des tourbières subarctiques sur des sites présentant un potentiel pour la paléoécologie afin que les données puissent être comparées de manière cohérente. La seconde, à Nain, visait à répéter cette technique d'échantillonnage pour des données écologiques actuelles dans un contexte différent dont la paléoécologie avait été documentée afin de croiser à la fois les données actuelles et passées avec celles des deux saisons sur le terrain.

A. Saison 2021 à Saint-Pierre & Miquelon (France)

L'idée initiale du protocole d'échantillonnage était d'évaluer, au sein de la tourbière, les effets des habitats environnants. En effet, le stress sévère associé aux tourbières est connu pour diminuer sur les bords de la tourbière. Par conséquent, un gradient allant du centre des habitats aux bords a été échantillonné sous la forme de trois unités d'échantillonnage : une au centre de la tourbière, une à proximité des habitats secondaires différents les plus proches et une à l'intérieur desdits habitats secondaires. L'étude paléoécologique nécessitait un bon niveau d'accumulation annuelle de tourbe afin d'optimiser la résolution temporelle de

chaque échantillon. De plus, la seule tentative passée d'étude palynologique sur a été réalisée sur la côte ouest de Miquelon et de Langlade. Les tourbes carottées contenaient malheureusement très peu de pollen. L'explication avancée pour la nature azoïque de ces tourbes tient en un contexte géographique très exposé aux vents dominants et pauvres en variété d'habitats locaux peu propices aux dépôts polliniques. La côte occidentale des îles a donc été évitée. Enfin, les sites devaient représenter une diversité de contextes paysagers, notamment au moins un site à l'intérieur ou à proximité d'un contexte urbanisé pour évaluer ses effets potentiels en tant que composant du paysage.

Avec ces besoins à l'esprit, un site par île a été sélectionné et étudié. Les sites sélectionnés sur chaque île qui répondaient aux critères susmentionnés comprenaient, sur Saint-Pierre, la "vallée du milieu" qui sera désignée par "ZS", "Mirande" sur Miquelon qui sera désignée par "ZM" et sur Langlade, le site de "l'étang du Goéland sud" appelé "ZL". Le site ZS se caractérise par sa proximité avec les zones actuellement anthropisés. ZM et ZL sont des sites plus naturels. ZM présente une plus grande proportion d'autres habitats dans le paysage et une plus grande influence de l'étang voisin, tandis que ZL offre un paysage de tourbière plus homogène.

Deux méthodes ont été sélectionnées, les pièges à fosse Barber et l'aspirateur thermique (= D-Vac). Les deux méthodes sont complémentaires, car les pièges à fosse sont une méthode passive, notamment sensible à l'activité des arthropodes et ont tendance à capturer des individus plus grands, tandis que le D-Vac permet de capturer des espèces plus petites et plus cryptiques qui ont tendance à ne pas être échantillonnées par les pièges à fosse. La standardisation de l'effort d'échantillonnage déployé devait atteindre deux objectifs : (1) être comparable entre les sites et les sous-sites ; (2) permettre un regroupement entre les pièges à fosse et le D-Vac. Pour ce faire, l'effort déployé consistait à réaliser 50 aspirations D-Vac de deux secondes, dispersées de manière aléatoire dans les 400 m² d'une unité d'échantillonnage formée par le carré de 20 mètres de côté délimité par la zone d'échantillonnage de 4 pièges à fosse. Lors de l'échantillonnage des habitats secondaires, qui servaient à des fins plus qualitatives que quantitatives, seuls trois pièges à fosse étaient installés. Ces trois pièges étaient placés afin d'éviter la pseudo-réplication et d'avoir toujours un rayon de 10 mètres d'habitats homogènes autour d'eux, mais la disposition carrée n'était pas suivie. Au lieu de

cela, les trois pièges étaient installés en suivant la forme du patch d'habitat secondaire.

Cela a donné lieu à Saint-Pierre et Miquelon à 72 pièges dans les tourbières et 26 dans les habitats secondaires. Ces pièges ont été installés de mi-juillet 2021 à fin août 2021 et récupérés et réinstallés toutes les deux semaines. Quatre sessions d'échantillonnage ont été menées avec le D-Vac, lors de la mise en place initiale des pièges à fosse et à chaque récupération, ce qui a donné 72 échantillons. Les relevés de végétation ont été effectués lors de la dernière récupération à la fin du mois d'août. Chaque relevé était associé à un piège à fosse. L'échantillonnage consistait en un carré de 1 mètre de côté avec le piège à fosse au centre. Les mesures de la végétation étaient le pourcentage de couverture de chaque espèce végétale identifiée, estimé visuellement.

Les variables environnementales ont été évaluées à deux échelles, locale et au niveau du paysage. Les variables locales étaient la température et l'hygrométrie de l'air, mesurées tout au long de la session d'échantillonnage toutes les 10 minutes via un enregistreur de données sur le terrain planté sur chaque sous-site, près du sol mais élevé sur un poteau pour éviter tout contact direct avec l'eau souterraine. La microtopographie des tourbières est un proxy connu de l'hygrométrie du sol et a été mesurée grâce à la photographie par drone

L'échantillonnage paléoécologique par carottage de la tourbe a été réalisé à l'aide d'un carottier russe qui a échantillonné des carottes semi-cylindriques de 50 cm de long avec un diamètre de 52 mm. L'ensemble de la colonne de tourbe a été échantillonné pour évaluer les âges d'accumulation de la tourbe, tandis que la partie analysée de la carotte correspond aux 2000 dernières années uniquement, sur la base de la datation au C14. Sur chaque site, quatre carottes ont été extraites parallèlement, une pour chaque modèle destiné à l'étude, à savoir les restes d'arthropodes, le pollen, les macrorestes végétaux et l'ADN environnemental. Les carottes destinées aux analyses d'ADN ont été traitées en dehors de ce projet de thèse.

Enfin, un site « bonus » a été échantillonné, celui de "l'Anse à Henry" au point le plus au nord de l'île de Saint-Pierre, dans une tourbière de pente, à 200 mètres d'un site archéologique en cours de fouilles. Deux pièges à fosse ont été installés et l'échantillonnage au D-Vac a eu lieu à la même fréquence que les autres

échantillonnages dans l'archipel. Des carottes de tourbe ont été extraites, révélant seulement 90 cm d'accumulation de tourbe. Cette zone a été initialement prospectée comme un site potentiel pour un site complet car proche du site archéologique, mais les surfaces des tourbières localement étaient trop petites. Étant donné que le dépôt tourbeux datait d'à peine un siècle, les données de ce site n'ont pas été traitées.

B. Saison 2022 dans l'archipel de Nain (nord-Labrador, Canada)

La campagne menée dans l'archipel de Nain a impliqué des efforts similaires pour l'échantillonnage des arthropodes, la collecte de données sur la végétation et les variables environnementales. Les sites étudiés étaient Oakes Bay sur Dog Island et South Aulatsivik. En raison des contraintes des sites, l'organisation spatiale et le nombre exact de pièges n'ont pas pu être reproduits exactement. Cela a entraîné la mise en place de 92 pièges Barber, y compris dans les habitats secondaires, actifs en juillet 2022. Le nombre associé d'aspirations avec le D-Vac était comparable au protocole de Saint-Pierre & Miquelon, mais sur une période beaucoup plus courte car la mission dans le nord n'a duré que trois semaines. Malheureusement, tous les contenus des pièges à fosses de Nain ont été perdus, ce qui, combiné à la courte durée de l'échantillonnage, a conduit à l'exclusion des données de cette campagne de terrain dans la thèse.

III. CHAPITRE 1: SPIDER AND VASCULAR PLANT ASSEMBLAGES IN SUBARCTIC PEAT BOGS ARE COMPLEMENTARY ECOLOGICAL INDICATORS OF VARIATION IN LOCAL AND LANDSCAPE FACTORS

Malgré la diversité qu'elles abritent et les services écosystémiques qu'elles fournissent, les tourbières demeurent mal comprises, particulièrement vis-à-vis de leurs réponses à des variations à de multiples échelles spatiales. De nombreux habitats subarctiques font face à des risques sévères liés aux changements climatiques globaux. Dans cette étude, en utilisant une approche multi-métrique, nous avons évalué les capacités indicatrices des plantes et des araignées en tant qu'indicateurs écologiques entre des tourbières contrastées d'un archipel Français

(Saint-Pierre et Miquelon) en Atlantique Nord. En 2021, des pièges Barber et de l'aspirateur thermique ont été utilisées pour collecter les araignées tandis que des relevés phytosociologiques ont servi à documenter la flore vasculaire. Un total de 69 espèces d'araignées et 38 espèces de plantes vasculaires ont été identifiées et les diversités taxonomique (TD) et fonctionnelle (FD, basée sur des traits relatifs à la dispersion, la taille et le fonctionnement dans l'écosystème) ont été estimées pour trois niveaux d'abondances relatives des espèces (Nombres de Hill $q=0$, 1 et 2) grâce au package iNEXT 3D pour la diversité alpha et iNEXT beta3D pour la diversité beta. Conformément aux attentes, les patrons de TD et FD sont fortement corrélés, et ce pour chaque nombre de Hill, mais également entre nombres de Hill pour les araignées, indiquant un effet étonnamment faible de l'abondance des araignées sur leurs patrons de diversités. A l'inverse, les différences entre les sites sont plus marquées pour la végétation quand la couverture d'échantillonnage est prise en compte ($q=1$ et $q=2$), cela pour la TD et la FD, ainsi que pour la diversité alpha et beta. Les RLQ et l'analyse en "Fourth corner" soulignent des différences significatives entre les sites qui sont liées à des traits fonctionnels de dispersions et des facteurs locaux pour la végétation. Finalement, les partitions de variances sur les assemblages soulignent l'importance des interactions entre les facteurs locaux et le paysage, pour les araignées et la végétation, et ce avec une importance relative importante des facteurs locaux pour la végétation. Notre étude révèle une grande complémentarité de l'utilisation des métriques et des assemblages des araignées et de la végétation comme indicateur des variations de conditions locales dans les tourbières, confirmant les changements rapides que traversent les habitats subarctiques.

IV. CHAPITRE 2: ORIBATID MITES AS BIOINDICATOR OF PAST CLIMATES: AN EXPLORATORY APPROACH USING CLIMATE RECONSTRUCTION METHOD AND A CASE STUDY FROM SAINT-PIERRE AND MIQUELON, FRANCE

Les oribates possèdent de nombreuses qualités en tant qu'indicateurs paléoécologiques du fait de leurs abondances, d'une écologie variée contenant des spécialistes et d'un bon comportement taphonomique permettant à leurs restes subfossiles d'être efficacement identifiés. Grace à ces qualités et au besoin en

paléoécologie d'améliorer les outils à sa disposition, cette étude cherche à éprouver le potentiel de ce modèle sous-utilisé que sont les oribates comme indicateurs au service de la reconstruction du climat passé. La reconstruction climatique, réalisée à l'aide de MCR (Mutual Climat Range) ou d'autres méthodes plus récentes de modélisation comme CRACLE, utilisent généralement des restes de végétation ou des coléoptères subfossiles mais ces restes sont difficiles d'identification et/ou rares. 46 jeux de données actuelles d'oribates répartis à travers l'hémisphère nord ont été utilisés pour la reconstruction climatique. Cela a été effectué en croisant les distributions connues de chaque espèce présentes sur chaque site, issues des bases de données GBIF, avec les données climatiques issues de WorldClim. Les reconstructions ainsi obtenues ont été comparées avec les données climatiques connues de chaque site et le niveau d'erreurs et ses drivers ont été analysés. Secondairement, un cas d'étude avec des données paléoécologiques d'oribates et de végétation, en tant que modèle de vérification, a été analysé pour éprouver la méthode. Globalement, les oribates démontrent un potentiel prometteur bien qu'en demi-teinte pour la reconstruction climatique. Le nombre d'espèces utilisées dans un modèle a eu un effet négatif sur la reconstruction climatique, malgré l'addition mathématique de données que cela implique. Les oribates pourraient, quand la somme de données disponibles augmentera, être à la base de reconstructions plus robustes mais pour l'instant les données d'oribates sur GBIF sont trop peu nombreuses pour des reconstructions fiables.

V. CHAPITRE 3: ATLANTIC SUBARCTIC PEAT BOGS ECOLOGY THROUGH A TWO MILLENNIA DYNAMIC, A TRANSDISCIPLINARY MULTI-TAXON APPROACH

Les deux derniers millénaires de l'Holocène récent correspondent à une période riche en variations tant sur le plan climatique qu'anthropique. Dans le contexte géographique de la côte Atlantique nord-est du Canada, la période climatique étudiée est connue pour être particulièrement variable et peu étudiée. Cette étude visait à mieux comprendre à la fois la dynamique fonctionnelle d'une tourbière, l'histoire environnementale locale de l'archipel de Saint-Pierre et Miquelon et à renforcer la compréhension de la dynamique climatique de la région.

Pour ce faire, les restes biologiques de plusieurs indicateurs ont été extraits des carottes de tourbe. La comparaison des restes sub-fossiles d'acariens oribates, des macrofossiles de végétation et du pollen a fourni, sur une période de deux millénaires d'accumulation de tourbe, des aperçus sur la dynamique des tourbières et le contexte climatique de l'archipel. Plusieurs variations liées au climat et à l'hydrologie locale, ainsi qu'à des événements d'incendie, naturels et éventuellement d'origine humaine, ont été observées. Ces dynamiques étaient associées à des patterns écologiques spécifiques des oribates ainsi qu'au développement de la végétation, tant des plantes vasculaires que des sphaignes à l'échelle locale, et croisées avec l'échelle plus large des réponses du pollen. Cette approche multi-taxons a permis une compréhension plus robuste et précise des modèles en jeu. En conclusion de cette étude, l'habitat de tourbière étudié est resté une tourbière océanique ombrotrophe sur presque toute la période étudiée. De plus, les modèles climatiques observés ici correspondaient aux variations historiques régionales spécifiques, contribuant ainsi à renforcer cette histoire climatique et à éclairer le cas jusqu'alors non étudié de Saint-Pierre et Miquelon.

VI. DISCUSSION GENERALE

A. Tourbière, un habitat complexe, résistant bien que sensible

Dans cette étude, nous avons observé les réponses des tourbières à un large spectre de variations, à l'échelle locale et paysagère, ainsi que sur une période de plus de deux millénaires. Un premier aspect à souligner est la résistance des tourbières, car malgré plusieurs variations climatiques, l'habitat est resté relativement stable. La végétation observée était principalement composée de sphaignes, caractéristiques des tourbières ombrotrophes. Ces habitats, pauvres en éléments nutritifs et à pH bas, abritent une flore spécialisée, notamment des plantes carnivores et des *Éricacées*. Les tourbières ombrotrophes sont alimentées par les précipitations et sont influencées par des facteurs locaux et paysagers, tels que la topographie et la proximité de la mer. Malgré leur résistance, les tourbières sont soumises à des variations, tant naturelles qu'en réponse à des changements environnementaux. Les variations spatiales sont observées à différentes échelles. Les conditions hydrologiques locales, telles que la microtopographie, influent sur

la biodiversité des tourbières. À l'échelle paysagère, la composition de l'habitat environnant et les facteurs tels que la proximité de la mer et les activités humaines affectent également les tourbières. Les variations temporelles, telles que les changements climatiques, influent sur la dynamique des tourbières. Les variations de températures et de précipitations affectent la croissance de la végétation et la disponibilité en eau, tandis que les événements tels que la fonte des neiges et les sécheresses et les incendies peuvent entraîner des changements significatifs dans l'habitat et la biodiversité des tourbières.

Les activités humaines telles que l'agriculture et l'exploitation forestière sont connues pour avoir des impacts sur les tourbières, bien que ceux-ci varient selon les régions. Les changements climatiques, tels que l'augmentation des températures et des événements météorologiques extrêmes, peuvent également affecter les tourbières en modifiant les régimes de précipitations et les températures. Les variations saisonnières, telles que la fonte des neiges et les périodes de sécheresse, ont également des impacts sur la dynamique des tourbières et la biodiversité associée. En comprenant ces variations et en évaluant les réponses des tourbières à différents facteurs, nous pouvons mieux appréhender l'importance de ces écosystèmes uniques et les menaces auxquelles ils sont confrontés. Cette capacité de réponse a été observée ici à travers l'espace et le temps et nous a renseignés sur l'histoire environnementale et climatique de l'archipel de Saint-Pierre et Miquelon.

B. Bioindication, un outil puissant

En utilisant plusieurs taxons comme indicateurs, nous avons accru nos connaissances à leur sujet. Chaque étude utilisant un taxon comme indicateur fournit de nouvelles données sur les occurrences des espèces utilisées, leurs réponses aux signaux environnementaux et donc renforce ou clarifie les schémas connus, voire découvre de nouvelles sensibilités. En biologie, cela peut signifier une meilleure compréhension de l'autoécologie des espèces ou, en biologie de la conservation, une meilleure compréhension de l'état des populations. Globalement, les outils d'indicateurs écologiques sont renforcés par leur utilisation, car plus les connaissances sur un taxon sont approfondies, plus d'informations peuvent être déduites de ces observations.

Les araignées ont montré une sensibilité à plusieurs signaux environnementaux et ont fourni une lecture fine de variations subtiles entre les habitats étudiés. Les réponses des araignées étaient en partie conformes à ce qui est décrit dans la littérature pour ce taxon, avec des réponses fortes de diversité bêta mais pas d'alpha. Les acariens oribates ont été utilisés de différentes manières dans cette étude. Le deuxième chapitre visait principalement à accroître notre connaissance de leur potentiel en tant qu'indicateurs de la reconstruction climatique. Cette étude a souligné l'importance relative de la sensibilité des acariens oribates au climat et à l'hydrologie, et a également mis en évidence les lacunes dans les connaissances sur les espèces globales face à des objectifs de reconstructions climatiques.

Les autres taxons utilisés dans cette étude, tels que les coléoptères carabiques et les fourmis, ont également contribué à l'augmentation des connaissances locales. Contrairement aux araignées et aux acariens oribates, la végétation avait déjà fait l'objet de nombreux inventaires dans l'archipel donc aucune connaissance naturaliste nouvelle n'émerge de cette étude. Sur le plan écologique cependant, l'utilisation de la végétation comme indicateur a permis de mieux comprendre l'impact des caractéristiques du paysage, notamment hydrologiques et anthropiques, sur la diversité des espèces dans les tourbières ombrotrophes de l'archipel.

VII. PERSPECTIVES

A. De nouveau bioindicateurs à explorer

Plusieurs bioindicateurs ont été utilisés dans ce projet, mais comme la multiplicité des indicateurs est bénéfique pour la compréhension écologique, nous examinerons des exemples d'autres indicateurs qui seraient pertinents pour approfondir les objectifs abordés tout au long de la thèse. Les indicateurs utilisés ici ont été choisis en raison de leur complémentarité, c'est la principale caractéristique visée pour proposer de nouveaux taxons modèles.

La considération des modèles présents en paléoécologie et absents en néoécologie, et vice versa, auraient été un ajout pertinent dans les deux contextes. Les taxons ont été sélectionnés pour leur complémentarité écologique. En effet,

les araignées, les acariens oribates et la végétation, respectivement prédateurs, détritivores et producteurs primaires, sont moins susceptibles d'être fortement corrélés les uns aux autres. Comme mentionné, il est possible de trouver des subfossiles d'araignées dans les tourbières et elles sont d'excellents indicateurs écologiques. De même, les acariens oribates présentent un grand potentiel en néoécologie et devraient être considérés pour de futures études dans l'esprit du premier chapitre de cette thèse. La végétation non vasculaire, en particulier les sphaignes, pourrait également être utilisée en néoécologie. Même si certains auteurs plaident pour une meilleure réponse des plantes vasculaires, l'utilisation croisée à la fois des sphaignes et des plantes vasculaires est porteuse d'informations complémentaires.

Les amibes sont utilisées dans plusieurs études paléoécologiques dans les tourbières car elles sont d'excellents indicateurs des niveaux de la nappe phréatique au fil du temps. L'ajout d'un indicateur avec une sensibilité spécifique au niveau de la nappe phréatique permettrait de mieux discerner les événements environnementaux.

Plus de métriques de diversité pourraient, dans l'esprit du premier chapitre, offrir une réflexion rétrospective grâce à la complémentarité qu'ils affichent avec les métriques utilisées. Par exemple, la diversité phylogénétique a une histoire croissante d'utilisation en néoécologie et même en paléoécologie. Ces métriques sont complémentaires à la diversité taxonomique et fonctionnelle utilisée ici et présentent une interaction particulière avec des conditions écologiques difficiles qui peuvent trouver des échos dans les habitats de tourbières.

B. Du pluridisciplinaire au multidisciplinaire

Tout d'abord, il convient de définir la subtilité entre les objectifs de pluridisciplinarité et de multidisciplinarité. La pluridisciplinarité est la manipulation de plusieurs disciplines en parallèle dans un projet sans croiser les thèmes, tandis que la multidisciplinarité vise une pratique de recherche collective cherchant la connexion et l'intégration des connaissances.

Cette connexion a été appelée dans la littérature scientifique dans le passé car un manque de communication entre plusieurs disciplines a été mis en évidence.

En effet, bien que les disciplines de la néoécologie et de la paléoécologie travaillent sur le même modèle d'étude et aient des objectifs similaires, elles peinent à coexister en raison des différences dans les méthodes et la nature des échantillons utilisés, mais aussi en raison d'un simple manque de compréhension et d'une inertie à modifier les habitudes de travail. Il existe quelques exemples intéressants qui croisent des données issues des deux disciplines mais cela demeure trop anecdotique et superficiel de notre point de vue.

C. Comment atteindre cet objectif ?

De nombreux écueils doivent être évités afin de créer un pont entre la paléoécologie et la néoécologie. Le premier peut être l'échelle de temps. En paléoécologie, la résolution temporelle doit être prise en compte lors de la discussion des taux d'accumulation des restes, qui peuvent varier au-delà de la comparabilité. Une comparaison des échelles de temps utilisées dans les deux sous-disciplines, souligne qu'il est possible d'utiliser les échelles de temps appréhendables comme la décennie. La nature des données, souvent qualitative en paléoécologie et quantitative en néoécologie, pourrait se rencontrer sur un terrain commun. Les méthodes de sous-échantillonnage aléatoire dans les assemblages néoécologiques pourraient répondre aux données paléoécologiques semi-quantitatives et constituer un moyen de construire des comparaisons. De même, cette connexion pourrait être réalisée en augmentant le nombre d'échantillons en paléoécologie afin d'obtenir des données quantitatives. Un tel effort est réalisé avec les proxies dont les restes sont les plus abondants dans le registre sédimentaire comme les pollens. La quantité de travail requise pour analyser d'autres restes paléoécologiques sur une échelle quantitative suffit à décourager ce genre de démarche. Pourtant, comme nous l'avons observé dans ce projet, les acariens oribates pourraient permettre une potentielle approche quantitative car la quantité de restes par volume de sédiments est élevée. La néoécologie pourrait avoir besoin, plus qu'elle ne le pense, du recul de la paléoécologie.

I. INTRODUCTION



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A. Thesis objectives

This research thesis aims broadly to understand the dynamics of sub-arctic peat bogs through the lens of bioindication. This objective can take as many forms as the complexity of the peat bogs habitat themselves. Peat bogs are habitats characterized by their abiotic conditions often contrasting to adjacent habitats and by their formation biology. The first point makes them an interesting object of ecological study and the source of conservation projects. The second point, the biology of their formation, makes the peat bogs' a natural history book as it accumulates slowly and preserves numerous remains that tells the tales of the environment in and around peat bogs. This last characteristic makes peat bogs a privileged habitat for palaeoecological studies.

The full complexity of peat bogs can be studied by a wide range of fields including biology, ecology, hydrology, chemistry, climatology and more, all interacting at various spatiotemporal scales. Directly tackling this complexity is beyond the reach of a single project. This specific project aims at reaching an understanding of the peat bog dynamics at different time scales, relying on the concept of bioindicators deducing environmental information from observed taxa's ecologies within the said environment.

This project will be divided in three different approaches using bioindications in order to enhance the understanding of peat bogs. The first chapter is a study of current arthropods and vegetation assemblages within sub-arctic peat bogs, studied through the lens of several diversity metrics and compared together across various peat bog's landscapes. These comparisons aim to shed light on the relationships between taxa, metrics and environmental parameters at different scales, highlighting their complementarity and respective sensitivities. The overall objective of this chapter is to both increase the knowledge of peat bog sensitivities to environmental parameters and on the taxa used as indicators themselves, concurrently increasing our knowledge and improved assessment tools.

The second and third objectives are paleoecological as they are studies of the peat bogs via the remains found within cores. This approach aims to understand the dynamic of the peat bog over the last two thousand years. This palaeoecological part of the study is divided in two chapters with distinct objectives. The first one aims at discovering and understanding the potential of

INTRODUCTION

oribatid mites as indicators of past climates within the frame of climatic reconstruction methods. Oribatid mites are an understudied taxa in the field of paleoecology, despite their high potential, and have never been used as a model taxon for climate reconstruction. As this taxon is widely present within subfossils records and is often identifiable to the species levels, it is pertinent to test how it can be used for palaeoecological purposes.

The second palaeoecological objective purports to understand peat bog dynamics over time through the comparison of several bioindicators, including both arthropods and vegetation with various sensitivities and scale of responses. Mirroring the first chapter, it relies on a comparison of arthropods and vegetation's as bioindicators of environmental cues. However, in contrast with the first chapter, the palaeoecological data are analyzed in a more qualitative fashion as the cues from the past required specific and rigorous precautions in their interpretations. The goal is to understand the natural history of the peat bog via the environmental history and in relation to the archipelago's climate. Secondly, through the comparison of indicator taxa this study will shed light on their specific sensitivities, highlighting where they strengthen or complete one another and by doing so, unravel the ecological history of the peat bogs.

Taken together these objectives capture various aspects of the peat bog's history up to present day, improving knowledge on both the habitats and on how to understand them.

B. Theoretical framework

1. ECOLOGICAL INDICATORS

1.1. What is an ecological indicator, definition and purpose

Ecology, is the study of the interactions between species and between species and their environments (Ramade, 2008). This short sentence leads to overwhelming levels of complexity (Parrott, 2010). Biodiversity comprises, among other compartment, over 1.5 million species and many more await discovery (Wilson, 2000). In addition, there is an urgency to monitor and protect biodiversity (Falk *et al.*, 2006) within an era so marked by human impacts that some scholars refer to as the "Anthropocene" (Crutzen, 2002; Dalby, 2013; Lewis & Maslin, 2015)

Paradoxically, faced with such needs, the means allocated to the study of environment don't seems to meet the needs (Waldron *et al.*, 2013; Barbier *et al.*, 2018). As highlighted within literature, the need for tools to assess biodiversity and ecological processes will grow (Hoffmann & Greef, 2003). Indeed, the incomplete knowledge of many taxa coupled with high extinction rates has been highlighted to justify the need for efficient and cost-effective tools that provide maximum information with limited resources (Samways *et al.*, 2010).

Among the solutions to aid ecologists in their study of the environment, the concept of bioindicators arose as early as early twentieth century (Hall & Grinnell, 1919) and grew in popularity since (Perrow & Davy, 2002; Moreno *et al.*, 2007; Turnhout *et al.*, 2007). Indeed, it is widely accepted that bioindicators present advantages in terms of efficiency compared to their costs (McGeoch, 1998; Bisevac & Majer, 1999; Rainio & Niemi, 2003; Pearce & Venier, 2005; Moreno *et al.*, 2007; Wilhere, 2008). Beyond the pecuniary considerations of a study (McGeoch, 1998), there are other aspects of bioindicators to consider justifying their use. Van Straalen (1996) poses the question: why use inferences from complex biological information to obtain information about environmental characteristics that could be measured directly? The author puts forward three scenarios justifying the use of bioindicators: The first scenario involves studies where measurements are tedious to perform other than through one or more indicator species. He cites examples of studies (see references in Van Straalen, 1996) on pesticides that

INTRODUCTION

degrade rapidly, sometimes within a few hours, but whose effects can be measured on arthropod communities for a few more weeks.

The second scenario is where the use of bioindicators adds value compared to direct measurements. The author cites ecological bioindicators that, in addition to providing information on environmental disturbances, also inherently inform us about their effects and the importance of the impact of these disturbances on the studied species. Many authors agree on this, as bioindicators are often functional components in their environment, and it is essential to obtain information on their responses to disturbances (Bisevac & Majer, 1999; Eyre & Luff, 2002; Longcore, 2003; Perner & Malt, 2003; Andersen & Majer, 2004; Andrés & Mateos, 2006 Gerlash *et al.*, 2013).

The third scenario mentioned by Van Straalen is where measurements are impossible, citing measurements of past conditions inferred from traces of arthropods taken from ancient sediments. However, this scenario has been refuted as part of the theoretical framework of bioindicators (McGeosh, 1998). Other authors have echoed Van Straalen's second scenario by emphasizing the additional information obtained when using bioindicators. For example, it has been suggested (Cristofoli *et al.*, 2010) that using spiders as indicators of wet heathland restoration not only highlighted restoration dynamics within the studied habitats but also provided detailed information on restoration mechanisms and the needs of environments that can serve as indications for improving future restoration actions. Similarly, a restoration study (Bisevac & Majer, 1999) demonstrated an improvement in restoration methodologies.

The bioindicator concept bears many definitions, The Oxford dictionary's definition state that a bioindicator is a species with a narrow range concerning one or more environmental factors, and when present, it indicates a condition or a combination of these conditions (Allaby, 1992). Similarly, the Encyclopedic Dictionary of Sciences, Nature, and Biodiversity (Ramade, 2008) defines bioindicators as "a term synonymous with biological indicators, designating plant or animal species which, due to their ecological characteristics, are the early indicators of abiotic or biotic changes in the environment due to certain human actions (=sentinel organisms)." Thus, it involves using species to obtain

information about the complex ecosystems they inhabit (Andersen, 1999). However, McGeosh (1998) suggests to further subdivide bioindication into several parts depending on conservation objectives: (1) biodiversity indicators, (2) environmental indicators, and (3) ecological indicators.

Biodiversity indicators, as defined earlier, serve to gather information about elements of the diversity of studied habitats. They are often employed in the current context of conservation, where issues of priority and management arise, and quantifying biodiversity can help make decisions by identifying hotspots (Samways *et al.*, 2010). There are differing opinions regarding the use of arthropods as indicators of diversity. Gerlach and colleagues (2013) argue that invertebrates are better indicators of biodiversity at large geographical scales (in which case the species involved must have similar dispersal abilities to be correlated) and that they lose robustness at regional or local scales. Indeed, correlations have been highlighted at the continental scale between the diversity of ground beetles (Coleoptera), bird diversity, and Lepidoptera diversity in North America (Pearson & Cassola, 1992). Nevertheless, numerous examples at smaller scales have shown successful results with the use of arthropods. For instance, the subfamily Ithomiinae (Lepidoptera: Nymphalidae) has allowed inferences about the richness of the entire order of Lepidoptera at local and regional scales in Neotropical environments (Beccaloni & Gaston, 1995).

In a somewhat different manner, studies aiming to measure spider biodiversity have succeeded in inferring their richness from observed web counts (Cardoso *et al.*, 2004; Gollan *et al.*, 2010). In both studies, richness is inferred from webs, and in the latter, this characterization of spider richness also serves to verify restoration dynamics. These cases dealt with indicators used to make inferences about specific taxa. Others have managed to highlight correlations between the diversity of several groups, such as centipedes in Turkey (Fattorini *et al.*, 2011) or Orthoptera in India (Jana *et al.*, 2006), with many other arthropods in their respective environments. Some studies have sought correlations between indicators of local diversity rather than with specific groups only. Bisevac and Majer (2002) highlighted that among the taxa they used (e.g., plants, ants, beetles, terrestrial vertebrates, springtails, birds, and spiders), the taxa most correlated with the overall diversity of the community were plants, beetles, and ants. Thus,

INTRODUCTION

to effectively complement the use of plants as indicators of diversity, ants and beetles are the taxa to target.

This conclusion aligns with that of different authors who suggest that to obtain robust results with biodiversity indicators, there should be a tendency to increase the number of taxa (Coelho *et al.*, 2009; Gerlash *et al.*, 2013) while keeping in mind the trade-offs between sufficient sampling efforts and the synthetic dimension of bioindicators as their goal is to reduce the measurement required (McGeosh, 1998). To achieve similar goals, Gerlash and colleagues (2013) highlight the use of threatened species as indicators of diversity. Indeed, being often sensitive to various disturbances, the habitats that house them are often of high quality and potentially support a rich biodiversity. However, this last example is not systematic; a study on a red-listed saproxylic beetle (Sverdrup-Thygeson, 2001) showed no correlations between this threatened species and the other taxa in its habitat. The absence of a link was explained by the highly specialized nature of this species, which distinguishes it from other taxa.

Environmental indicators are characterized by the responses they show to variations in their environment and are therefore used to detect them (McGeosh, 1998). A study by Spellerberg (1991) examined different types of environmental indicators, identifying five subsets. (1) The first is that of sentinels. These are species introduced into a given environment to detect a disturbance as soon as it occurs. The approach seems uncommon, and examples are rare, especially with arthropods. The most well-known example of their use is that of canaries in mines (Spellerberg, 1991), whose death signaled the presence of gas. (2) The second subset contains detectors. These are species naturally present in the environment that will show a response (behavioral changes, different mortality rates, etc.) to changes in their habitat. An example of the impact of sulfur dioxide pollution was measured using ant communities in Australia (Hoffmann *et al.*, 2000). (3) The third type consists of exploiters. These indicate, by their presence, the probability of the presence of pollution or disturbance. A well-known example is the larvae of Chironomidae, which increase in density in disturbed environments (Rosenberg & Resh, 1993). (4) The fourth subset is that of accumulators. These indicators accumulate chemicals in themselves in such a way that it can be measured. A study on the concentrations of lead and cadmium in different habitats used various

arthropods, including spiders, as accumulators (Maelfait & Hendrickx, 1998). This study also highlighted the quality of spiders as accumulators due to their position in the trophic network and warned of the importance of stability between accumulator species used to compare sites due to significant interspecific variation in accumulator quality. (5) Finally, test organisms in laboratories were used to compare the toxicity of different pollutants or determine their concentration. An example of a laboratory study on the impact of sublethal doses of pesticides on the behavior of spiders showed that the concentrations present had a significant impact on the exposed species, with possible repercussions on their fitness (Royauté *et al.*, 2015). The study also highlighted an unexpected facet of pesticides, which even at reduced doses for environmental reasons, persist in causing problems for biodiversity. Environmental indicators are therefore valuable tools in conservation, especially in the studies mentioned above with pesticides that degrade rapidly, and where indicators help assess their concentrations.

Many ecological indicators rely heavily on arthropods (McGeosh, 2007). Their goal is to understand anthropogenic impacts on biocenosis, making them the most crucial bioindicators (McGeosh, 1998) and they serve to highlight distinct environmental variables in space or time (Gerlash *et al.*, 2013). They have a dual interest; more than just informing about the environment, studies using these indicators also obtain information about their study model (Van Straalen, 1996). Indicator species may also be relevant for conservation (Scott *et al.*, 2006) or economic interests (Kevan, 1999), making it doubly interesting to study them. An intriguing example of spatial variation is the use of genetic characteristics of spider subpopulations, which has highlighted landscape fragmentation issues (Maelfait & Hendrickx, 1998). To illustrate the use of ecological indicators over time, the most convincing example is that of restoration indicators (Gerlash *et al.*, 2013). Historically, the first studies to highlight this concept were those using changes in ant communities as indicators of the restoration dynamics of former mining sites in Australia (Majer, 1983; Andersen, 1997).

2. PEAT BOGS, A PECULIAR HABITAT

2.1. Definitions and formation

Peat bogs are habitats defined firstly by the presence of peat. The threshold to be considered a peat bog is a peat accumulation of at least 30 to 40cm, with the exception of some arctic peat bogs where the harsh conditions lead to extremely slow accumulation (Payette & Rochefort, 2001). Peat is the name of vegetal organic matters that accumulates as the conditions of its deposit inhibit decompositions (Rydin *et al.*, 2013). Peat is mainly composed of the dominating vegetation of this habitats namely moss, sedges and reed (Bonn *et al.*, 2016). The conditions that allow peat accumulation can vary but the constant is high hydrology as this results in low degradation and therefore accumulation of peat reside in wet anoxic conditions (Rydin *et al.*, 2013). Those condition can be found either within a lake ongoing eutrophication that fills up and becomes a peat bog or within a topographical depression in which water accumulates. This importance of water explains why the arctic, subarctic and boreal climates host the majority of peat bogs as they are characterized by frequent rain and fog that feeds peat bog hydrology and limits evaporation (Payette & Rochefort, 2001).

2.2. High conservation stakes

Peat bogs are amongst the most and endangered habitats on the planet (Pinceloup *et al.* 2020), covering 4 million of km² across the globe (Rydin *et al.*, 2013). While their important functions within ecosystems are largely accepted within the scientific literature (Bonn *et al.*, 2016), these humid habitats currently suffer the dual threats of destruction from encroaching agriculture and urbanization (Poulin *et al.*, 2004) and extraction. Indeed, the ecosystem services associated to peat bogs are numerous as thereafter listed by Bonn and colleagues (2016). They can be exploited for fruit production, game wildfowls and fish species harboring, or their use for peat flavored whiskey or excavated and burnt for heating are usages that can be cited. Amongst the regulating services there are bioremediations, dilution and sequestration of water waste and mediation of water flows. There is a whole sub discipline of studies that focus on quantifying and restoring the carbon sequestration capability peat bogs. Lastly for ecosystem

services, cultural services are linked to peat bogs, for instance all the outdoor activities that occur within the peat bogs. There are also spiritual and cultural associations with the peat bogs as natural habitats. There are also historic cultural outputs linked to peat bogs as sacred places like cemeteries. Finally, within the cultural services there are intellectual usage of peat bogs. For instance, their ability to store environmental cues and cultural artefacts throughout time, used by scientists, also fall down the purview of cultural services.

The other intrinsic value of peat bogs resides in the biodiversity they shelter (Marshall & Finnamore, 1994). The harsh constraint of peat bog tends to drive their diversity down, few species can withstand these conditions compared to other habitats (Gore, 1983; Joosten *et al.*, 2008), yet this diversity is of high conservation values as the species that live there are sometimes not found elsewhere (Spitzer & Danks, 2006). As well, the cold microclimates of peat bogs have often made those habitats a refuge for species linked to cold climates from ancient ice ages, known as refugia (Stenøien *et al.*, 2011).

The conservation value of bogs is rooted in those aforementioned qualities but the urgency to protect them resides in their state of conservation worldwide. Covering about 4% of the globe's surface, peat bogs are threatened by human activities (Poulin *et al.*, 2004). Agriculture, forestry, peat extraction or electricity production impacts peat bog all over the world, yet the degradation is not homogenous (Bonn *et al.* 2016). Canadian peat bogs are relatively untouched with 90% of peat bogs remaining intact, some European countries on the other hand have seen most of their peat bogs damaged, as is the case for 85% of the bogs of the Netherlands (CPG in Bonn *et al.*, 2016). Furthermore, as the extent of their surfaces diminish disconnections of peat bogs within the landscape is a pressing issue as their specialized fauna tends to have lower dispersal abilities (Rydin *et al.*, 2013) and are therefore more sensitive to disconnection. For instance, the case of the spider *Dolomedes plantarius* in Europe, a species that is specialized in aquatic environments like peat bogs and that need a connectivity of water to disperse, which it lacks and therefore its population is dwindling (Pearson, 2008).

INTRODUCTION

2.3. A spectrum of different habitats

Following the disambiguation of the many names bestowed to peat bogs by Rydin *et al.* (2013) there are many different types of peat bog. Those variations can be ordered on a crossed gradient of richness and wetness (the wetness gradient tends to follow tree cover gradient) (Fig. 1).

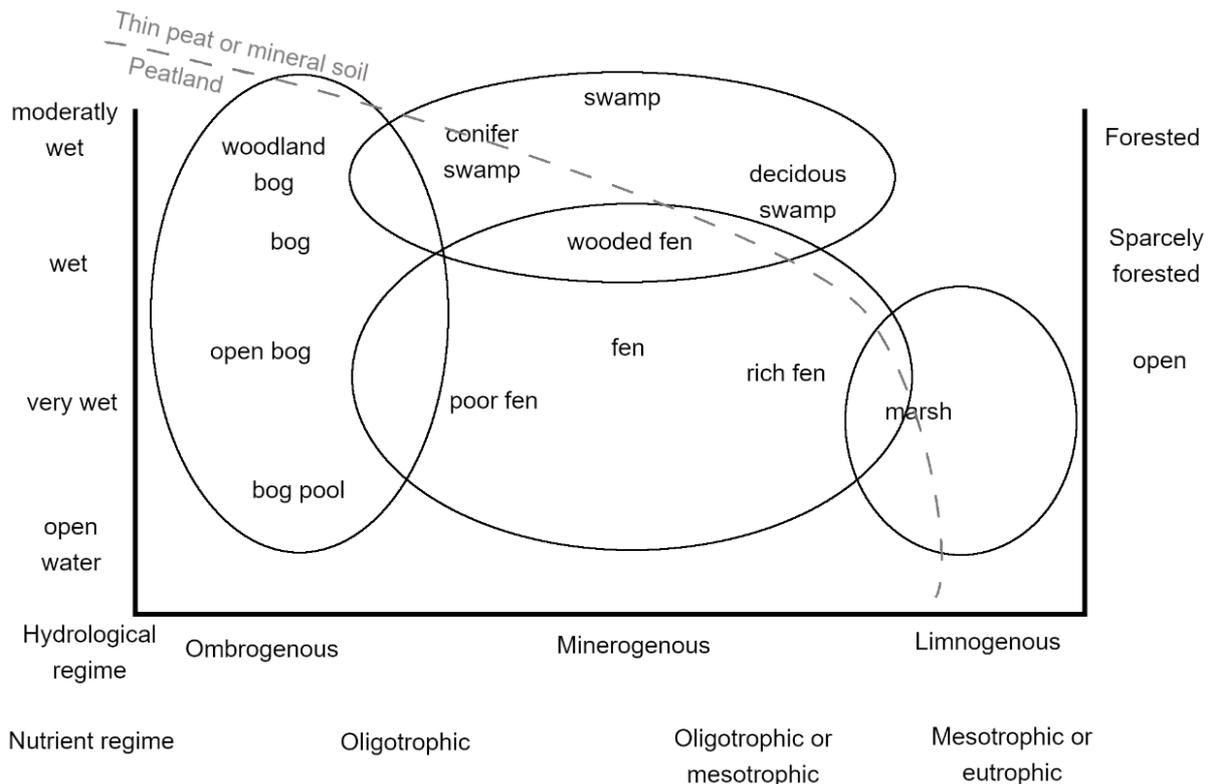


Figure 1 Adapted from Rydin *et al.* 2013: the classification of different peat bog depending on wetness, hydrological regime, level of tree cover and nutrient regimes.

Depending on the formation conditions relative to the crossed hydrological and nutrient regimes, the peat bog will be either “poor” or “rich”, nutrient and vegetation wise (Lourenco *et al.*, 2023). Ombrogenous peat bog, at the bottom of the richness gradient get its name from the main source of water that allows for peat accumulation, rain. *Ombros-* “rain” and *-genous* “born in” or “originated” in ancient Greek. Due to the topography that prevents runoff water to get to the peat bog or the accumulation of peat that ends up in a dome shape that can no longer access the nutrient of runoff water, only rain feeds the ombrogenous peatbogs, hence the nutrient poverty. That kind of peat bog is usually known under the

simple name "bog" and can vary in wetness and forest cover. Those variations are not necessarily encompassing the whole bog and can express themselves as a mosaic of wetness within a specific bog. Among the bogs, the Canadian Atlantic coast harbors a richer bog where some poor fen species are observed while the rest of the assemblages are bog specialists. An explanation to this specificity is the vicinity of the bog with the sea that led to the importation of nutrients caused by the salt spray (Damman & Dowhan, 1981; Wells, 1996; Payette & Rochefort, 2001).

Minerogenous peat bogs, called fens, get part of their water from run-off from richer water that brings in nutrients and allows more plant species to thrive. From the Latin *Mineralis* "minerals" and the same the ancient Greek *-genous* as ombrogenous. There is a spectrum of richness within fens from poor to rich depending on the amount of nutrients available. This quantity of nutrients is mainly driven by the nature of the soil in contact with the run-off water before it gets to the fen.

2.4. Endogenous stress and specialized biodiversity

The specific conditions of these bogs include high humidity, low pH, low nutrient availability, anoxic stratum, accumulation of toxic substances which are often subjected to wind and sun (Rydin *et al.*, 2013). Those conditions make the life within the bog harsh and lead to many species' specialization (Minayeva & Sirin, 2012). Tussock formation, the floating mattresses of vegetation or the resistance to submersion are adaptations often observed on bog that protect vegetation against flooding (Rydin *et al.*, 2013). Some plants are known to be adapted to low pH through secretion of acidic substances (citric and oxalic acid) next to their roots to facilitate the absorption of some nutrients that, already rare, have a reduced potential of absorption by plants at low pH (Ström *et al.*, 1994). The nutrient poor environment is met by plants through adaptations like nutrient conservation (Bubier *et al.*, 2011), and long-lasting foliage (Rydin *et al.*, 2013). Amongst the most distinctive of those poor nutrient adaptations, there are the carnivorous plants that compensate the lack of nutrients in the soil by consuming arthropods. The northern pitcher plant *Sarracenia purpurea* (Fig. 2.1) and the

INTRODUCTION

sundew *Drosera rotundifolia* (Fig. 2.2) are two highly common carnivorous plants within nutrient poor bogs (Ellison & Gotelli, 2002; Stewart & Nilsen, 1992) in the Saint-Pierre & Miquelon archipelago.



Figure 2 Example of carnivorous plants in Saint-Pierre & Miquelon's bog. *Sarracenia purpurea* (1) from Langlade and *Drosera rotundifolia* (2) from Miquelon. (Photographers: Pascaline Caudal & Dominique Marguerie respectively).

Fauna within peat bogs is also submitted to their conditions. Amongst the known adaptations, their small size limits the need for nutrients, tolerance to extreme condition and anoxia as well as microhabitat selection that avoids the severe conditions or polarization of life cycle for either short time spans within favorable windows or long slow development with dormant stages providing resistance to severe condition are described (Rosenberg & Danks, 1987). Numerous aquatic species are peat bog specialists but with adaptations not restricted to peat bogs but to aquatic environments (Rydin *et al.* 2013). For vertebrates, even if they mostly use peat bogs sporadically or during specific life stages, some adaptations have been observed like specific resistance to low pH in the skin of amphibians (Mazerolle, 2005) or in eggshells (St-Louis & Breebaart, 1991).

Biodiversity in peat bogs is therefore considered composed of K strategists with great longevity and slow development and by highly polyvalent generalists (Minayeva & Sirin, 2012). This definition is echoed in arthropods with oribatid mites theorized as K strategists (Norton 1994) which among the taxa with most peat bog specialized species (Behan-Pelletier & Lindo, 2023).

3. MULTIPLICITY OF MODEL: COMPLEMENTARITY THROUGH TIME AND SPACE

3.1. *Arthropods, a world of ecological diversities and usages in neo- and paleoecology*

3.1.1 Arthropods

Arthropods, due to their immense diversity, are richest in terrestrial environments (Wilson, 1987; Hamilton *et al.*, 2010; Basset *et al.*, 2012), and their functional roles (Rosenberg *et al.*, 1986; Oliver & Beattie, 1996; Samways *et al.*, 2010), play a significant role in ecology. Arthropods have a substantial history of use in bioindication, primarily in aquatic environments and increasingly in terrestrial environments since the late 20th century (Andersen, 1997; McGeosh, 1998; Moreno *et al.*, 2007). This diversity has been a criterion that several authors have considered in their choice of study models for bioindication (Rosenberg *et al.*, 1986; McGeosh, 1998; Rainio & Niemi, 2003; Samways *et al.*, 2010). Other criteria have also been highlighted that contributed to the popularity of arthropods as bioindicators. Among these criteria is their ability to respond quickly to disturbance. Due to their small size, very short generation times, and abundance, they are sensitive to various disturbances, leading to rapid, easily observable, and quantifiable responses (Rosenberg *et al.*, 1986; Kremen *et al.* 1993; Weaver, 1995; McGeosh, 1998; Perner & Malt, 2003; Pearce & Venier, 2005; Oliver & Beattie, 1996; Samways *et al.*, 2010; Gerlach *et al.*, 2013). Furthermore, their great functional diversity (guilds, life history traits, etc.) allows for analysis from relevant study perspectives, considering the variety of responses to disturbances that arthropods offer as functional communities (Maelfait & Hendrickx, 1998; Longcore, 2003; Rainio & Niemi, 2003; Schirmel *et al.*, 2012; Koivula, 2011; Cristofoli *et al.*, 2010).

3.1.2 Spiders

There are more than 50 000 known species of spiders (World Spider Catalog, 2023) and expected as much still to be found (Hamilton *et al.*, 2010; Basset *et al.*, 2012) are the most diverse group of animals almost exclusively composed of predators. There are a few exceptions like *Bagheera kiplingi*, a jumping spider that can shift its regime to hibiscus sprouts for up to 90% of its diet depending on the competition pressure within its habitat (Meehan *et al.*, 2009). Likewise, web

INTRODUCTION

weavers eat some pollen as it recycles its web, and ambush hunters and cursorial species are known to feed on pollen or nectar in flowers (Suetsugu *et al.*, 2014). Yet even *B. kiplingi* can't survive solely on plant material (Nyffeler *et al.*, 2016). These exceptions highlight the vast diversity of spiders, something considered a "megadiverse" taxon (Malumbres-Olarte *et al.*, 2017). This diversity express itself in every continent and habitats (Foelix, 2011). Amongst the spectrum of diversity expressed within spiders, the guilds are particularly rich. As mentioned earlier, spiders are mainly considered predators and therefore guilds within spiders discriminates between the ways of hunting (Cardoso *et al.*, 2011). The main categories are the web weavers, the ambush hunters and the active hunters. Those categories have forms and are linked to environmental variations (*e.g.* Braschi *et al.*, 2021). Within the context of North American peat bogs, spiders are amongst the taxa with the highest number and proportion of specialized species (Payette & Rochefort, 2001; Spitzer & Danks, 2006). Among those, aquatic specialist like *Dolomedes striatus* (Fig. 3) thrive in bogs where adaptations like the ability to walk on water is an asset (Suter, 2013). This specialization and diversity make them great bioindicators (Cristofoli *et al.*, 2010), and possibly diversity indicators (Rubio, 2016), environmental indicators (Maelfait & Hendrickx, 1998) or ecological indicators (Scott *et al.*, 2006).

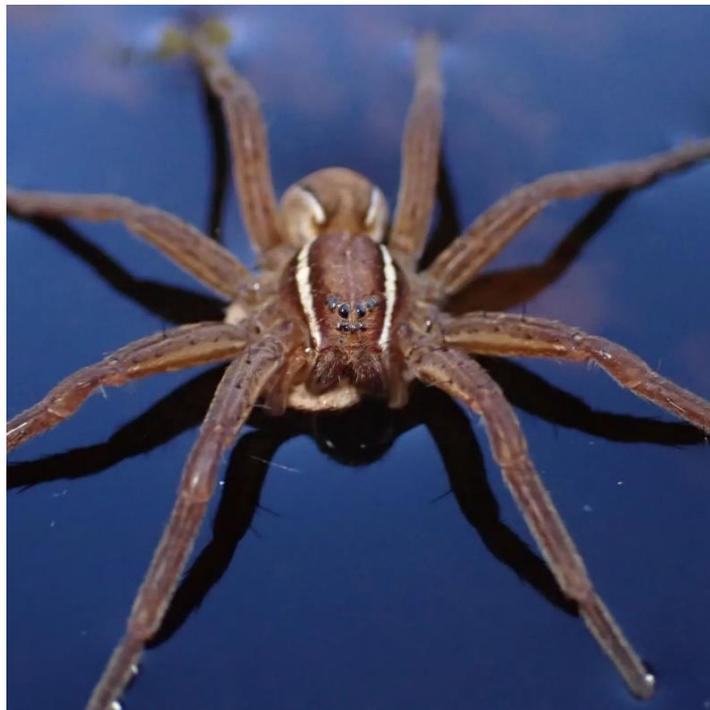


Figure 3 *Dolomedes striatus* female with cocoon, observed walking on water in a bog. Miquelon, chemin des boeufs, 2021. Photographer: Axel Hacala.

Within the palaeoecological remains, despite Scott (2003) that concluded on the strong potential of spiders as sub fossil remains for palaeoecological study (e.g. Fig. 4), there is only a few examples of spider sub fossils. They are often noted in paleoentomological studies. Bennike and colleagues (2008) noted the presences of spiders in peat cores and used the order level in combination with other arthropods to conclude to a dryer period within a core with cues of aquatic habitats. Short *et al.* (1994) observed several spiders remains (13 individuals out of 121 arthropod individuals) but didn't identify theme further than the order *Aranae* either and drew no conclusions from their presence. Other examples used the information linked to spiders like Borsher (1988) that drew conclusions on human activities from abundant remains of Linyphiidae.

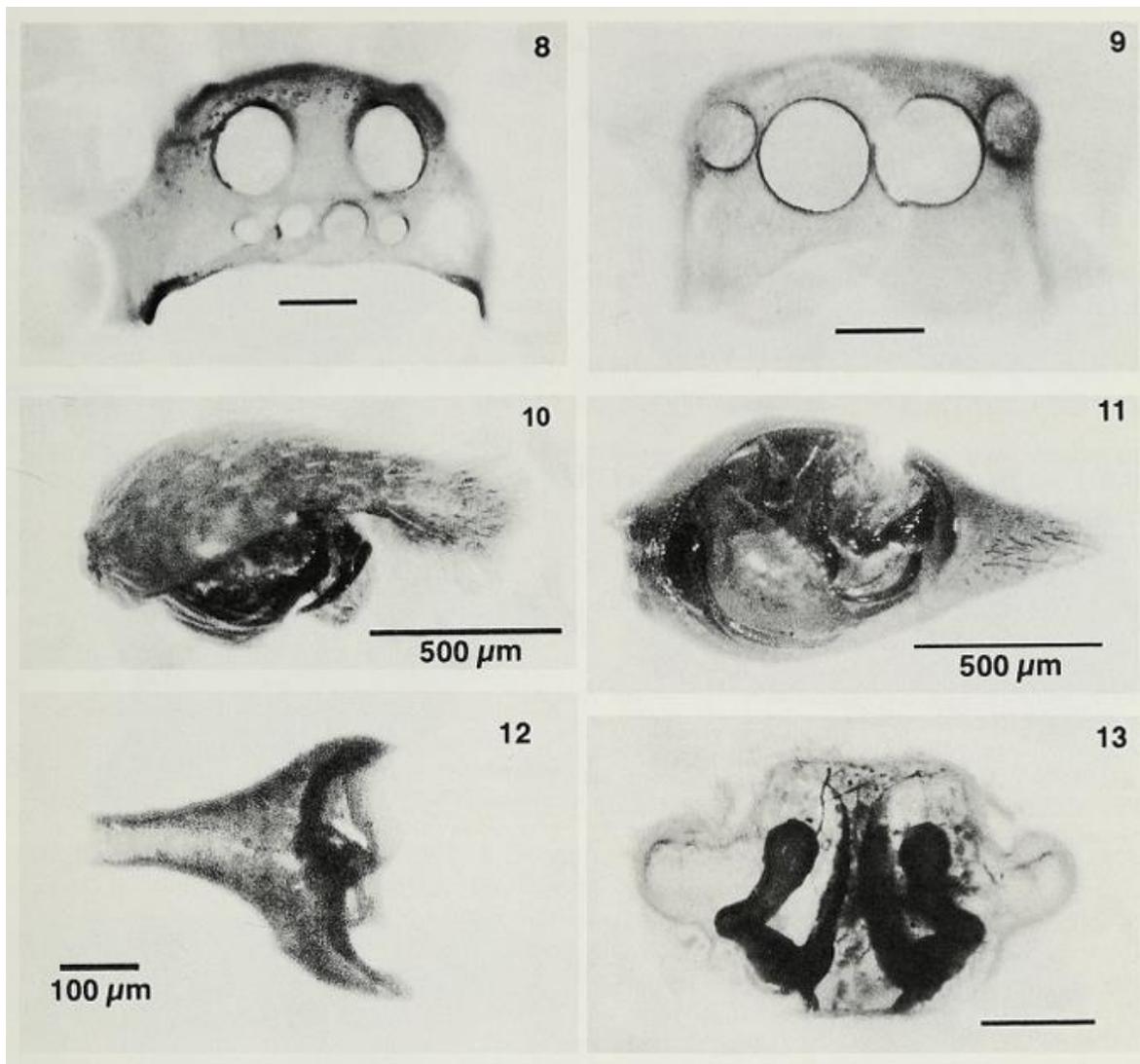


Figure 4 Example of Spider's sub-fossil from Scott (2003) that were identifiable. 8: *Lycosidae* cephalothorax; 9: *Salticidae* cephalothorax, possibly *Neon reticulatus*; 10: Male palp similar to *Trochosa terricola*; 11: Male palp similar to *Alopecosa pulverulenta*; 12: Palpal tibia from *Erigone atra*; 13: Epigynum from *Pardosa pullata*.

3.1.3 Oribatid mites

Oribatid mites represent a rich suborder of acarida with over 13 000 species (Behan-Pelletier & Lindo, 2023). They are among the first animals that lived on land with fossils examples dating to the Devonian (Norton *et al.*, 1988) and a much earlier origin is theorized as a molecular clock analysis suggest (Schaefer *et al.*, 2010). These soil dwelling arthropods display a diversity of feeding guilds including primary and secondary decomposers, which may be mycophagous, phytophagous and predatory (Sheu & Maraun, 2004). They are the most numerous arthropods in most environments with densities that can reach 425×10^3 ind/m² (Behan-Pelletier & Bissett, 1994; Behan-Pelletier & Lindo, 2023).

They present a singular ecology with a slow development, reproduction and resources assimilation which lead them to be considered K-strategist species (Norton, 1994). Albeit unusual for such small beings as K strategists are often larger creatures (Pianka, 1970), their rhythm of life and reproduction suggest a K strategy, or at least a "slow strategy" (Behan-Pelletier & Lindo, 2023). The great diversity of defenses mechanisms present within oribatid mites enforces the definition of a K-strategy and is also linked to a greater survival rate (Pianka, 1970). Those defensive mechanisms are either mechanical or chemical. Mechanical

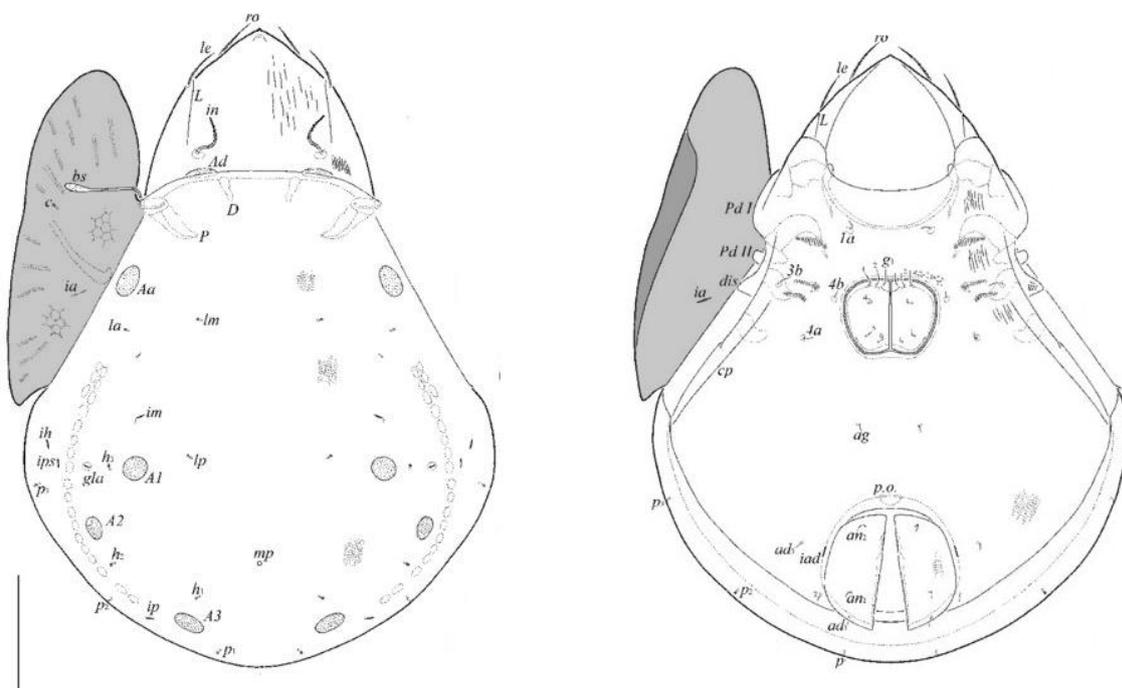


Figure 5 Example of a pteromorph, highlighted in darker grey, on a *Galumna perakensis*. Dorsale (left) and ventral (right) views. Only one pteromorph is represented per individuals but is usually symmetrical. Scale bar 100 μ m. Figure adapted from Ermilov & Kalúz (2019).

defenses start with sclerotization and mineralization resulting in a hardened cuticle. Beyond composition, the forms of the cuticles can come into play with pteromorph, a winglike structure that protects the legs (Fig. 5) or tectum, a specific junction of cuticle plate forms that protect the junctions by having a plate covering the other. Amongst the physical defenses, the Ptycoidy should be mentioned, it's a body form that allows the legs of the mites to retract within the body and the front apsis closes off, thus their nickname of "box mite" (Sanders & Norton, 2004).

Amongst the chemical defences found in oribatid mites, there are ceroteguments produced on their cuticles that prevent predation through protection and camouflage but also reduces transpiration and protection from infections (Raspotnig *et al.*, 2008). Finally, the opisthonotal glands can be found in a variety of forms and produce a diversity of substances (Sakata & Norton, 2001; 2003). These substances have a repellent role against large predators like beetles but less against smaller predator like gamasid mites that are more blocked by physical defences (Brückner *et al.*, 2016). Amongst the toxic components used by Oribatid mites, there are alkaloid that are accumulated by frogs after oribatid consumption and used by the frog as a defence mechanism (Saporito *et al.*, 2007).

Amongst the palaeoecological remains, Oribatid mites are not always discussed beyond a simple mention (e.g. Short *et al.*, 1994). This scarcity in the palaeoecological literature might be explained by the difficulty of identification of the taxa (Baker, 2009). When Oribatid mites do are used as palaeoecological model taxa, they have suggested great potential (Schelvis, 2020). They are found in abundant quantities in palaeoecological contexts, and are preserved enough (Fig. 6) so that over 80% of them can be identified to species level (Schelvis, 1990; 2020). This good level of identification can be attributed to their good preservation state as often, only distal parts of their body like legs are absent (Krivolutsky & Druk, 1986). When the identification is not possible at such a fine taxonomic level, generic identification can still bear information as they can be associated to biofacies (Erickson *et al.*, 2003). Markkula and colleagues (2018; 2020) has highlighted past permafrost dynamics in subarctic peat bogs based on the bioindication potential of oribatid mites. Erickson & Solod (2007) described past climatic and hydrological events in USA from past oribatid mite assemblages

INTRODUCTION

found within lake sediments. Those assemblages were clustered into biozones that allowed for the discrimination of various climatic variations during the study period and highlighted the Pleistocene-Holocene boundary. Polyak *et al.* (2001) studied a colder and wetter climate in New Mexico 3200 to 800 years ago based on oribatid mites, while Larsen *et al.* (2006) used the presence of aquatic species of oribatid mites to strengthen conclusions of wet phases in a multitaxa studies of lake sediments.

3.2. Vegetation, a timeless tool for ecology

3.2.1 Current vegetation community

Vegetation is the most used indicator taxa in ecology (Kuiper *et al.*, 2014) and were among the model taxa at the beginning of ecology as a discipline through the first studies of phytogeography (Von Humboldt, 1807). Vegetation was the main indicator that led to the creation of bioregions (De Candolle, 1820). This historical predominance of vegetation as indicators still echoes nowadays as Humboldt data that led to phytogeography were re-used in 2015 by Morueta-Holm and colleagues to illustrate the variations of vegetation over 200 years of climate changes (Fig. 7).

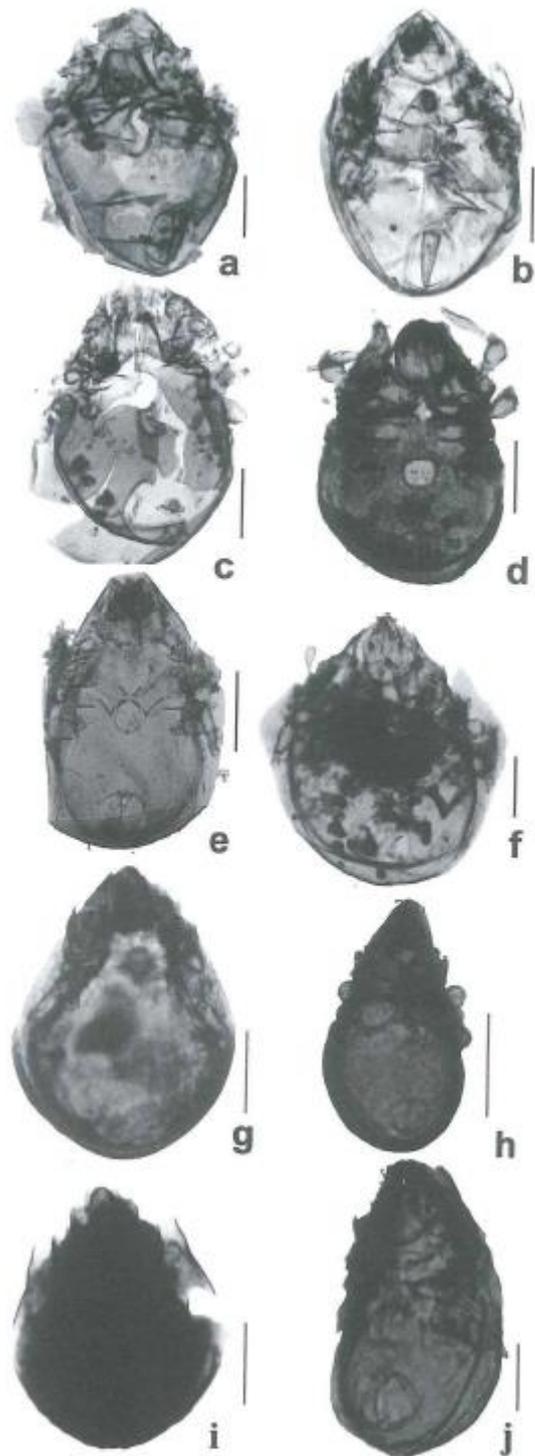


Figure 6 Example of oribatid mites sub-fossils from Erickson *et al.* (2003). A: *Limnozetes onondaga*; B: *Xylobates lophotrichus*; C: undetermined ceratozetoid; D: *Carabodes radiatus*; E: *Oripoda* sp.; F: *Naiazetes reevesi*; G: *Pelopsis bifurcatus*; H: *Suctobelbella* sp.; I: *Peloptulus* sp.; J: *Tectocephus velatus*.

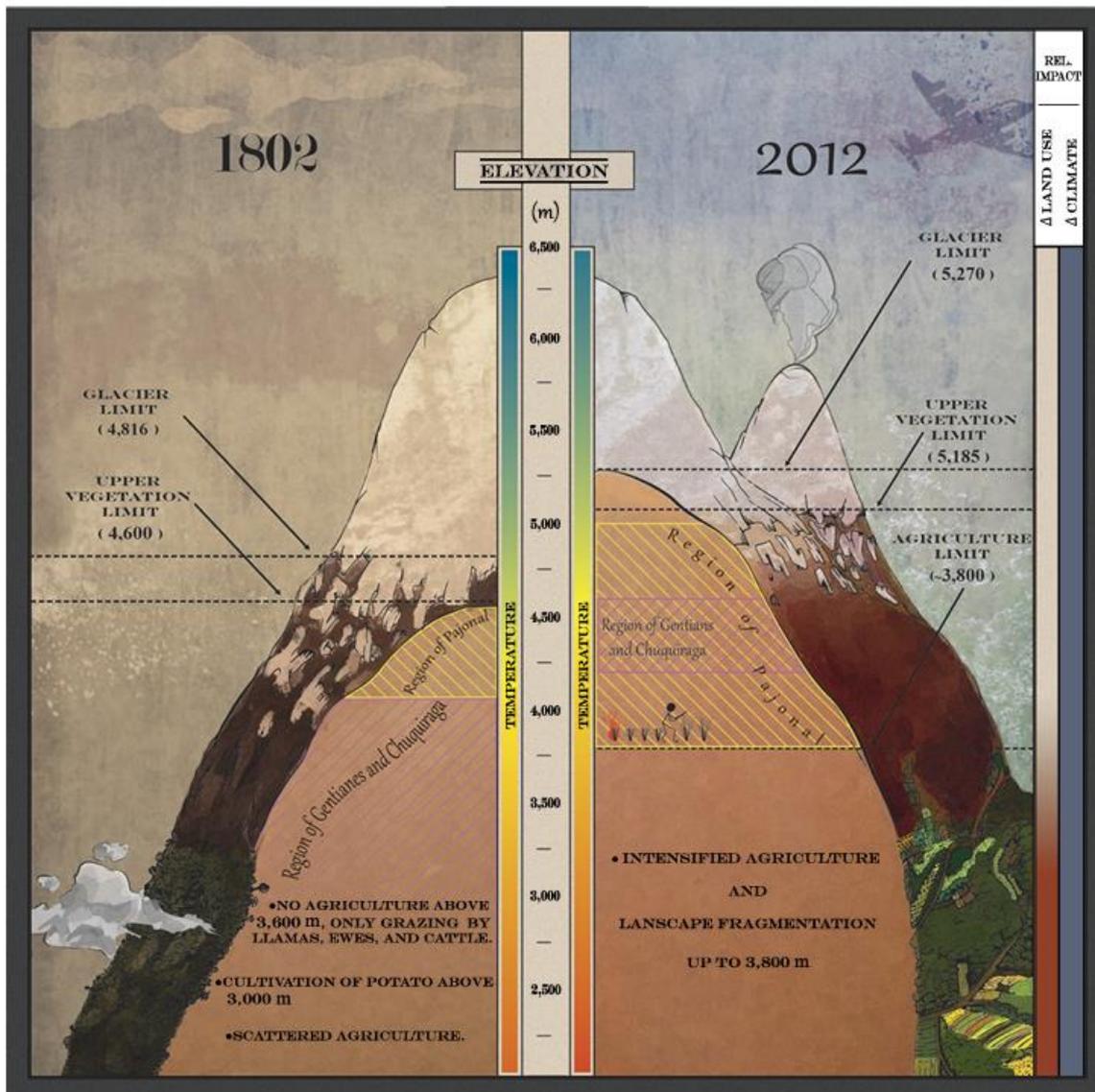


Figure 7 Morueta-Holme *et al.* (2015) adaptation of Humboldt "Tableau de la nature" to display the altitudinal variations of vegetations belts over 2010 years.

Vegetation ecology and biology is well known enough for precise indicators values to be drawn from each species. For instance, in Europe there is a widespread use of Ellenberg values (Ellenberg, 1950; Hill *et al.*, 1999). These values allow us to infer ecological conditions (e.g. humidity, light, continentality etc...). Vegetation is also frequently used as an ecological indicator of environment patterns as most studied habitats have been conceptualized through their vegetation (LaPaix *et al.*, 2009). For instance, forests are mainly analyzed through their vegetation composition (Francis *et al.*, 2000), so are grasslands (Sellers *et al.*, 2001) and wetlands (Maltby & Barker, 2009). Furthermore, past vegetation remains have been extensively used in paleoecology.

3.2.2 Pollen records

Vegetation in paleoecology is mostly known through pollen analysis (Foucault, 2021). Pollen, the reproductive male gamete is spread through the environment, either through air, water or transported by fauna. The biological characteristics of the pollen itself makes it highly resistant (Havinga, 1967) and the diversity of shapes and micro sculpture on their surfaces make them identifiable even after long periods of time up to 250 million years (Hochuli & Feist-Burkhardt, 2013). The often-high taxonomic resolution achievable with pollen, the high quantity of identifiable pollen grains within a sample makes their results robust (Riding, 2021) and can even go through rarefaction calculations to strengthen the results (Nikkeshi *et al.*, 2021). This ability to give a landscape scale quantitative overview of vegetation, even at low taxonomic resolution, can lead to broad understanding of landscapes and associated climates (Richard, 1988). Through modelling efforts and by combing pollen data with vegetation characteristic (relative and estimated pollen production, pollen fall speed, current vegetation and sampling sites characteristics) it is even possible to reconstruct past vegetation landscapes (Serge *et al.*, 2023).

3.2.3 Vegetation remains

Vegetation macro remains, are vegetation cues retrievable in paleo-deposits. They include stems, leaves or reproductive parts like seeds (Fig. 8). Contrary to the pollen that gives information about the communities all around the sampling point, macro remains highlight local patterns. Indeed, the materials under study are the plant parts that once lived at the sampling points. There is always bias possibility from plant materials coming through runoff water or various external sources. This risk is similar to the many sources of variation linked to paleoecology and is dealt with by heeding caution in interpretations. The locality of the samples is an interesting trait of the macro remains as it makes this method very complementary to pollens and, when used alone, doesn't have to worry about the provenances of the samples. Macro remains have the advantage of offering a good taxonomic resolution. Indeed, far more often than with pollen alone, the macro remains can be identified to species, sometime, contextualizing what the pollen display in parallel (Birks & Birks, 2000). The macro remains have been used to understand environmental and climate of past habitats in paleoecology (Birks, 2003) and to follow anthropic activities in archaeology (Roy *et al.*, 2021).

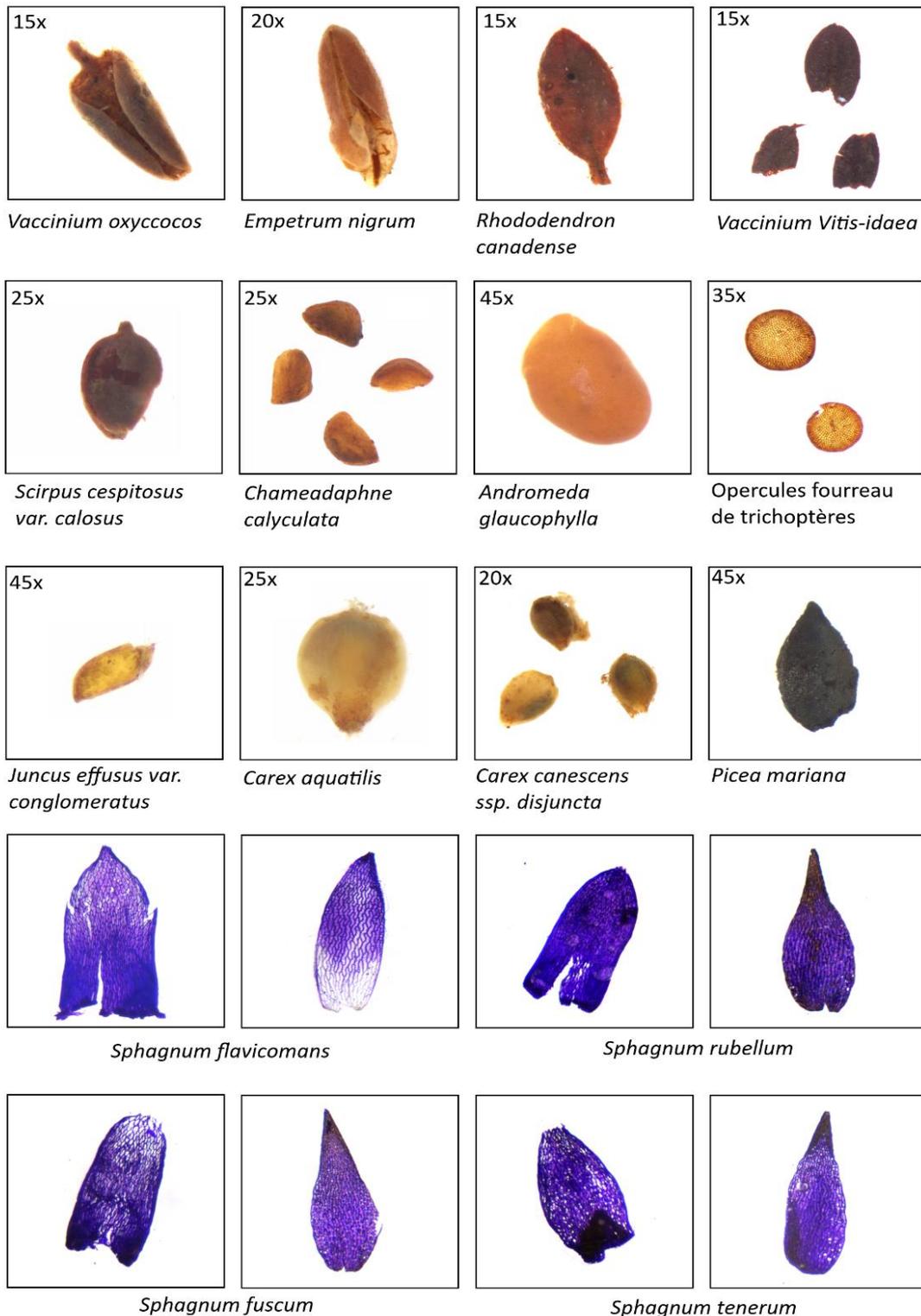


Figure 8 Example of macrofossils both, leaves and seeds, from an analysis performed by the Centre d'étude nordique (Québec, Canada) on samples from the peat core of Saint-Pierre (ZS1). Image from a report by Marie-Eve St-Pierre and Najat Bhiry.

4. ECOLOGY, CLIMATOLOGY AND HISTORY: STUDYING A NORTH AMERICAN FRENCH ARCHIPELAGO

4.1. *Geological and climatic context of Saint-Pierre and Miquelon, a sub-arctic enclave*

4.1.1 **Broad geological and climatic context**

The archipelago of Saint-Pierre and Miquelon is situated off the east coast of Canada, 17km from the shores of the Burin peninsula in the south of the island of Newfoundland. It is composed of three main islands, Saint-Pierre, Miquelon and Langlade. The last two islands are linked together by a sandy tombolo (Fig. 9) since the 18th century (Aubert de la Rüe, 1933). Saint-Pierre is the smallest island with a 26km² surface area while the other two have a combine surface area of 216km². Several smaller and uninhabited islands are present in the archipelago, the most notable being the Ile au Marins, the Grand Colombier, the Ile aux Vainqueurs and the Ile aux Pigeons in a decreasing order of size.



Figure 9 The great double tombolo that links the islands of Miquelon and Langlade. Photo taken from Langlade facing north to Miquelon. (Photographer: Patrick Hacala)

Geologically the archipelago belongs to the Canadian Shield, and more precisely in the Greenville province, hence rocks from the most recent Precambrian orogeny (Payette & Rochefort, 2001). The entire geology and landscape of the archipelago are affected by periglacial phenomena (Saint-Yves, 1962) and traces

of the last ice age include moraines, erratic blocks (Fig. 10) and eroded hill tops (Robequain, 1952; Aubert de la Rüe, 1970). The geological nature of islands within the archipelago varies with Saint-Pierre and Miquelon are volcanic in nature while Langlade is composed of metamorphic rocks (Aubert de la Rüe, 1933).



Figure 10 Erratic block in Saint-Pierre.

The mean temperature of the archipelago is 5.5 °C, with a maximum in August of 15.7 °C and a January minimum of -2.97 °C (mean values calculated from 1933 to 1987, Muller *et al.*, 2012). Despite its position at a meridional latitude the archipelago is described as a subarctic enclave, inheriting its cold conditions from the Labrador current running down from the Arctic Circle (Aubert de la Rüe, 1970). Indeed, while boreal habitats are described in the archipelago, the low topography is submitted to strong winds and harsh climates resulting in a tundra habitat, often characteristic of higher latitudes and or altitudes (Muller, 2008). Another main characteristic of the archipelago is the high hygrometry of its climates, linked to the great amount of fog. The Grand Bank of Newfoundland, where the archipelago is situated, is one of the two foggiest places of the world, characterized by the meeting of cold water from the Labrador current and the warmer water of the Gulf Stream (Lewis *et al.*, 2004). In history, this weather resulted in many shipwrecks (Fig. 11) that might have participated in the formation of the aforementioned tombolo.

4.1.2 Main habitats

The main habitats of the archipelago are boreal forest, peat bogs, tundra and subarctic heathlands.

The boreal forest (Fig. 12) is dominated by *Abies balsamea*. Other resinous essences are present including *Picea mariana* and *P. glauca* as well as *Larix laricina* in damp areas. Amongst the deciduous trees, some *Betula papyrifera* can be noted along with other species, often in the vicinity of streams, but they are a minority. In more open landscapes, often close to the resinous forest and in disturbed areas another Betulaceae, *Alnus crispa*, is very common. The resulting habitat is described as a hyper oceanic birch and fir forest (Muller *et al.*, 2012). The *Abies balsamea* forests on the archipelago is heterogeneous in form as they range from regular forest with trees up to 15 meters high to dwarf rampant forest that can be considered “krummholz” and which are formed through anemomorphosis (Muller *et al.*, 2012).

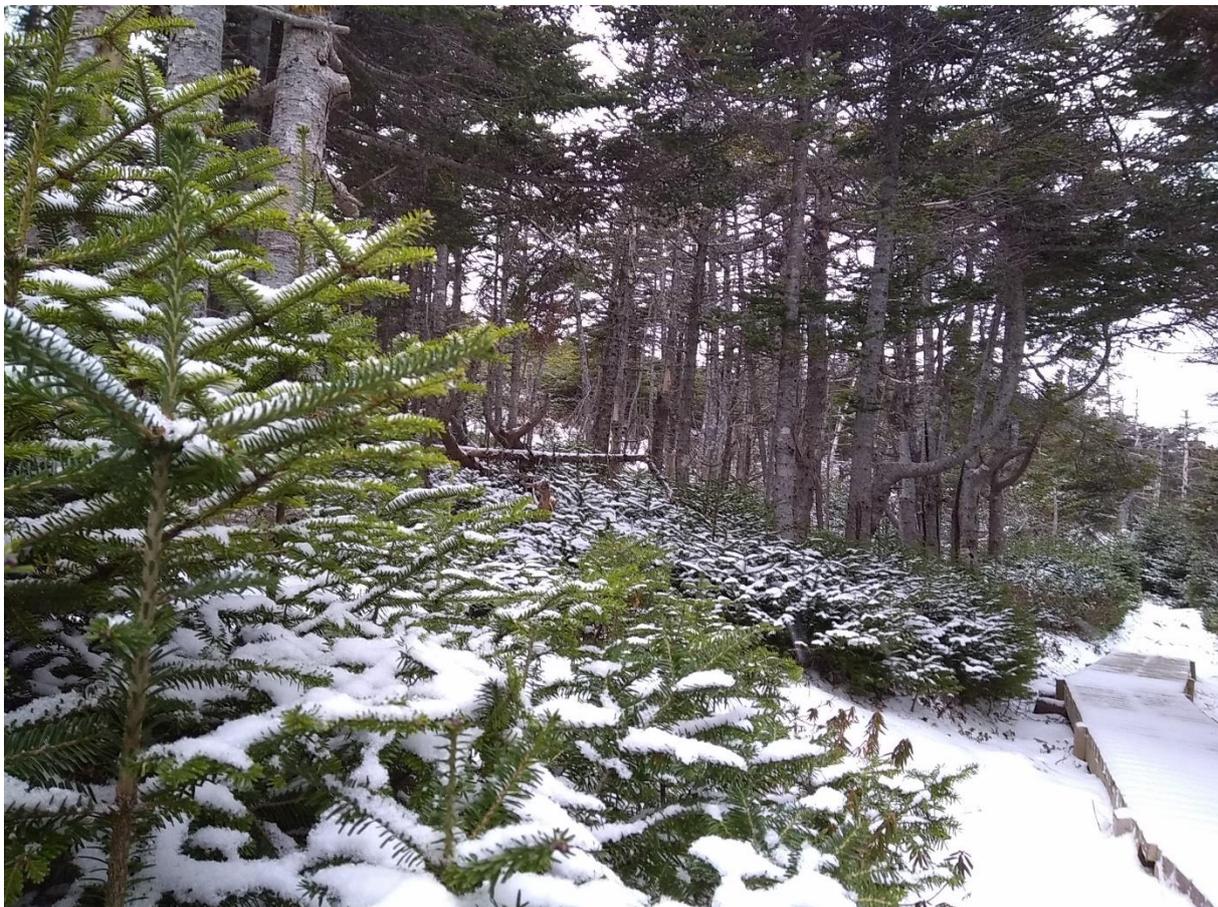


Figure 12 Example of *Abies balsamea* in a boreal forest of Saint-Pierre Island in winter.

INTRODUCTION

The peat bogs of the archipelago are either minerotrophic slope fens or the dominant ombrotrophic bogs which are characterized locally by the presence of some species related to poor minerotrophic fens as its common for Atlantic littoral bogs (Damman & Dowhan, 1981). Covering large surface area of the archipelago, mostly in Miquelon and Langlade, the bogs form blanket of peat bogs scattered with thermokarstic ponds.

Tundra habitats, are characterized by short *Ericaceae* like *Emptrum eamesii* and small flowers like *Diapensia lapponica* (Muller, 2008). These species grow close to the ground enduring the strong winds and shallow soils of the hilltops of the archipelago. This habitat is highlighted as an indicator of the specifically cold climate of the areas as such vegetation is considered arctic-alpine and is usually associated to higher latitudes and altitudes (Muller, 2008). Locally those rocky landscapes are called the “mornes” which could be translated to “bleak”.

The subarctic heathlands are shrubby habitats dominated by *Ericaceae* species, mainly *Rhododendron groenlandicum* (Fig. 13) in the archipelago, a species known to be highly competitive and dominant in poor habitats where it thrives with the help of mycorrhizal networks (Hébert & Thiffault, 2011). Amongst the other highly common species, the sympatric *Kalmia angustifolia* and *Vaccinium angustifolium* are numerous in the open habitats of the archipelago.



Figure 13 *Rhododendron groenlandicum*, in flower. (Photographer: Patrick Hacala)

4.1.3 Broad human history.

▪ ***North American Indigenous occupations***

There is a long history of indigenous occupations on the archipelago, spanning 5000 BP (Leblanc & Rabottin, 2000) to 325 BP (Marchand *et al.*, 2023). The 5000 BP date is subject to debate amongst archeologists as Marchand *et al.* (2023) choose not to conclude on the age of Archaic maritime cultures on the archipelago due to lack of evidence. The island of Saint-Pierre is the most meridional site where this culture left traces of its occupation and is therefore a site of great importance for our understanding of North American indigenous cultures (Marchand *et al.*, 2023). The occupation appears heterogeneous through time with different groups succeeding one another with gaps of several centuries between occupations (Marchand *et al.*, 2023).

▪ ***European colonization***

While the waters around the archipelago were used by European fisherman since 1504, the first settlement by the French was established in 1604 (Aubert de la Rüe, 1933). The next two hundred years were highly turbulent as France and England battled over the colony. During those conflicts the archipelago saw its structures burned and its population shipped away numerous times. In fact, the territory changed hands seven times until 1814 when it permanently became part France (Aubert de la Rüe, 1933).

4.1.4 Climatic variation through the last two thousand years

The area's climate during the last two millennia is known for its heterogeneity (Peros *et al.*, 2016). This variability expresses itself at various scales as the region experiences through various climatic events (Peros *et al.*, 2016). This is expressed geographically as all continents were not affected equally (Mann *et al.*, 1999) or synchronously (Piilo *et al.*, 2019). The area around Newfoundland was subjected to the Labrador current and sea ice influences (Sicre *et al.*, 2014), and experienced different climates and a delayed pattern (Finkenbinder *et al.*, 2022; Foucault, 2021) with high variability and temperature patterns due to the influence of the sea's surface water influence (Rashid *et al.*, 2023).

4.1.5 Medieval Climate Anomaly

The Medieval Climate anomaly (=MCA) was a warm period noted in Europe between the 9th and 14th centuries (Foucault, 2021). In the area of interest for this project, the study of Newfoundland sheds light on the climatic specificity of the area. The MCA locally was delayed to the 11th century and likely began with a cold event before getting warmer (Finkenbinder *et al.*, 2022). This event would be linked to ice melts in Greenland that affected southern coastal territory like Newfoundland (Sicre *et al.*, 2014) and most likely the archipelago of Saint-Pierre and Miquelon.

4.1.6 Little Ice Age

The Little Ice Age (=LIA), as its name suggest, was a colder period at the end of the Holocene experienced in the northern hemisphere (Foucault, 2021). This climatic event started after the cascading effect from high solar activity that led to a great intrusion of warm Atlantic water in the Nordic seas that partially melted sea ice and Fjord glaciers which then weaken the sub polar gyres, leading to the start of the LIA (Lapointe & Bradley, 2021). The LIA's effect on the Newfoundland regions, encompassing the archipelago, is complex and debated as the sea influences lead to opposite climate outcomes between the coast and the open seas as well as various warn and cold event within the period (Rashid *et al.*, 2021).

4.1.7 Anthropogenic warming

The last century is characterized by global rising temperatures (Chen *et al.*, 2021). This recent climatic era is highly variable, both temporally and geographically (Walther *et al.*, 2002) but the general trend is for increased energy within the planetary system linked to Greenhouse Gas Emissions (Chen *et al.*, 2021). These impact both ecological (Walther *et al.*, 2002) and human populations (Zandalinas *et al.*, 2021). In the context of the archipelago of Saint-Pierre and Miquelon, climate change is a perceived as a concrete issue (Philippenko *et al.*, 2021) and it is a threat to the archipelago as its climate is dictated by its oceanic setting (Aubert De la Rüe, 1933) and the islands themselves are highly sensitive to water level rise (Oppenheimer *et al.*, 2019) and coastal erosion (Collins *et al.*, 2019).

II. MATERIAL AND METHODS: THESIS COURSE AND ACTIONS JUSTIFICATIONS.



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To answer this project's questions, two field campaigns were organized. One in the archipelago of Saint-Pierre & Miquelon in 2021 and one in the archipelago of Nain, Labrador in 2022 (Fig. 14). The first campaign's objectives included the assessment of current peat bog arthropod and vegetation biodiversity on sites that had potential for paleoecology in order for the data to be coherently compared. The second one, in Nain, aimed at repeating this sampling technique for current ecological data in a different context whose paleoecology had been documented in order to cross both current and past data with the data from the two field seasons.

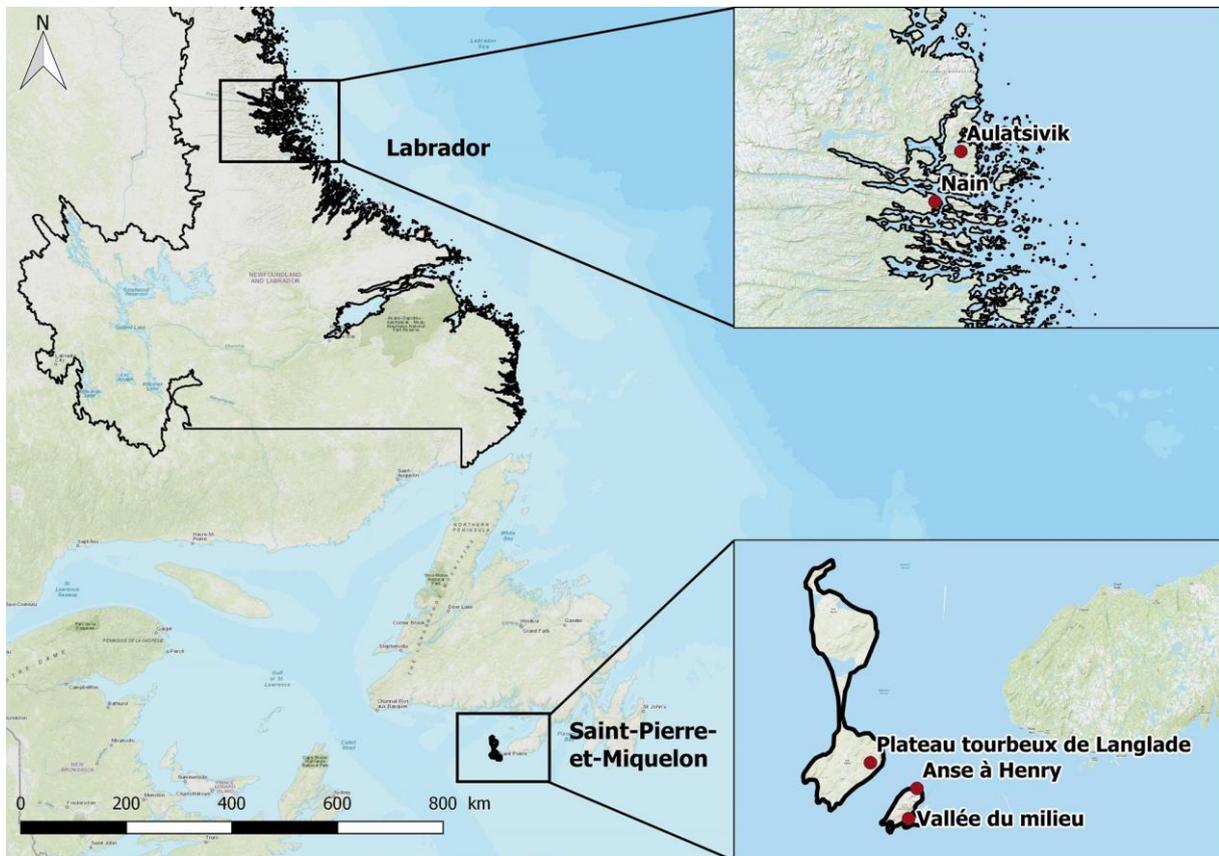


Figure 14 Map of the two areas sampled. Up north the archipelago of Nain and down south the archipelago of Saint-Pierre & Miquelon.

A. The 2021 season on Saint-Pierre & Miquelon (FRANCE)

This sampling campaign started by questioning local naturalists and stakeholders in order to reduce the possible number of study sites to consider before arriving on the archipelago. The criterion on which the sites were chosen was the comparability of habitats, as only peat bogs comparable to each other, were surveyed. In order to be able to deploy sufficient and comparable sampling methods, the sites needed to be of a large enough surface area. Indeed, the epigeic arthropod sampling methods need to be associated with homogeneous habitats across the whole surface. These were sampled by each trap and those chosen surfaces could not overlap between traps as it would lead to pseudoreplication (Topping & Sunderland, 1992).

The first idea of the sampling protocol was to assess, within the peat bog, the effects of surrounding habitats. Indeed, the harsh stress associated to peat bogs is known to diminish on the edges of the peat bog (Payette & Rochefort, 2001). Therefore, a gradient from the center of the habitats to the edges was sampled in the form of three sampling units, one in the center of the peat bog, one in the vicinity of the closest habitats and one within the said secondary habitats. Each of the peat bogs sampling units was composed of 4 traps in a square with 10m sides (Fig. 15). In order to assess such patterns, three sub sites must be present at each locale, close enough to remain within the same ecological context but distinct enough not to create pseudoreplication. Secondly the palaeoecological study required a good level of peat accumulation in order to

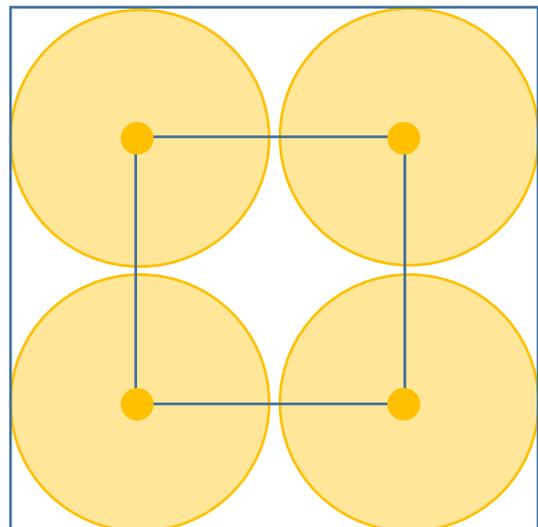


Figure 15 Schematization of one sampling units. Each yellow circle is the capture area on pitfalls traps placed at its center. The inner circle of 10m side represented the minimum distance between the pitfalls to avoid pseudoreplication while the outer square is the limit of the sampling unit, where the D-Vac aspirations are randomly distributed.

optimize the temporal resolution of each sample. Furthermore, the only past attempt at a palynological study on the archipelago was on Miquelon, on the west coast, and resulted in poor samples (Lavoie comm. Pers.). It was hypothesized that the west coast, subjected to dominant winds and with few other local habitats

present, was less propitious for pollen deposits. Finally, the sites needed to represent a diversity of landscape contexts, notably at least one to be within or close to an urbanized context to assess its potential effects as a landscape component.

With these needs in mind, one site per island was selected and surveyed. The selected sites on each island that fit the aforementioned criteria included, on Saint-Pierre the "vallée du milieu" that will be referred to as "ZS", "Mirande" on Miquelon that will be referred as "ZM" and on Langlade the site of "étang du Goéland sud" called "ZL". ZS site is characterized by a proximity to anthropized areas. ZM and ZL are more natural sites with ZM displaying a greater proportion of other habitats within the landscape and a greater influence from the nearby pond while ZL has a more homogenous peat bog landscape.

A first survey of sub sites insides within each selected site was done to link potential sampling sites with potential peat coring locations. To do so, exploratory pedological survey using a corer was performed throughout the sites in order to estimate the depth of the peat's accumulation (Fig. 16).

Three sub-sites per sites were selected for coring, one of those three having the greatest peat accumulation observed on the site (ZS1 = 90cm; ZL2 = 225; Zm2 = 250cm).

Once the sites were chosen, sampling began. Since the peat bogs we sampled were all open habitats with low vegetation it was decided to



Figure 16 Example of pedological exploration on ZM. (Photographer: Tristan Briand)

only sample the epigeic fauna. To do so, two methods were selected, the pitfall traps and the thermic aspirator (=D-Vac). Pitfall traps (110 mm in diameters and 150 mm deep) were set and half-filled with a salted solution (250 g L^{-1}) with a drop of odorless soap. The D-Vac was an inverted leaf blower (RYOBI Model Rbv26b, 15 cm tube diameter, $720 \text{ m}^3/\text{h}$ suction capacity). The two methods are complementary as the pitfall traps is a passive method, that is notably sensitive

MATERIAL AND METHODS: THESIS COURSE AND ACTIONS JUSTIFICATIONS.

to arthropod activity and therefore tend to capture larger individuals (Boetzl *et al.* 2018) while the D-Vac allows to capture smaller and more cryptic species that tend to be missed by the pitfalls (Amiar *et al.*, 2023).

The sampling effort standardization deployed needed to achieve two objectives: (1) being comparable across the sites and sub-sites; (2) allow pooling between pitfalls and D-Vac. To do so the effort deployed was to make 50 D-Vac aspiration of two seconds, randomly dispersed within the 400m² of one sampling unit formed by the 20m sided square delimited by the sampling zone of 4 pitfalls (Fig. 15).

When sampling the secondary habitats, which were serving more qualitative than quantitative purpose, only three pitfall traps were set. Those three traps were set in order to avoid pseudoreplication and still have a 10m radius of homogenous habitats around them but the square disposition was not followed. Instead, the three traps were installed following the form of the secondary habitat patch.

This resulted in 72 traps in peat bogs and 26 in secondary habitats. Those traps were set from mid-July 2021 to the end of August 2021 and retrieved and set back every two weeks. Four sampling sessions were conducted with the D-Vac, at the initial set up of pitfall trap and at every retrieval resulting in 72 samples (see figure 17-19 for spatialization).



Figure 17 Saint-Pierre site (ZS) sampling spatialization. The pitfall traps being represented with red dots.

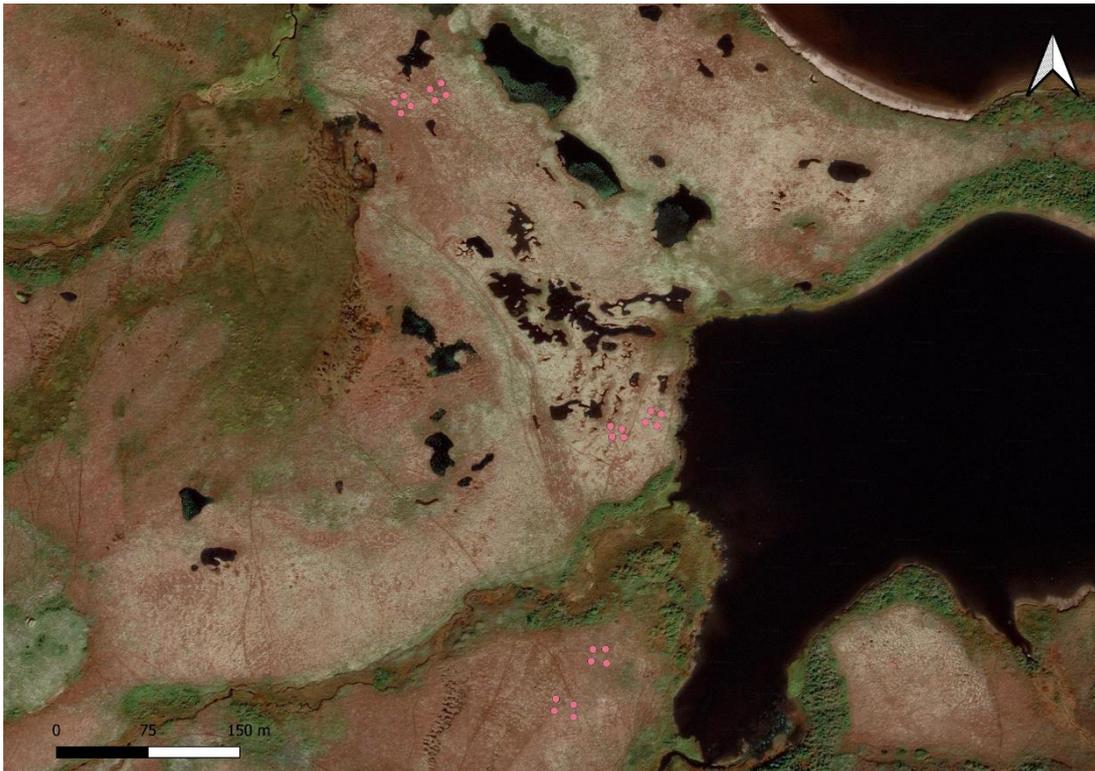


Figure 18 Miquelon site (ZM) sampling spatialization. The pitfall traps being represented with pink dots.



Figure 19 Langlade site (ZS) sampling spatialization. The pitfall traps being represented with red dots.

MATERIAL AND METHODS: THESIS COURSE AND ACTIONS JUSTIFICATIONS.

Vegetation relevés were done at the last retrieval at the end of august. Each relevés were associated with a pitfall trap. The sampling consisted in a 1m sided square with the pitfall at its center. The vegetation measurement was percentage cover of each plant species which were estimated visually.

Link to this sampling campaign, environmental variables were assessed. Environmental variables were assessed at two scale, locale and at landscape level. Locale variable were temperature and hygrometry, measured throughout the sampling session every 10minutes via field data logger (©Tinytag Plus 2 - TGP-4017) planted on each sub-sites, close to the ground but elevated on a pole to avoid direct contact with ground water (Fig. 20). The loggers were encased in a white plastic aerated case that prevent direct contact with rain and standardize and limited direct sun effect through the high albedo of the case. The brut hygrometry and temperature once measured were transformed through calculation of minimum, maximum, mean and SD (=standard deviation) values, calculated at the month scale.

Microtopography of bogs is a known proxy of soil hygrometry (Rydin *et al.*, 2013) and was measured through drone photography (model: ©FC6310S 8.8mm; flight altitude 55m; Resolution of 1.4cm/px and altitude precision to the level of 1cm)



(Fig. 21). A Five-meter buffer around each sampling point (Fig. 21) was assessed and variation of micro topography was computed as well as rugosity index (based on the ruggedness index of topographic heterogeneity by Riley *et al.*, 1999) with GIS (QGIS.org 2022). Mean, standard deviation, delta between minimum and maximum height of topography as well as mean and standard deviation of the rugosity index were computed.

Landscape variables were assessed through GIS after a mapping of the different habitats in a 500m radius around the sampling points. Minimal distance between habitats common to every site (*Abies balsamea* dominated forest, ponds and pools) as well as the surfaced covered by every present habitat (m²) in each trap's 500m buffer was assessed (Fig. 22).

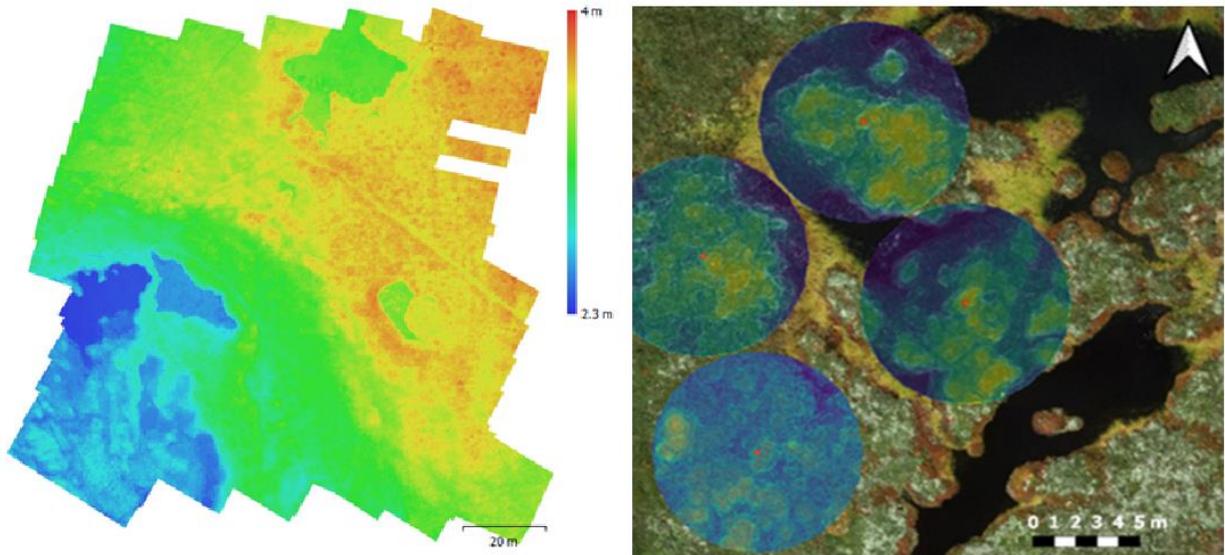


Figure 21 Example of micro-topography assessment based on drone imagery. The raster of topographical variation of a sub-site (right) and the 5m buffer around each pitfall traps (red dot) on ZS1 (left).

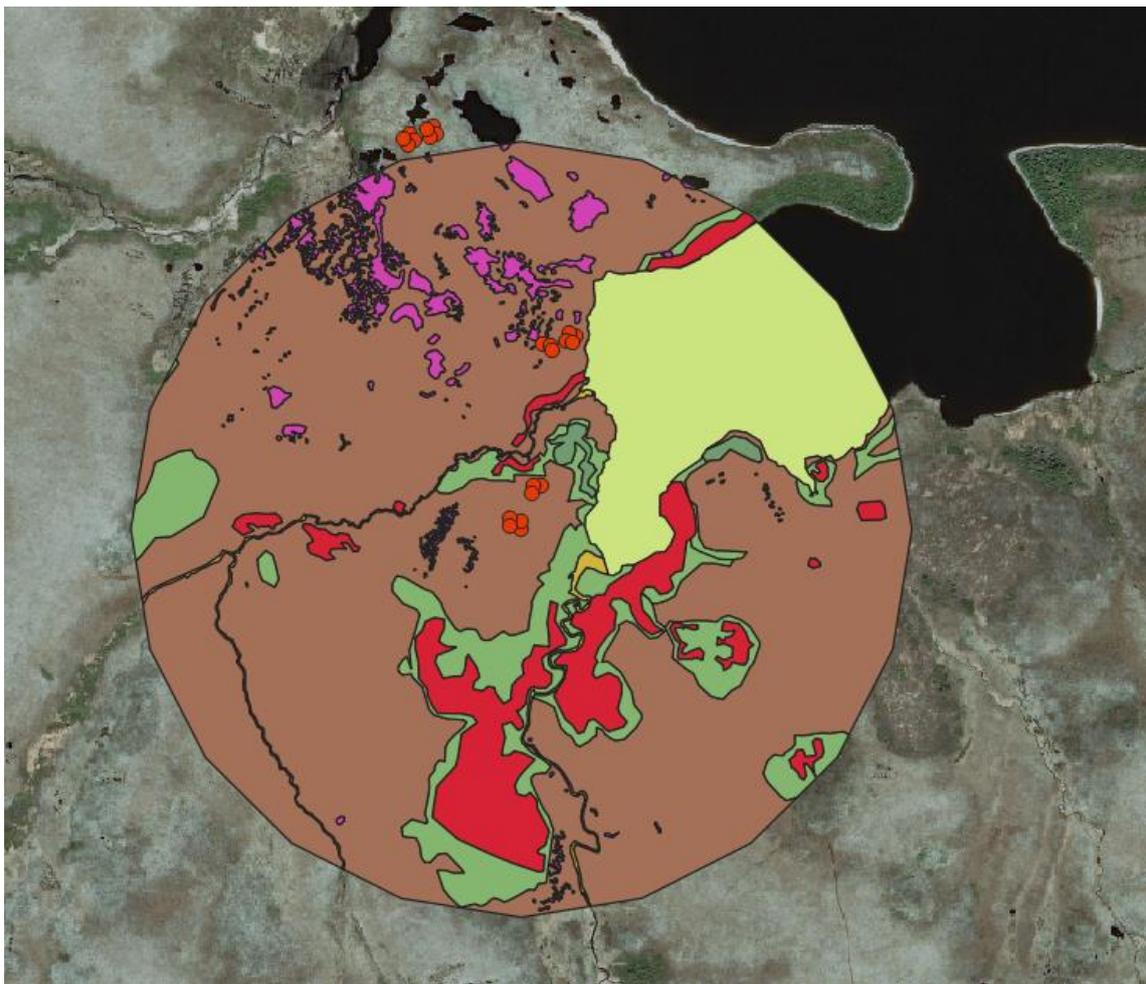


Figure 22 Example of landscape habitat assessment with the example of ZM. Brown: Peat bogs; Light green: sub-arctic heathlands; Dark green: *Larix laricina* woods; Red: *Abies balsamea* woods; Pink: pools; Light yellow: ponds; Dark yellow: rivers; Red dots: pitfall traps.

MATERIAL AND METHODS: THESIS COURSE AND ACTIONS JUSTIFICATIONS.

Palaeoecological sampling, peat coring, were done using a Russian corer (Fig. 23) that sampled 50 cm long semi-cylinder cores with a 52mm diameter. The whole column of peat was sampled to assess the ages of peat accumulation while the analyzed portion of the core corresponds to the last 2000 years only, based on C14 dating. On each site, four core were extracted, one for each model aimed for the study, hence arthropods remain, pollen, vegetation macro remains and environmental DNA. The DNA core was always dig first to limit the potential contaminations linked to impurity on the corer. Gloves were worn and, between each extraction, the corer and all tools were disinfected with bleach to avoid DNA contaminations of the cores. When extracting the other cores, only a thorough cleaning with water of the corer and the tools was done.



Figure 23 Illustration of peat coring with the extraction of the DNA cores in ZS1. The core extraction (left) and the wrapping of the sampled core (right). (Photographer: Sylvie Allen-Mahé).

Lastly as bonus site was sampled, the one of “Anse à Henry” (Fig. 24) at the northernmost point of Saint-Pierre Island. Two pitfall traps were set and retrieved and D-Vac sampling occurred all at the same rates as other sampling in the archipelago. Peat cores were extracted but with only 90cm of peat accumulation. This area was initially prospected as a potential host for a full site as there is an archeological site 200m away from the peat bogs but surfaces of the peat bogs locally were too small.



Since the bottom of the core was dated to only a century old, this site data were not treated further.

Figure 24 Anse à Henry bonus site. (Photographer: Dominique Marguerie).

B. The 2022 campaign of Nain archipelago (Labrador, Canada)

The Nain archipelago's campaign had a similar effort deployed for the arthropods, vegetation sampling and environmental variables. The studied sites were Ox Bay in Dog Island and South Aulatsivik. Due to sites constraints, the spatial organization and exact number of traps couldn't be exactly replicated. Indeed, the northern sites were already studied and strong of many archeological information which led to less flexibility in sites locations. This led to 92 pitfall traps, secondary habitats included, that were active in July 2022. The associated number of D-Vac aspiration was comparable to Saint-Pierre & Miquelon protocol yet far less spaces in time as the mission in the north was only 3 weeks long. Likewise, the pitfall traps were only set for a few days. While the pitfall traps sampling effort is directly link to time of activity, we will never know how such a short sampling time affected the campaign as every sample of pitfall traps from Nain were lost. Adding to it the great time associated to sample sorting in a short calendar, remaining data from the Nain campaign were not used in the thesis and are kept for future projects.

C. Sample treatment

The current samples from pitfall traps and D-Vac were sorted and stored in ethanol 70%, following concentration trade-off that favors morphological conservation of specimens (Marquina *et al.*, 2021).

The peat samples from the core designated for arthropods macro remains were subdivided in 1cm thick slices for a mean volume per sample of 6.33 ± 1.6 ml and stored in a cold room (4°C). The samples were wash with water on a 250µm sieve and then the arthropods remain were manually sorted under 40x magnification. One sample every 3 cm was processed. The arthropod remains found this way were stored in 70% ethanol. Those sorting were effectuated by the PhD student himself and several trainees throughout the project.

Identification of arthropods was done for spiders, ants and ground beetles under x40 magnification with respectively Paquin & Dupérré (2003), Hicks (2018) and Evans (2010). Spider data were analyzed (see chapter 1) while ground beetle and ants were identified but not exploited as the sampled abundance were too low to provide robust representation of natural assemblages (see appendix 1). Oribatid mites identification was done using Behan-Pelletier & Lindo (2023) and morphological comparison with the Canadian National Collection of Insects &

Arachnids at the Agriculture and Agri-Food Canada in Ottawa. Identification was done under microscopic magnification (x400) in lactic acid (70%) and specimens too dark for identification were left in the same solution for a few hours to make them more translucent and ease the identification (Krantz & Walter, 2009).

D. Study sites

1. SAINT-PIERRE SITE, ZS

The Site from Saint-Pierre is called "ZS" and is subdivided in three sub-sites (ZS1, ZS2 & ZS3). This site is characterized by its proximity from anthropic areas and from the sea and by the greater amount of surrounding boreal habitats of forest and heathlands (Fig. 25). The said forests are vastly dominated by *Abies balsamea* while the heathlands are composed of ericaceous plants, mainly *Rhododendron groenlandicum* and *Kalmia angustifolia* or *Vaccinium angustifolium*. Anthropized areas vary in intensity of transformation, from ruderal vegetation's area to highly urbanized zones. The ruderal vegetation ranges from closing environment dominated by *Alnus crispa* or invaded by exotic *Renoutheria japonica* to meadows of grass-type plants accompanied by ruderalisation indicating genus like *Taraxacum* and *Rumex* or the invasive *Senecio jacobaeae*. Those ruderal habitats are either linked to human activities (human constructions as garden and road borders) or meadow enriched, grazed and trampled by horses in enclosed parks.



Figure 25 : ZS1 subsites. (Photographer: Patrick Hacala)

2. MIQUELON AND LANGLADE SITES, ZM AND ZL

The site from Miquelon is called "ZM" (Fig. 26) and is subdivided in three sub-sites (ZM1, ZM2 & ZM3) while the site from Langlade is called "ZL" (Fig. 27) and is subdivided in three sub-sites (ZL1, ZL2 & ZL3). Those sites were chosen as the natural end of the anthropized "gradient". Both sites are characterized by large homogeneous surfaces of peatlands and of various open water habitats (ponds and pools) while forest and heathland cover are lower within the landscape. The sites specificities between the two that can be highlighted are the greater cover of pond in Miquelon as the sites is border by a great pond called Mirande, a 3.4km long body of freshwater bordered by peat lands. Likewise, Miquelon sites is the only site with forest cover of Tamaraks, *Larix laricina*, a coniferous species associated to damp areas and peat bogs (Marie-Victorin *et al.*, 2002).

E. Methods performed by colleagues

Vegetation macrofossils were sorted and identified by the Centre d'études nordiques (Québec, Canada) while pollen were treated, identified and studied in the Laboratoire Chrono-environnement (Besançon, France). Datation based on C14 was done by the Laboratoire de Radiochronologie of the Centre d'études Nordiques from Laval University (Québec, Canada). Chronomodelisation was performed by Philippe Lanos (CNRS, Geosciences Rennes) and Dominique Marguerie (CNRS, ECOBIO). Drone imagery acquisition was done by the DTAM (La Direction des Territoires, de l'Alimentation et de la Mer) of Saint-Pierre and Miquelon. Any participation by a peer to a chapter is specified in the authors list.

F. Thesis manuscript outline

The Thesis manuscript thereafter is organized in chapter as aforementioned but with a specificity of form: they are written as individual research articles. The neoecological first part is composed of the chapter one, an article already published in the journal Ecological indicators. The second part, paleoecology, is divided into two chapter that albeit being in the form of articles, are not yet submitted but are destined for it.



Figure 26 Miquelon sites from the south. (Photographer: Tristan Briand)



Figure 27: Example of peat bogs surrounding the Langlade sites. (Photographer: Pascaline Caudal)

III. NEOECOLOGY



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Spider and Vascular Plant Assemblages in Subarctic Peat Bogs are Complementary Ecological Indicators of Variation in Local and Landscape Factors.

Axel Hacala^{1,*}, Manuel Salgueiro-Simon², Allison Bain³, Dominique Marguerie¹, Julien Pétilion^{1,4}

¹ UMR CNRS 6553 Ecobio, Université de Rennes, 263 Avenue du Gal Leclerc, CS 74205, 35042, Rennes Cedex, France

² Université de Brest. Laboratoire Géoarchitecture, Territoires, Urbanisation, Biodiversité, Environnement, F-29200 Brest

³ CELAT Research Centre, Université Laval, Québec, Canada

⁴ Institute for Coastal and Marine Research, Nelson Mandela University, Gqeberha, South Africa

Corresponding author: axel.hacala@gmail.com, +33 6 16 50 76 52

Author contributions:

Axel Hacala: Conceptualization, Methodology, Investigation, Resources, Formal analysis, Writing - Original Draft, Writing - Review & Editing, Project administration, Funding acquisition. **Manuel Salgiero:** Formal analysis. **Allison Bain:** Conceptualization, Writing - Review & Editing, Supervision, Project administration, Funding acquisition. **Dominique Marguerie:** Conceptualization, Methodology, Investigation, Resources, Writing - Review & Editing, Supervision, Project administration, Funding acquisition. **Julien Pétilion:** Conceptualization, Methodology, Investigation, Resources Writing - Review & Editing, Supervision, Project administration, Funding acquisition.

HIGHLIGHTS

- High complementarity between spider and vascular plants as ecological indicators in peat bogs.
- High complementarity between diversity metrics in the understanding of ecological patterns.
- Landscape and local factors as interwoven structuring drivers of community in peat bogs.

RESUME

Malgré la diversité qu'elles abritent et les services écosystémiques qu'elles fournissent, les tourbières demeurent mal comprises, particulièrement vis-à-vis de leurs réponses à des variations à de multiples échelles spatiales. De nombreux habitats subarctiques font face à des risques sévères liés aux changements climatiques globaux. Dans cette étude, en utilisant une approche multi-métrique, nous avons évalué les capacités indicatrices des plantes et des araignées en tant qu'indicateurs écologiques entre des tourbières contrastées d'un l'archipel Français (Saint-Pierre et Miquelon) en Atlantique Nord. En 2021 des pièges barbers et de l'aspirateur thermique ont été utilisés pour collecter les araignées tandis que des relevés phytosociologiques ont servi à documenter la flore vasculaire. Un total de 69 espèces d'araignées et 38 espèces de plantes vasculaires ont été identifiées et les diversités taxonomique (TD) et fonctionnelle (FD, basée sur des traits relatifs à la dispersion, la taille et le fonctionnement dans l'écosystème) ont été estimées pour trois niveaux d'abondances relatives des espèces (Nombres de Hill $q=0$, 1 et 2) grâce au package iNEXT 3D pour la diversité alpha et iNEXT beta3D pour la diversité beta. Conformément aux attentes, les patrons de TD et FD sont fortement corrélés, et ce pour chaque nombre de Hill, mais également entre nombres de Hill pour les araignées, indiquant un effet étonnamment faible de l'abondance des araignées sur leurs patrons de diversités. A l'inverse, les différences entre les sites sont plus marquées pour la végétation quand la couverture d'échantillonnage est prise en compte ($q=1$ et $q=2$), cela pour la TD et la FD, ainsi que pour la diversité alpha et beta. Les RLQ et l'analyse en "Fourth corner" soulignent des différences significatives entre les sites qui sont liées à des traits fonctionnels de dispersions et des facteurs locaux pour la végétation. Finalement, les partitions de variances sur les assemblages soulignent l'importance des interactions entre les facteurs locaux et le paysage, pour les araignées et la végétation, et ce avec une importance relative importante des facteurs locaux pour la végétation. Notre étude révèle une grande complémentarité de l'utilisation des métriques et des assemblages des araignées et de la végétation comme indicateur des variations de conditions locales dans les tourbières, confirmant les changements rapides que traversent les habitats subarctiques.

ABSTRACT

Despite their specific biodiversity and the ecosystem services they furnish, peat bogs remain poorly understood, especially in terms of their responses to changes at multiple spatial scales. Many subarctic peat systems face acute risks, due to current global change. In this study, using a multi-metric approach, we assessed the relative value of plants and spiders as ecological indicators in contrasted peat bogs of a French archipelago (St. Pierre-et-Miquelon), located in the North Atlantic. In 2021, pitfall trapping and suction sampling collected spiders while phytosociological relevés were used to document vascular plants. A total of 69 species of spiders and 38 species of vascular plants were identified, and both taxonomic (TD) and functional (FD, based on traits related to dispersal, size and ecosystem functioning) diversity were then estimated for three levels of species relative abundance (Hill numbers $q=0$, 1 and 2) using the iNEXT 3D package for alpha diversity as well as iNEXT beta3D for beta diversity. As expected, patterns of TD and FD were highly correlated for each Hill number, but also between Hill numbers for spiders, indicating a surprisingly low effect of species abundance on (spider) diversity patterns. On the contrary, differences between sites were more visible for plants species when species coverage was considered ($q=1$ and $q=2$), for both TD and FD, and for alpha and beta diversity. RLQ and Fourth corner analyses indicated differences based on functional traits between sites which were significantly associated with relationships between dispersal modes and mostly local factors for plant assemblages. Finally, variance partitioning on assemblage composition showed the importance of an interaction between local and landscape factors for both plants and spiders, with a relatively high importance of local factors alone for plants. Our study thus revealed the high complementary of spider vs. plant assemblage-based metrics as indicators of changing local conditions in peat bogs, confirming these both experience rapid change in subarctic climates.

Key words: alpha diversity, beta diversity, taxonomic diversity, functional diversity, iNEXTbeta3D, 4th corner analysis, wetlands, St. Pierre and Miquelon

1. INTRODUCTION

Peat bogs are amongst the most unusual (Minayeva & Sirin, 2021) and endangered habitats on the planet (Pinceloup *et al.*, 2020), covering 4 million of km² across the globe (Rydin *et al.*, 2013). While their important functions within ecosystems are largely accepted within the scientific literature (Bonn *et al.*, 2016), these humid habitats currently suffer the dual threats of destruction from encroaching agriculture and urbanization. Different types of peat bogs are generally classified within a gradient of available nutrients linked to their hydrology (Rydin *et al.*, 2013). The habitats studied here are bogs (*sensu* Rydin *et al.*, 2013), or more specifically, they are ombrotrophic peat bogs which draw their ecological specificities from their harsh environmental conditions. They are characterized by saturated hydrology, high acidity and a scarcity of nutrients (Rydin *et al.*, 2013). These conditions lead to important levels of specialization in the biodiversity they host (Minayeva & Sirin, 2021), enhancing both their conservation value (Scott *et al.*, 2006) and the interpretive challenges they represent (Räsänen *et al.*, 2023). Bogs of the North American Atlantic coast are unique habitats characterized by a combination of species considered specialist species exclusive to poor bog plants and few minerotrophic ones (Damman & Dowhan, 1981; Wells, 1996).

These types of conditions have been previously studied and even if variations in landscape were highlighted as key driving factors (Andersen *et al.*, 2011), the scale and environmental cues present in the published literature are often too localized (a local variable within a given landscape, e.g., Andersen *et al.*, 2011) or too large - at the continental scale (climatic perspectives, e.g. Robroek *et al.*, 2017) to properly understand the dynamics of peat bogs. In addition, peat bog diversities are often studied by simply comparing different types of peat bogs (Payette & Rochefort, 2001) instead of assessing the variation within a single type of peat bog.

There is therefore a need to improve the knowledge of these habitats and their diversity. Ecological indicators may be used as a tool to efficiently assess habitat ecology (McGeosh, 1998) and to inform about specific indicators themselves (Van Straalen, 1996), however, as previously stated, it is better to use multiple taxa to assess habitat complexity as different taxa may have diverged ecological sensitivities, potentially revealing complementary responses (Samways *et al.*, 2010; Fattorini *et al.*, 2011).

Amongst the ecological indicators to be documented, spiders were selected, as they are a highly diverse taxon with more than 50,000 known species worldwide (World Spider Catalog, 2023). They have a broad enough ecology to have colonized most terrestrial ecological niches on the planet (Foelix, 2011) and they fit the requirement of a good indicator species (McGeosh, 1998; Gerlash *et al.*, 2013) due to their abundance, diversity, ease of sampling, identifiability, and numerous specialized species. In addition, spiders are amongst the taxa with the highest number and ratio of specialized animal species in Canadian peat bogs (Payette & Rochefort, 2001; Spitzer & Danks, 2006), leading to their successful use as indicator taxa (Scott *et al.*, 2006; Buchholz, 2016). The second taxon considered are vascular plants, the most commonly used indicator of ecological variations in peat bogs (e.g., Kuiper *et al.*, 2014; Robroek *et al.*, 2015) and often one of the primary means, after hydrology, of distinguishing different types of peat bogs (Rydin *et al.*, 2013). The combined use of spiders and vegetation is based on their known complementarity when faced with different ecological processes (Pétillon *et al.*, 2014; Hacala *et al.*, 2020). As spiders are almost exclusively predators, their responses are often uncorrelated with the diversity of local vegetation (Lafage *et al.*, 2019) and their sensitivity to landscape features differs largely across vegetation types, including in wetlands (Lafage *et al.*, 2015). The two taxa thus display different responses to ecological cues and variable degrees of correlation between diversity metrics, and their ecological indicator values can be expected to differ globally across spatial scales. The use of multiple diversity metrics will better serve conservation of peat bog as those metrics are complementary (Tucker *et al.*, 2018; Hacala *et al.*, 2021; Robuchon *et al.*, 2021; Morel *et al.*, 2022) while also contributing to the overall understanding of habitat biodiversity and conservation values (see Webb *et al.*, 2002 in recent literature). The combined use of multiple metrics is found in the recent literature (for arthropods but also more commonly with vegetation: Hacala *et al.*, 2021) and appears essential for a holistic understanding of habitats (Devictor *et al.*, 2010). For instance, the combined usage of taxonomic and functional diversities demonstrate their complementarity as ecological metrics (Leroy *et al.*, 2014; Campbell *et al.*, 2010; Wong *et al.*, 2019; Ridet *et al.*, 2021). As for the order of diversity based on Hill numbers (*sensu* Chao *et al.*, 2014), they allow for the understanding of the weight of rare and dominant species within an assemblage that could not be properly assessed solely with diversity indices (Schwartz *et al.*, 2000; Gaston & Fuller, 2008; Jain *et al.*, 2014). Finally, the complementarity of

alpha and beta diversities allows for the assessment of an assemblage's composition and serves to untangle environmental sensitivities (Socolar *et al.*, 2016). Within peat bogs, the complementarity of multi-metric approaches has highlighted distinct patterns of biodiversity, which can be observed between taxonomic and functional diversity with vegetation (Robroek *et al.*, 2017) and entomological (Diptera) communities (Taillefer *et al.*, 2018), between alpha and beta diversity with vegetation (Fontaine *et al.*, 2007) and within diversity orders with spiders (Scott *et al.*, 2006). To the best of our knowledge, these diversity components are complementary, yet have never been used on a single project.

This study aims to understand the complementarity of contrasted taxa and several metrics as ecological indicators of local and landscapes features within peat bogs. As previously stated, this approach has not been previously undertaken in the study of subarctic Atlantic bogs, an often-overlooked habitat (Sikes & Callegari, 2020). For example, arthropod diversity knowledge can vary by 20-fold from subarctic to temperate regions (DeWaard *et al.*, 2019), indicating the need for specialized studies. These knowledge gaps within the subarctic region have been highlighted specifically for Canadian subarctic peat lands (Warner *et al.*, 2006). This state of knowledge combined with the current global changes affecting these habitats at a higher rate (Elmqvist *et al.*, 2004; Limpfen *et al.*, 2021) stresses the need to improve our knowledge of them.

We hypothesize (1) a high complementarity between taxa as they are known to display different responses to environmental variables (Hacala *et al.*, 2020; Pétilion *et al.*, 2014) and spatial scales (Lafage *et al.*, 2015); (2) a redundancy in taxonomic and functional diversity as the two metrics are generally highly correlated (Pavoine *et al.*, 2013; Hacala *et al.*, 2021), notably in the case of vegetation (Cadotte *et al.*, 2013); (3) that diversity orders will display complementarity by untangling the effects of stressful environments which tend to drive dominance patterns (Perner & Malt, 2003); and (4) that studying alpha and beta diversities will reinforce the complementarity of both taxa as ecological indicators (for both taxonomic and functional diversity), as reported from other habitats (e.g., Lafage *et al.*, 2015; Hacala *et al.*, 2020).

2. MATERIAL AND METHODS

2.1. Study sites

Peat bogs were sampled on three sites on the archipelago of St. Pierre and Miquelon (Fig. 28): St.-Pierre (46.7696 E, -56.1862 N), Miquelon (47.0729, -56.3329) and Langlade (46.8258, -56.3093). These were selected to represent a spectrum of comparable ombrotrophic bogs within contrasted landscape contexts. All three sites were subdivided into three sub-sites of comparable peat bog habitats. St. t. Pierre is characterized by a landscape context composed of anthropogenic areas as well as forest and subarctic heathlands, while the Langlade and Miquelon sites are characterized by large areas of peatland and open water habitats. These two sites resemble each other in terms of landscape composition but they vary in terms of local structure and landscape organization (*e.g.* the distance between landscape elements and sampling points are greater within Miquelon). The mean temperature of the archipelago is 5.5 °C, with a maximum in August of 15.7 °C and a January minimum of -2.97 °C (mean values calculated from 1933 to 1987, Muller *et al.*, 2012).

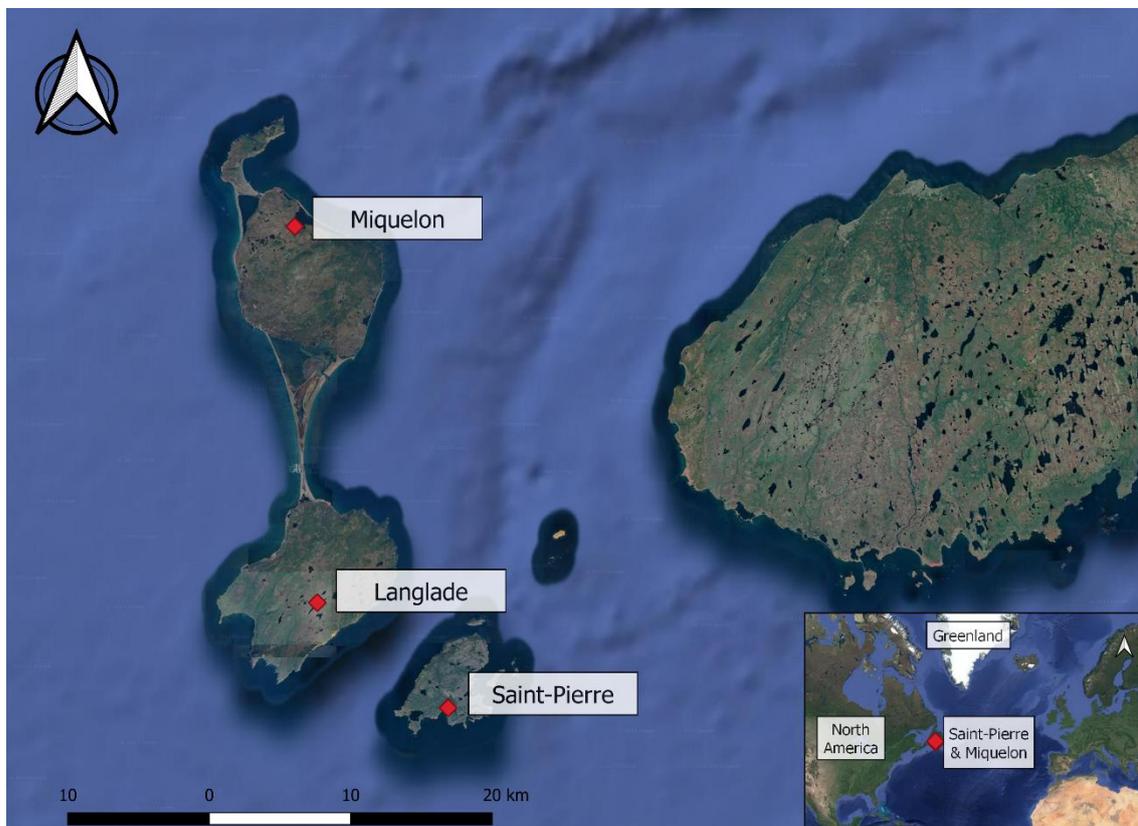


Figure 28 Map of St. Pierre & Miquelon. The red dots indicate the three study sites.

2.2. Arthropod Sampling and Vascular Plant Characterization

In 2021, eight pitfall traps (110 mm in diameter and 150 mm deep) were set on each of the sub-sites for a total of 72 traps. Each trap was associated with a botanical relevé within a square meter where a percentage cover of each plant species was visually estimated. Spatially, groups of four traps were set at least 10 m apart to avoid edge effect and pseudoreplication (Topping and Sunderland 1992). Each group of four traps formed a sampling point and each trap was set within a five-meter radius of a homogeneous habitat based on dominant vegetation. These were half-filled with a saltwater solution (250 g. L⁻¹). A drop of odorless dish soap was added in order to break the surface tension and improve arthropod capture. The contents were collected every two weeks from mid-July to the end of August 2021.

Sampling with a suction sampler was performed every two weeks, resulting in four capture sessions, using an inverted leaf blower (15 cm tube diameter, 720m³/h suction capacity). Sampling consisted of 50 times two seconds randomly distributed aspirations across a 20 m side square corresponding to the area sampled by each group of 4 pitfall traps. This resulted in 72 aspiration samples. For the analysis, spiders from the four pitfall traps and the associated suction samples were pooled together as well as the vascular plants data from the four associated relevés.

2.3. Identification

Spider samples were sorted in the laboratory, transferred to ethanol 70%, and stored at the University of Rennes, France. Identification to species level was undertaken using Paquin & Dupérré (2003) on adult spiders, while vascular plant identification was done in the field using Marie-Victorin *et al.*, (2002).

2.4. Environmental Variables

Environmental variables were assessed at two scales, that of local and landscape. Local variables were air temperature and hygrometry and were measured every 10 minutes via field data logger (©Tinytag Plus 2 - TGP-4017) during the 45-day sampling season, with one data logger for each sub-site.

Minimum, maximum, mean and standard deviations were computed. Microtopography of bogs is a known proxy of soil hygrometry (Rydin *et al.*, 2013) and was measured through drone photography (model: ©FC6310S 8.8 mm; flight altitude 55m; Resolution of 1.4cm/px and altitude precision to the level of 1 cm). A five meter buffer around each sampling point was assessed and variations in the microtopography were calculated along with the rugosity index (based on the ruggedness index of topographic heterogeneity by Riley *et al.*, 1999 with GIS QGIS.org, 2022). Mean, standard deviation, delta between minimum and maximum height of topography as well as mean and standard deviation of the rugosity index were also calculated.

Landscape variables were assessed through GIS after mapping the different habitats in a 500 meter radius around the sampling points (mapped based on 2012 aerial images at 1 m resolution from BD ORTHO®). Minimal distance between habitats common to all sites (*Abies balsamea* dominated forests, ponds and pools) as well as the surfaced covered by every present habitat (m²) in each trap's 500 meter buffer was assessed.

2.5. Functional Traits

Two criteria were set to select the traits: (1) they must be reported as drivers of species assemblages and (2) they must be available in published literature. The functional trait definition provided by Violle *et al.* (2007) and followed by Wong *et al.* (2019) was used, with the exclusion of environmental preferences as they are not, strictly speaking, a functional trait. Three traits were selected for spiders: dispersal abilities (ballooning), body size and trophic guild. For vascular plants, dispersal mode (by water, wind, zoochory and vegetative local dispersal), seed mass, plant height and SLA (specific leaf area) were chosen. These traits are known to be linked to environmental responses in both spiders (Schirmel *et al.*, 2012) and in vegetation (Garnier & Navas, 2012; Laine *et al.*, 2021). When these traits were not present in the literature, the value from the closest species within the genus was used.

2.6. Statistical Analysis

Potential pattern in diversity metrics (TD & FD, alpha and beta) between sites were assessed with rarefaction curved from iNEXT.3D (Chao *et al.* 2021) and

iNEXT.beta3D packages (Chao *et al.*, 2023). This method was selected to account for the possible influences of sampling coverage and dominance patterns through the comparison of different diversity orders (Hills number of $q=0; 1; 2$). The tests were run with 40 knots and 200 bootstrap replications. Potential significant differences were assessed through the absence of overlapping confidence intervals on iNEXT.3D curves (Chao *et al.*, 2014).

To assess trait association with a site's specificity, three matrices were analyzed simultaneously through an RLQ analysis containing the following information: L (species abundance across samples), R (environmental characteristics of samples) and Q (species traits), which crosses traits and environmental variables weighted by species abundances. For this, the RLQ function of ade4 package (Dray *et al.*, 2007) was used. In addition, following the method in Borcard *et al.* (2018), a Fourth corner analysis was done to assess the pairwise relationships between traits and environmental variables as a complementary method to the RLQ as proposed by Dray *et al.* (2012, 2014) as it allows to link the traits and environment matrices that were both tied to the assemblage matrix within the RLQ.

To assess the relative importance of local and landscape variables, alpha diversity, and multiple regressions were done with a stepwise model selection procedure by AIC (Akaike, 1974), implemented in the MASS R package (Venables & Ripley, 2002) on rarefied taxonomic and functional diversity based on Chaos estimator with the BAT package (Cardoso *et al.*, 2015). Relative contributions of explicative variables to the model were estimated using the relaimpo package (Grömping, 2006) with the R^2 contribution averaged over orderings among regressors (Lindeman *et al.*, 1980; Chevan & Sutherland, 1991). To assess the relative importance of local and landscape impacts on spiders and vascular plants communities as well as on beta diversity (both taxonomic and functional) a variance partitioning was done following Borcard *et al.* (2018) and Lafage *et al.* (2015). Taxonomic beta diversity was based on Bray Curtis distance while functional distance matrixes were based on kernel density n-dimensional hypervolume methods (Mammola & Cardoso, 2020) implanted in the BAT package (Cardoso *et al.*, 2015). All data analyses were conducted using the free software R-3.6.2 (R Development Core Team, 2021).

3. RESULTS

Taxonomic alpha diversity compared through rarefaction curves at different orders of diversity displayed contrasting results between spiders and vascular plants (Figs. 29 & 30; see appendices A & B for the species lists and associated traits values per taxon for spiders and vascular plants respectively).

No significant differences were observed between sites in the spider assemblages regardless of the diversity order (Fig. 29). For vascular plants assemblages, a higher taxonomic diversity was observed in St. Pierre in the three orders, except for Langlade's assemblages with $q=0$ that appear to be rich (Fig. 29.B). This pattern highlights that the previous differences between St. Pierre and Miquelon were not due to rare species alone but dominant ones as well. Lastly, it can be observed for $q=2$ (Fig. 29.B) that the plant assemblages from Langlade and Miquelon are not significantly different. On the other hand, the St. Pierre assemblages of vascular plants are higher in diversity with a pattern of dominance shared between more species.

This pattern was also observed for functional alpha diversity with no differences between sites for spider assemblages, regardless of the diversities' orders and the same relationship between sites for each order of diversity of vascular plant assemblages (Fig. 30 A & B) with the exception of Langlade and Miquelon which are not being different for $q=1$ (Fig. 30.B).

Taxonomic beta diversity compared through rarefaction curves at different order of diversity displayed close patterns between spiders and vascular plants (Fig. 31, A&B). No significant differences were observed for $q=0$ and $q=1$ for both spider and vascular plants assemblages. For $q=2$, spider assemblages were less divergent between Langlade and Miquelon than between St. Pierre and Miquelon and St. Pierre and Langlade. No differences were observed for vascular plants at order $q=2$.

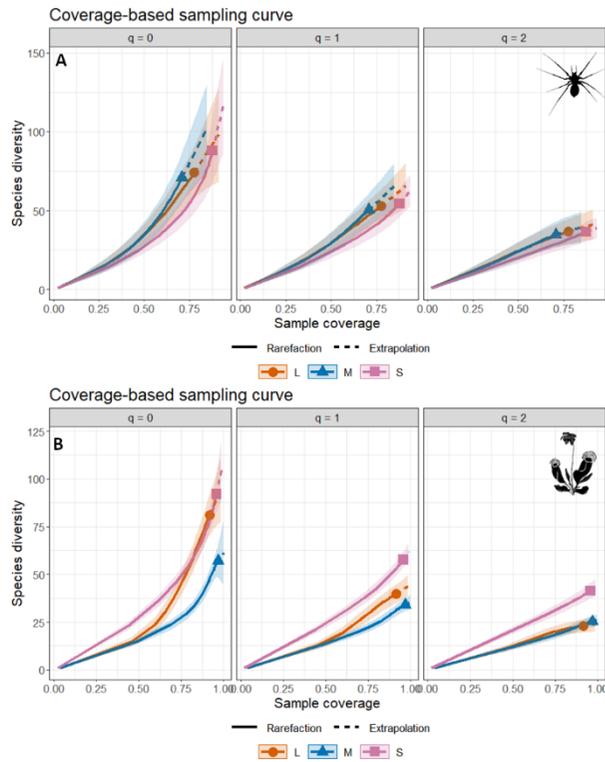


Figure 29 Spider (A) and vegetation (B) alpha taxonomic diversity against sample coverage comparison between sites: S= St. Pierre; L= Langlade; M= Miquelon. The interval of confidences of each curve is based on a bootstrap following Chao et al. (2021).

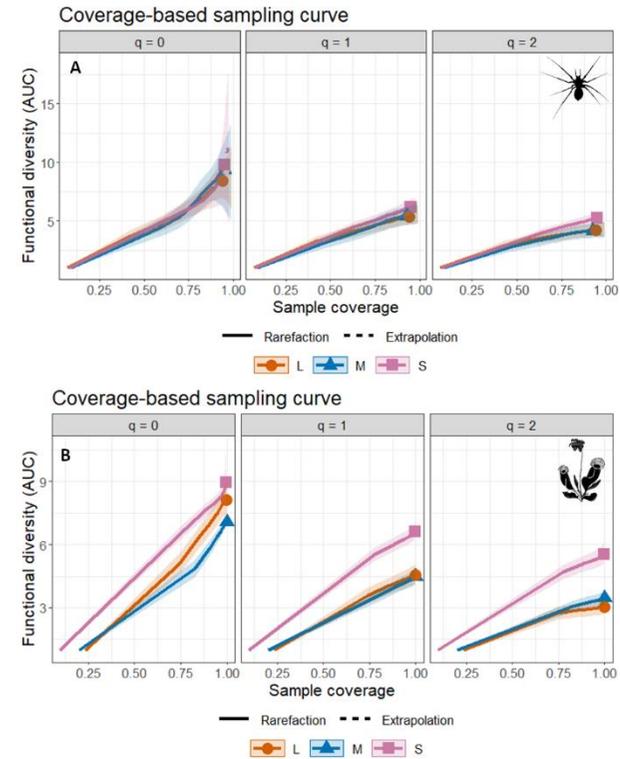


Figure 30 Spider (A) and vegetation (B) functional diversity against sample coverage comparison between sites: S= St.Pierre; L= Langlade; M= Miquelon. Functional diversity AUC corresponding to the area under the curve for the functional distinctiveness profile based on functional diversity calculation from Chao et al. (2021). The interval of confidences of each curve is based on a bootstrap following Chao et al. (2021).

Functional beta diversity compared through rarefaction curves at different orders of diversity also displayed close pattern between spiders and vascular plants (Fig. 31, C & D). No significant differences were observed for $q=0$, while $q=1$ and 2 displayed patterns of differences with various degrees of strength. Spider beta diversity for both $q=1$ and $q=2$ displayed an intermediate pattern with St. Pierre and Miquelon differences being significantly higher than those of Miquelon and Langlade. The differences between St. Pierre and Langlade can be considered intermediate with no observable differences from the two other pairings. Vascular plants beta diversity for $q=1$ displayed a significantly lower divergence between Miquelon and Langlade than for the other two pairings of sites while $q=2$ displayed no differences.

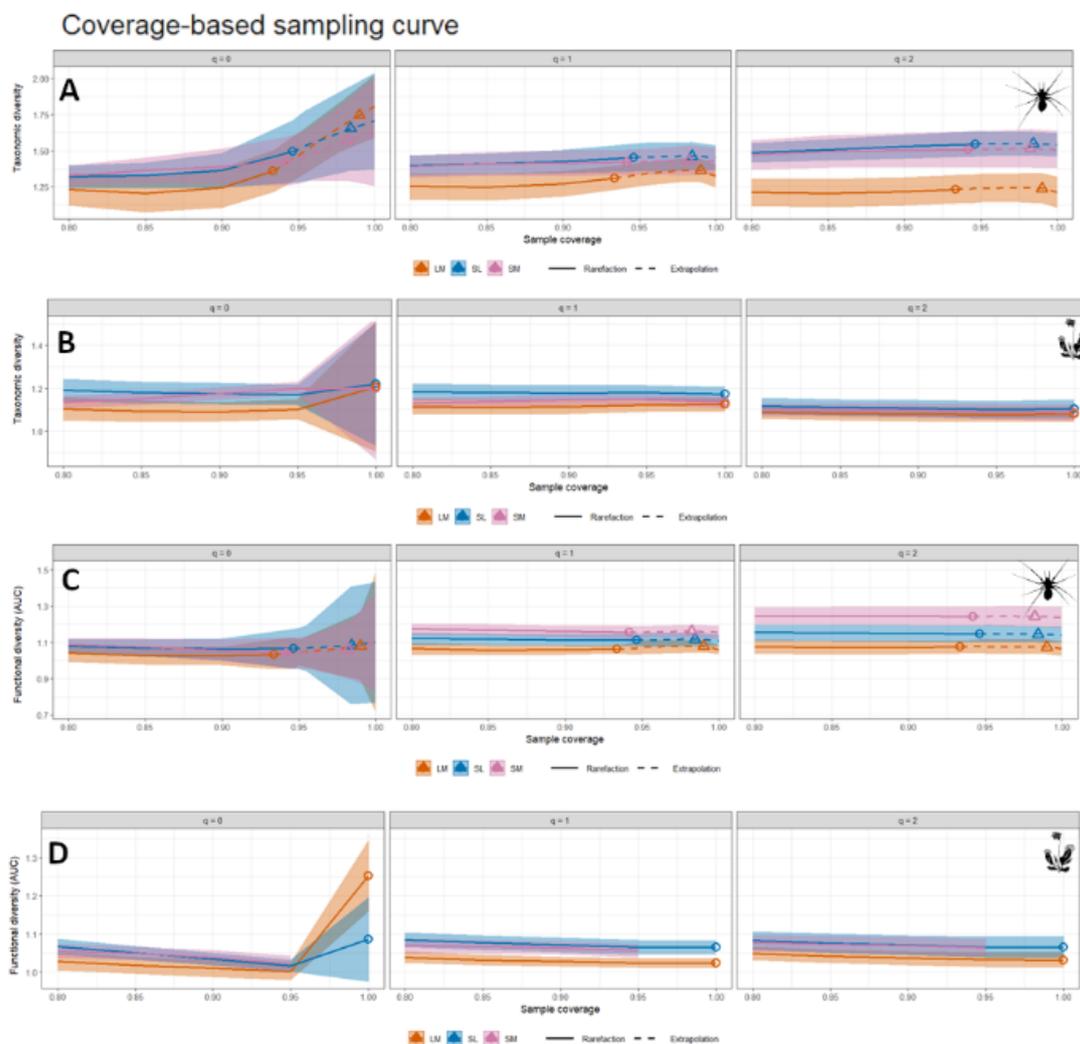


Figure 31 Spider (A & C) and vegetation (B & D) beta taxonomic (A & B) and functional (C & D) diversity against sample coverage comparison between sites: S= St. Pierre; L= Langlade; M= Miquelon. Functional diversity AUC corresponding to the area under the curve for the functional distinctiveness profile based on functional diversity calculation from Chao et al. (2021). Confidence interval of each curve is based on a bootstrap following Chao et al. (2021).

3.1. RLQ

Both spider and vascular plant assemblages displayed separated groupings with a specificity of the sub-site ZS1 being isolated from the rest of the St. Pierre assemblages and other sites (Fig. 32 & 34). One difference between the spiders and vascular plants was that the plant assemblages of Langlade and Miquelon were close together (Fig. 34).

For spiders, the first axis (81.54% of projected inertia) separated the sub-site characterized by anthropogenic feature (ZS1 in St. Pierre) and the complex mosaics of natural landscapes (ZS2 and ZS3) from the more natural and homogeneous sites of Langlade and Miquelon (Fig. 32). The projected spider's functional traits on this axis (Fig. 33.A) highlighted larger spiders - the sheet web weaver guild and ballooning spiders for the anthropogenic and complex landscapes, while natural sites were more linked to the guilds of specialist hunters, space web weavers and non-ballooning spiders. Along the same axis, the projected environmental variables (Fig. 33.C) were linked to cover of other habitats (forest, heath and coastal habitats) or anthropogenic ones such as roads and urban areas for the anthropogenic and complex landscapes while local topographic variable and humid habitat covers drive the right side, linked to the assemblages of natural habitats.

The second axis (12.31% of projected inertia) separated the spider assemblages from Miquelon and Langlade. The projected traits associated to this separation linked Langlade's spider assemblages to orb web weavers and ambush hunters while Miquelon's assemblages were associated with space web weavers and specialists (Fig. 33.B). The projected environmental variables associated with Langlade's spider assemblages (Fig. 33.D) were the cover of wet grassland and meteorological variables while those from Miquelon were tied to the distance of the nearest woodlands of both *Abies balsamea* and *Larix laricina* along with meteorological variables.

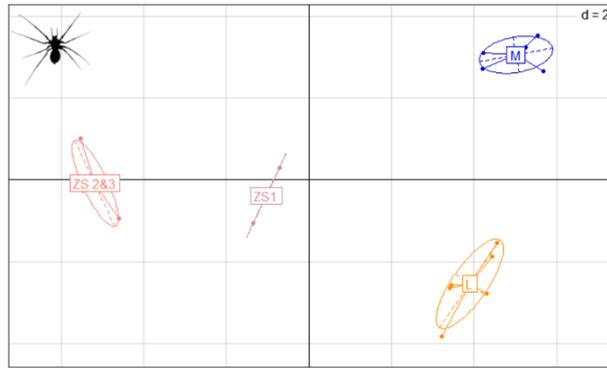


Figure 32 4 RLQ projection of spider assemblages. Sites L= Langlade; M= Miquelon; ZS1, ZS2 & ZS3 = the three sub sites of St. Pierre.

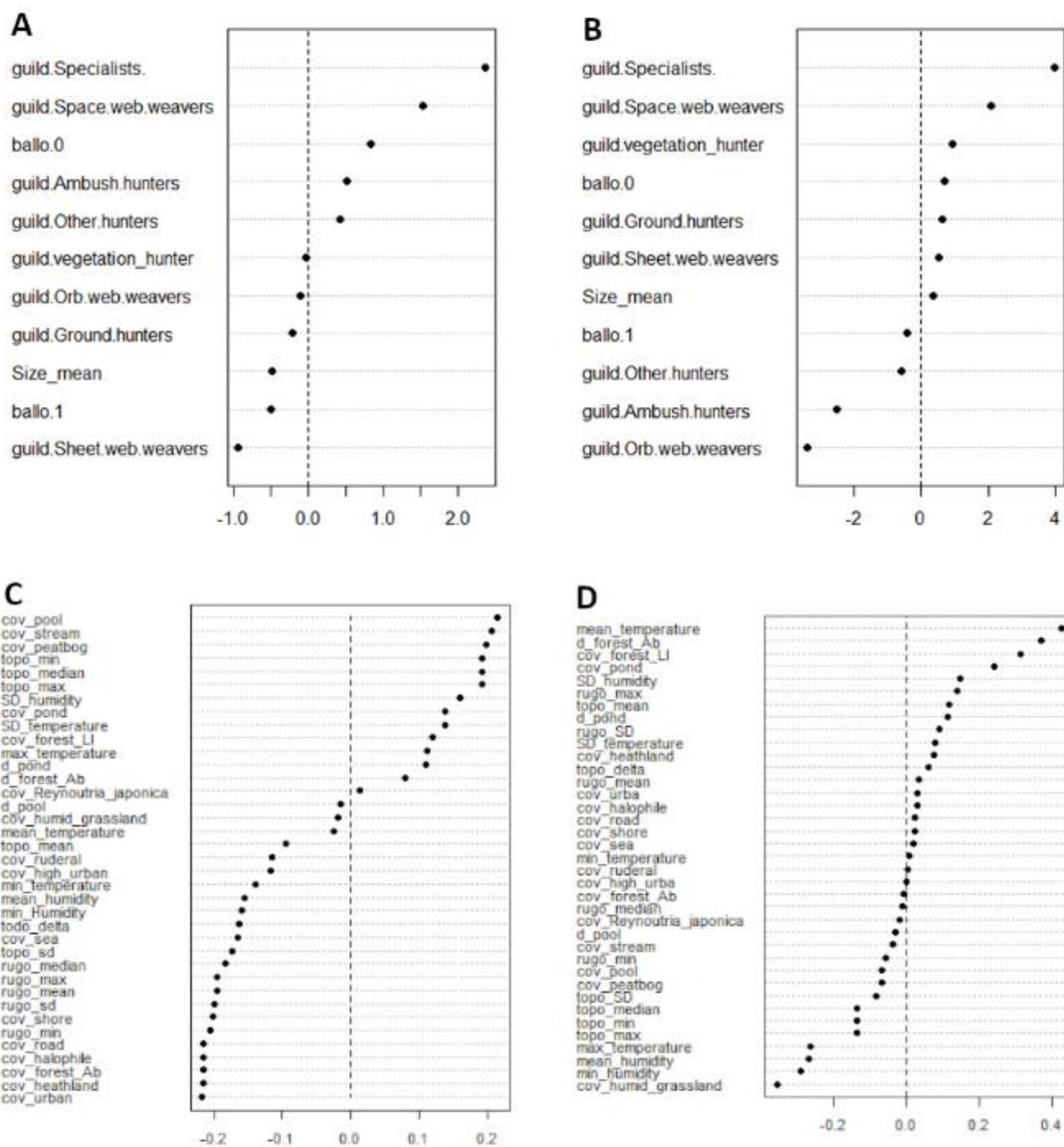


Figure 33 The projected weight of each traits of spider’s assemblages link to the first (A) and second (B) axis and the projected weight of each environmental variable link to spider’s assemblages on the first (C) and second (D) axis. The dashed line was added to help visualize the 0.

For the vascular plants, the first axis (71.13% of projected inertia) also separated the natural sites (Langlade and Miquelon) from the anthropogenic and complex landscapes of St. Pierre (Fig. 34). The main functional trait of vascular plants projected along this axis was air dispersal, associated with St. Pierre's vascular plant assemblages. The environmental variables projected on the first axis (Fig. 35.A) were linked to hydrology: microtopographic measures (maximum, median, minimum) and cover of wet habitats (ponds and bogs), all associated with natural sites, while the other sites were associated with the cover of different habitats (heathland, *Abies balsamea* forest, road, coastal vegetation and urbanized areas) and heterogeneity of microtopography (SD, mean, median and maximum rugosity) (Fig. 35.C).

The second axis (20.28% of projected inertia), which distinguishes the vascular plant assemblages from sites close to urban areas, was associated with traits of light seeds, zoochory and close vegetative dispersal (Fig. 35.B). Likewise, the environmental factor associated with this segregation was the cover of an invasive plant, *Reynoutria japonica*, a species associated with disturbed areas and dense human occupation (Fig. 35.D; see appendix 2 for numerical details of each RLQ's projected weight values).

3.2. Fourth-Corner Analysis

The fourth-corner analysis did not highlight any pairwise relationships between spider traits and other variables. For vascular plant assemblages, the mode of dispersal by wind was significantly and positively affected by SD and delta of topography, the mean, median, SD and maximum of rugosity and habitat cover of mild urbanization and halophyte vegetation.

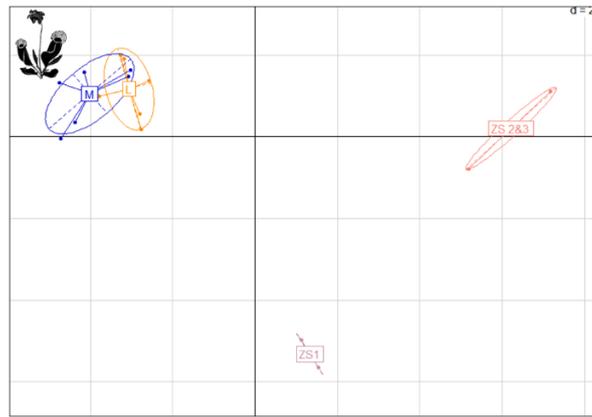


Figure 34 RLQ projection of vascular plant assemblages. Sites L= Langlade; M= Miquelon; ZS1, ZS2 & ZS3 = the three sub sites of St. Pierre.

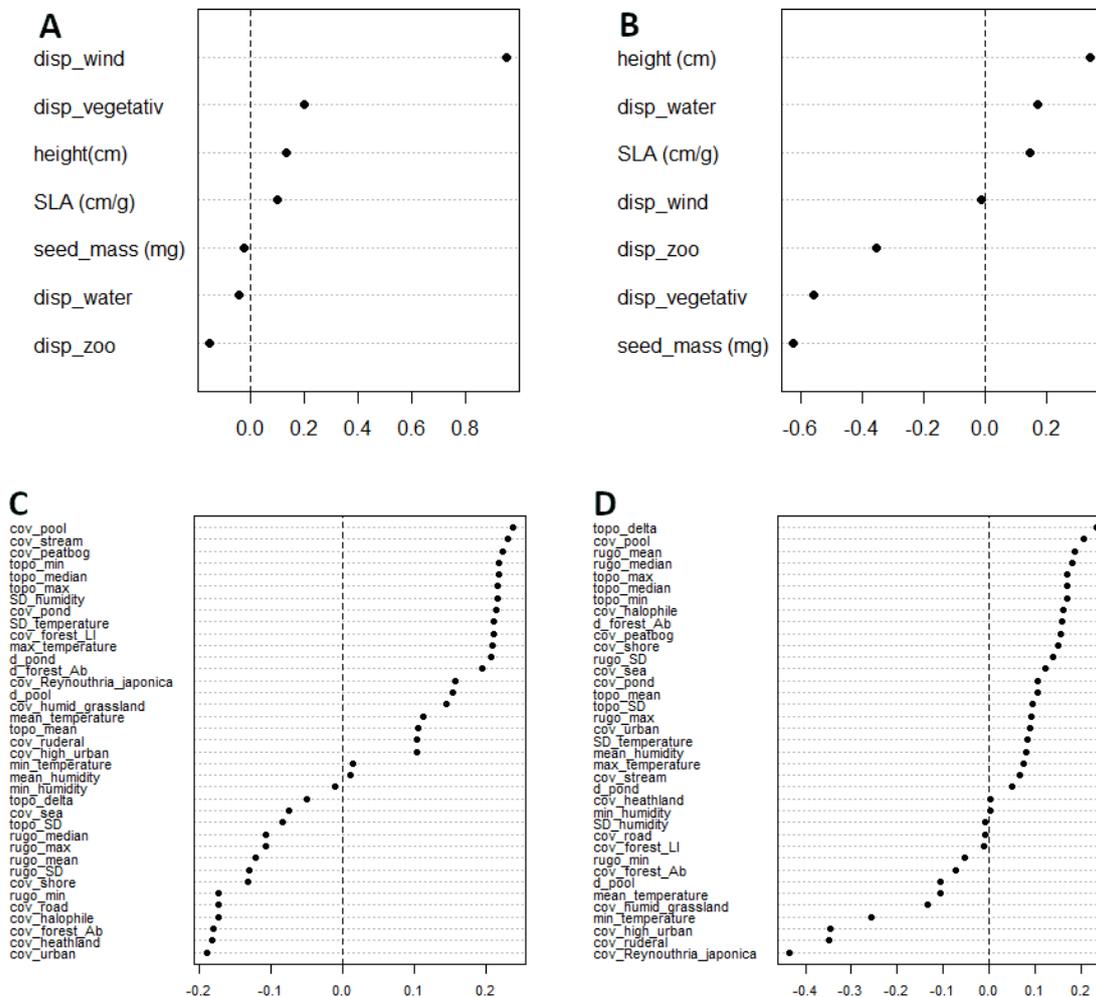


Figure 35 The projected weight of each trait of vascular plants assemblages links to the first (A) and second (B) axis and the projected weight of each environmental variable links to vascular plants assemblages on the first (C) and second (D) axis. The dashed line was added to help visualizing the zero.

3.3. Variance Partitioning

The models largely explained spiders' taxonomic ($R=0.96$; $p < 0.001$) and functional ($R=0.84$; $p < 0.001$) diversities as well as and vascular plant alpha taxonomic ($R=0.36$; $p < 0.001$) and functional ($R=0.65$; $p < 0.001$) diversities. The local and landscape variable impacts of alpha diversity displayed contrasting responses between spiders and vascular plants (Fig. 36). While spiders responded to several variables for both taxonomic and functional diversities (Fig. 36.A & B), whereas vascular plants only responded to landscape variables (Fig. 36.C & D). Spider alpha diversity varied between taxonomic and functional with a slightly higher percentage attributed to landscape variables rather than local ones (53% vs. 47%) and a strongly higher percentage for landscape variables with functional diversity (74% vs. 16%). Spider alpha diversity was rather evenly distributed amongst landscape variables for both taxonomic and functional diversities while a striking 45% of variance was attributed to the local variable "mean topography" in taxonomic diversity against a 16% for functional diversity. Vascular plants' alpha diversities, both taxonomic and functional, responded to four landscapes variables. Taxonomic and functional diversities shared three variables: cover of urbanized habitat, of highly urbanized habitats and of bogs. Distance to wood was associated with taxonomic diversity and distance to ponds to functional diversity alone. It can be observed that between taxonomic and functional alpha diversity of vascular plants, there was a shift in the relative variance explained by the categories. Only 52% of the variance was explained in the taxonomic diversity model and half of it was due to the distance to the nearest *Abies balsamea* forest while for functional diversity model, 78% of the variance was explained and 42% of it came from the combined cover of urbanized and strongly urbanized areas.

Regardless of the metrics, spider assemblages displayed higher variance explained overall than vascular plants (taxonomic: 99% vs. 51%; functional: 90% vs. 78%, spiders vs. plants respectively). The variance partitioning between local and landscape environmental variables both for spider and vascular plant assemblages' composition displayed a high interaction (Tab. 1) and indicated the stronger importance of landscape rather than local variables with various degrees of strength. Spider assemblages had a sevenfold higher influence from landscape versus local variables where it was only slightly higher for vascular plant

assemblages. In the model selection, the spider assemblages displayed a sensitivity for the cover of humid grasslands and roads at the landscape scale, to the minimal rugosity of topography, and the mean and maximum temperature at the local scale. The vascular plant assemblage’s model selected for the covers of ponds, humid grasslands and moderately urbanized areas at the landscape scale and minimal and standard deviation of rugosity as well as mean temperature at the local scale.

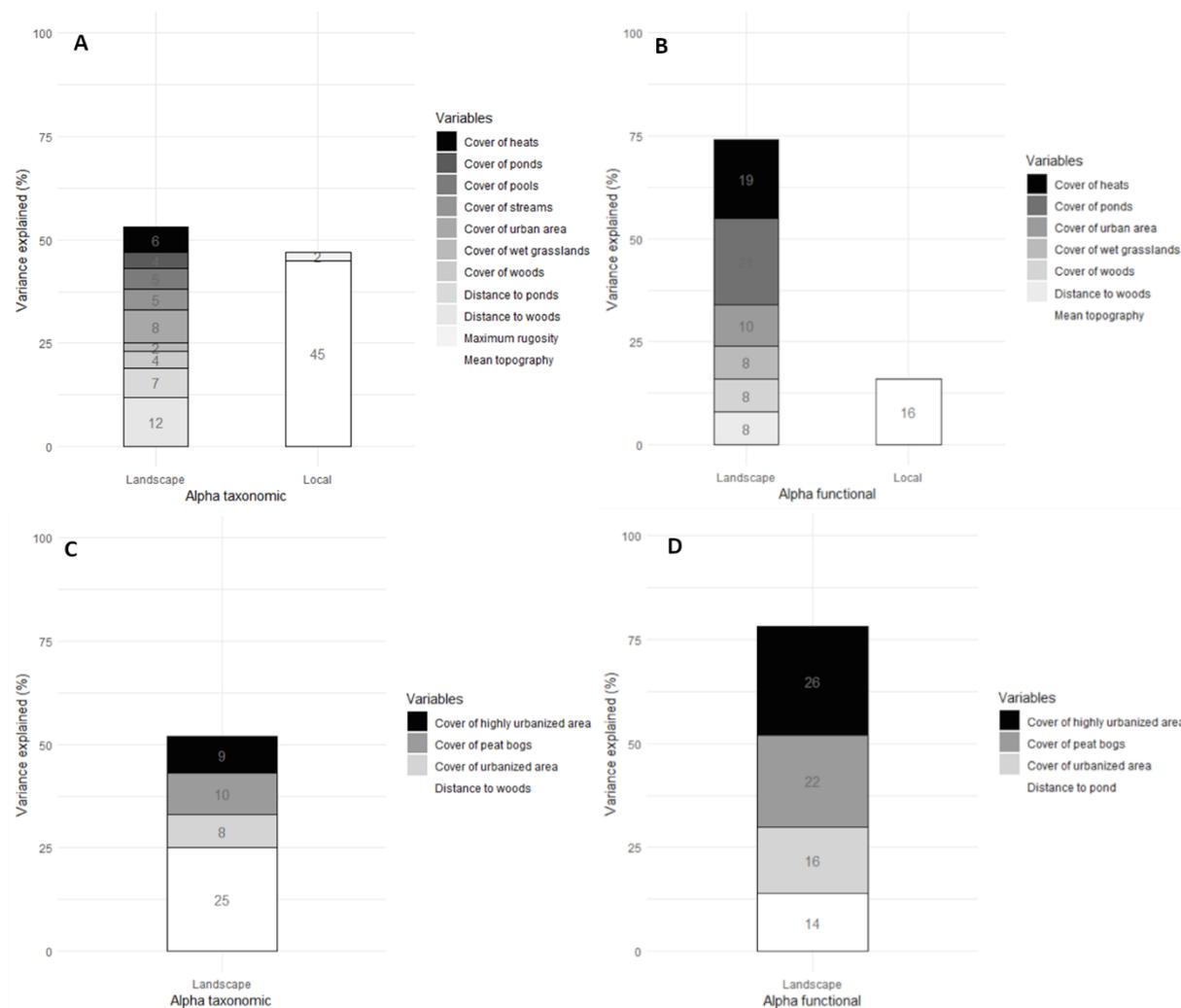


Figure 36 The relative variance explained by environmental variables in alpha diversity models for: (A) Spider taxonomic diversity; (B) Spider functional diversity; (C) Vascular plant taxonomic diversity; (D) Vascular plant functional diversity.

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Table 1 Variance partitions between landscape and local variables for community and beta diversity following Borcard et al. (2018). Statistical significance threshold of each partition was set for $p < 0.05$ *; 0.01 **; 0.001 ***. NA value corresponds to models that failed to converge

Variance partitions		Local		shared	landscape	unexplained	
Composition							
Spider		1%	***	22%	7%	***	70%
Vegetation		5%	***	29%	8%	***	58%
Taxonomic diversity	β						
Spider		7%	***	32%	29%	***	32%
Vegetation		14%	***	45%	20%	***	21%
Functional diversity	β						
Spider		NA		NA	NA		NA
Vegetation		8%	***	17%	32%	***	43%

The variance partitioning between local and landscape environmental variables both for spiders and vascular plant beta diversity displayed higher variance proportions explained by landscape variables, with the exception of spider functional beta diversity for which no partition of variation was significant. Similarly, spider taxonomic beta diversity displayed higher differences between landscape and local proportions of variations explained, while a high proportion of the overall explained variation was linked to correlation between variables. In the model selection, the spider beta taxonomic diversity displayed a sensitivity for mean and standard deviation of height of microtopography, maximum temperature and mean and standard deviation of air humidity for local variables. Landscape variables for spider beta taxonomic diversity included cover of natural habitats (*Abies balsamea* forests, heathlands, peat bogs, ponds, sea and *Larix laricina* forests) and urbanized habitats (highly urbanized area and ruderal vegetation) as well as distance from natural habitats (*Abies balsamea* forest, ponds and pools).

The vascular plants' beta taxonomic diversity displayed a sensitivity for mean, median and delta of height of microtopography, standard deviation of rugosity as well as mean and standard deviation of air humidity for local variables. Landscape variables for the vascular plants beta alpha diversity included cover of natural habitats (*Abies balsamea* forests, wet grasslands, peat bog, ponds and sea) and urbanized habitats (urbanized areas, roads, ruderal vegetation).

While it was not possible to make comparisons between spiders and vascular plant's functional beta diversity, a pattern was observable for vascular plant taxonomic and functional beta diversity. These were characterized by a higher proportion of variance explained by landscape variables. The beta functional diversity of vascular plants displayed a sensitivity for minimal, mean and standard deviation of temperature for local variable as well as distance to natural habitats (*Abies balsamea* forest, ponds and pools), cover of natural habitats (heathland, wet grasslands, peat bogs, ponds and streams) and cover of urbanized habitats (both ruderal vegetation and highly urbanized areas).

4. DISCUSSION

4.1. Pattern of diversities

Spiders and vascular plants displayed similar responses for a given metric, but for a given taxon, metrics revealed different responses to changes in environmental conditions. The joint numerical response between taxonomic and functional diversity is not surprising considering their intrinsic mathematical relationship (Pavoine *et al.*, 2013), but even though close to each other, taxonomic and functional diversity displayed varying patterns that may have ecological significance. Lack of differences between facets of spider alpha diversity was also reported in other ecological studies where spider assemblage's differences resided in turnover patterns without notable alpha diversity differences (Bell *et al.*, 1998; Coccia & Fariña, 2019; Hacala *et al.*, 2020). The pattern observed here is very likely to match previous results considering the marked dissociation of the communities in the RLQ community analysis. This first variation of responses between metrics highlights the complementarity of alpha and beta diversities in the context of our bogs, validating our hypothesis. The vascular plants assemblages, regardless of the metric used, had higher diversities within St.

Pierre, only matched by the assemblages from Langlade when considering richness, and highlighting the importance of rare vascular plant species in Langlade. It is known that ombrotrophic peat bogs close to the sea on the Atlantic Canadian Coast are more diverse due to the presences of species usually associated with poor minerotrophic peat bogs (Damman & Dowhan, 1981; Glaser, 1992). Additionally, the richer the peat bog, the more it is known to have its richness impacted by landscape heterogeneity (Vitt *et al.*, 1995). One explanation of the higher vascular plant richness of St. Pierre sites could come from their greater proximity to the coast, enriching the bog. Likewise, the specific habitat mosaic around the St. Pierre sites is associated with higher topography which may also lead to bog enrichment through runoff after rains. One or both of those explanations could lead to an increased permeability in colonization from neighboring vascular plant habitats. Indeed, ZS2 and ZS3 higher diversities are linked to species often associated with other habitats (*e.g. Dantonina spicata, Sanguisorba canadensis* and *Abies balsamea*). The lower richness of ZS1 could be linked to the influence of adjacent urban areas as expected at this spatial scale (Bonn *et al.*, 2016) yet further measurement to assess such impacts might be required to demonstrate more conclusive results.

The relationship between the diversities of vascular plant assemblages of the more natural habitats of Langlade and Miquelon revealed the patterns of sites specificities. The higher taxonomic Shannon diversity of Langlade vascular plant assemblage over that of Miquelon is observed as well with taxonomic richness but not with Simpson taxonomic diversity. These results highlight the importance of rare species within Langlade assemblages while Miquelon ones have no species that are not present at least in one of the other two sites. Those rare species unique to Langlade have high degrees of specialization (Payette & Rochefort, 2001) and this would appear to indicate local factors rather than colonization by surrounding habitats species. In addition, when dominant species are given more weight through Simpson diversity, Langlade and Miquelon's assemblages display no differences in taxonomic diversity. This pattern was expected as dominant bog specialist sedges like *Trichophorum cespitosum* (Payette & Rochefort, 2001) lower the evenness. When considering functional diversities, the Shannon diversity patterns between Langlade and Miquelon resemble the Simpson one which indicates a global functional redundancy. This is to be expected in a habitat as harsh as a bog (Robroek *et al.*, 2017).

The variation of sensitivity and therefore responses of our taxa and metrics here indicate how their potential as ecological indicators is displayed. The richness inclined response of vascular plants makes up for the low evenness and dominated assemblages in harsh habitats, like those found in bogs.

4.2. The Composition, Traits and Environment

The RLQ analysis highlighted differences in assemblages between all sites for both taxa with the only exception of Langlade and Miquelon for which vascular plants assemblages were close together. This general pattern of differences indicates that even within a small archipelago, in closely comparable habitats with high environmental filters, there can be a high variation in composition. The closeness of Miquelon and Langlade here echoes the diversity pattern described earlier with the beta diversity curves and the shared dominant species. Another assemblage divergence observed is the separation of the ZS1 from the two other sub-sites of St. Pierre with both taxa. This pattern was discussed through the lower richness of this sub-site in the vascular plants' assemblages, this is also seen with the spiders and the disturbances may be an explanation for this pattern as well (Pétillon & Garbutt, 2008). Indeed, the reduced richness of arthropod assemblages in disturbed settings is an inconsistent response discussed in the literature (lower in Pétillon & Garbutt, 2008 and unchanged in Hacala *et al.*, 2020). However, a highly stressful environment found in many bogs may filter out generalist species that compensate species loss in other perturbed environments, leading to the assemblages of both taxa being potential indicators of disturbance with the bog.

The RLQ analysis highlighted links between this sub-site and both environmental variables and traits of the associated assemblages. For the spider assemblages, the link is unclear for the ZS1 sub-site as it is in an alignment with the rest of St. Pierre sub-sites in the RLQ. As a whole, they are associated with sheet web weavers, ballooning spiders and bigger spiders. The sheet web weavers from St. Pierre assemblages are known to inhabit woodlands and open habitats (*e.g. Agelenopsis utahana*: Paison, 1997, and several Linyphiidae species like *Bathyphantes pallidus*: Buddle, 2001). The environmental variables associated with those assemblages are the cover of surrounding habitats including the *Abies balsamea* forest, subarctic heathland, and the coastal and urban areas. These results highlight the effects of the surrounding habitats that allow for spider colonization in an undisturbed bog, as they can manage the bog conditions without

being specialists. Another explanation may be derived from the interaction of an edge effect in a smaller bog in a complex landscape since edges of bogs are known to have reduced environmental filters (Payette & Rochefort, 2001) facilitating colonization by surrounding spiders. Thus, the variations within the spider compositions appears to be an indicator of the influence of the landscape matrix settings on the bogs.

The vascular plant assemblages associated traits and environmental variables for St. Pierre sites, contrary to spiders, are different between the ZS1 sub-site from that of ZS2 and ZS3. The variable that drove ZS2 and ZS3 vascular plant assemblages are rugosity measures of microtopography and cover of the different neighboring habitats. The local heterogeneity together with the impacts of both forest, heath and sea in the landscape concur with our previous hypothesis. Thus, they may be enriched due to the closeness of the sea (Damman & Dowhan, 1981), which may reduce the filters which ease the colonization from pools of species in adjacent habitats. The sensitivity of vascular plant assemblages to local parameters of heterogeneity could be linked to edges effects and enhanced diversities by increasing the number of ecological niches within the bog, thereby affecting the composition of the assemblages (Thuiller, 2006). The one trait associated with those sub-sites is dispersal by wind. As noted in the literature, shrubs and tree species are among the most likely species to disperse from wind and from surrounding habitats into a peat bog (Campbell *et al.*, 2003). Likewise, St. Pierre sites are characterized by the higher abundance of species tolerant to bogs but thriving in other habitats like *Abies balsamea* and Ericaceae shrubs like *Rhododendron groenlandicum*. Only the results from the Fourth corner analysis linking wind dispersal to environmental variables might not be due to direct impacts from the environment or adaptation but rather a correlation to St. Pierre sites as the environmental variables are all higher for these sites and the wind dispersal trait is the one associated to its assemblage. For the ZS1 assemblages, the main traits are small seed mass and vegetative dispersion. For the vascular plants, this sub-site is distinct from the others due to the absence of species rather than their presence, it is thus futile to draw any conclusions about these traits.

The two most natural sites are set apart from St. Pierre in the RLQ through a pattern linked to guild traits (specialist and space web weaver) and non-ballooning species. The guild traits associated with both sites were likely statistical artefacts as they were only represented by few individuals. Indeed, it is known that

multivariate analysis such as that of the RLQ are sensitive to rare occurrences (Cao *et al.*, 2001). However, the non-ballooning trait may be explained by specialist bog species that would not be prone to passive long-distance dispersal which would allow them to stray, as observed with spiders in other constraining habitats (Bonte *et al.*, 2003). All environmental variables globally associated with the sites on Langlade and Miquelon were linked to hydrology, whether it was local with microtopography (Payette & Rochefort, 2001) or at the landscape scale and including ponds, streams and the bogs themselves. Such a sensitivity echoes commensurate findings within similar geographical and environmental contexts (Pellerin *et al.*, 2009). This pattern highlights how spider assemblages are good indicators within natural bogs for they are less impacted by other habitats and are linked to the prevalence of water within ecosystems.

When considering vascular plants, the sites of Langlade and Miquelon were not separated by any specific traits but the same environment variables of the spiders, the hydrological variables. This concurs with bogs being rather homogeneous in their traits along geographical gradients (Robroek *et al.*, 2017) while composition can vary, seen here through the variability of hydrology between landscapes which is a known key driver within peat bogs (Rydin *et al.*, 2013).

The assemblages of Langlade and Miquelon displayed differences on the RLQ for spiders only and were overlapping for vascular plants. The differences between Langlade and Miquelon for spider assemblages were linked to both traits and their environments but the traits were the same guild represented by too few individuals to be considered a robust pattern. The environment variables driving the differences between the spider assemblages of the two sites are linked to landscape composition. Spiders from Miquelon appear sensitive to the distance to the nearest forest of *Abies balsamea* and the cover of *Larix laricina* while those of Langlade are linked to wet grasslands cover. Amongst the species only present in Miquelon, one of the more abundant was *Neoantistea agilis*, a species associated with forests near open water (Draney, 1997). Likewise, amongst the species only found in Langlade, there are species associated not only with bogs but open wet habitats like *Arctosa raptor* (Koponen, 1994).

Confirming our previous results, the variance partitioning displayed an important part of the variances explained by the landscape variables. The spider's assemblages and beta diversity's higher ratio (one to seven for the community and

four to one point five for beta taxonomic diversity) highlight their higher sensitivity to landscape contexts rather than to vegetation (Lafage *et al.*, 2015). This could be linked to the fundamental differences between spiders and plants, as spiders are mobile (Gerlash *et al.*, 2013) and less dependent on water chemistry (Bonn *et al.*, 2016), they are potentially less impacted by local environmental filters than plants are. On the other hand, the alpha diversity of vascular plants was only associated with landscape variables, whereas spiders responded to both local and landscape factors. This result resonates with the higher alpha richness pattern observed for St. Pierre's site. It could be linked to the landscapes that enriched the bog and added fen-related species, as the variables selected by the models are those associated with St. Pierre sites. It should also be noted that the greatest part of the explained variance is associated with the interaction of the landscape and local variables, highlighting the interwoven nature of these scales within peat bogs. This interconnectedness might be the source of the low and absent responses of the Fourth corner analysis as it tests for pairwise responses between traits and environmental variables and cannot assess their joint effects.

4.3. Conclusion

This paper explored the use of multi-metrics and multiple taxa ecological indicators as they represent the complexity of natural environments. Concurring with our first hypothesis, vascular plant and spider assemblages displayed different responses which explain several aspects of the environmental settings examined here. This complementarity of indicators expresses itself through the respective sensitivity of the metrics used as they capture different angles of the studied system's ecology. The complementarities expected in hypotheses 1, 3 and 4 interact collectively. The redundancy of hypothesis 2 linked to the harsh nature of bogs was also observed, yet within the redundancy, the trait approaches within beta diversity consolidated our understanding of beta diversity pattern. This multi-taxa and multi-metric approach highlights the complementarity of different indicators and their respective sensibilities, providing insight on their potential future application and use in bog conservation and restoration status studies or the assessment of environmental disturbances. Indeed, this study highlights peat bogs' sensitivity to many intertwined environmental cues and suggests methods to untangle them. Faced with the urgency of peat bog conservation and restoration that requires an ability to assess habitat dynamics, such methods are

paramount (Bonn *et al.*, 2016). Likewise, a better understanding of bogs within their landscapes could help for conservation prioritization as the landscape context is known to be impactful (Payette & Rochefort, 2003). A potential next step toward further improvements in related studies should employ multiply joint indicators. A known complementarity within measures of diversity could be the addition of phylogenetic diversity (Cadotte *et al.*, 2013; Hacala *et al.*, 2021; Ridel *et al.*, 2021), as diversity metrics has proven to be an important tool of biodiversity conservation (Faith, 1992; Rodrigues *et al.*, 2005). Another improvement could come from adding taxa associated with different scales and environmental processes and with a different trophic regime which could lead to a better understanding through complementarity. Oribatid mites are recognized as indicator taxa in peat bogs (Lehmitz *et al.*, 2020; Behan-Pelletier & Lindo, 2023). Yet they are a relatively poorly known taxa (Behan-Pelletier & Lindo 2019) and should be tested in future similar studies. Their use could make an important addition to the models used here to improve both our knowledge of bog biodiversity as well as the multitaxa indicator as a tool.

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IV. PALEOECOLOGY



A. Oribatid mites as bioindicator of past climates: an exploratory approach using climate reconstruction method and a case study from St. Pierre and Miquelon, France.

Axel Hacala^{1,*}, Valerie Behan-Pelletier², Dominique Marguerie¹, Julien Pétillon^{1,3}, Allison Bain⁴

¹ UMR CNRS 6553 Ecobio, Université de Rennes, 263 Avenue du Gal Leclerc, CS 74205, 35042, Rennes Cedex, France

² Invertebrate Biodiversity Program, Research Branch, Agriculture and Agri-Food Canada, K.W. Neatby Bldg., Ottawa, Ontario, Canada.

³ Institute for Coastal and Marine Research, Nelson Mandela University, Gqeberha, South Africa

⁴ CELAT Research Centre, Université Laval, Québec, Canada

Corresponding author: axel.hacala@gmail.com, +33 6 16 50 76 52

RESUME

Les oribates possèdent de nombreuses qualités en tant qu'indicateur paléoécologiques du fait de leurs abondances, d'une écologie variée contenant des spécialistes et d'une résistance permettant à leurs restes subfossiles d'être efficacement identifiés. Grace à ces qualités et au besoin en paléoécologie d'améliorer les outils à sa disposition, cette étude cherche à éprouver le potentiel de ce modèle sous-utilisé que sont les oribates comme indicateurs au service de la reconstruction du climat passé. La reconstruction climatique, réalisé à l'aide de MCR (Mutual Climat Range) ou d'autres méthodes plus récentes de modélisation comme CRACLE, utilisent généralement des restes de végétation ou des coléoptères subfossiles mais ces restes sont soit difficiles d'identification et/ou rares. 46 jeux de données actuelles d'oribates répartis à travers l'hémisphère nord ont été utilisés pour la reconstruction climatique. Cela a été effectué en croisant les distributions connues de chaque espèce présentent sur chaque sites, issues des bases de données GBIF, avec les données climatiques issue de WorldClim. Les

reconstructions ainsi obtenues ont été comparées avec les données climatiques connues de chaque site et le niveau d'erreurs et ses drivers ont été analysés. Secondairement un cas d'étude avec des données paléocéologiques d'oribates et de végétation, en tant que modèle de vérification, a été analysé pour éprouver la méthode. Globalement, les oribates démontrent un potentiel prometteur bien que variable pour la reconstruction climatique. Le nombre d'espèces utilisé dans un modèle a eu un effet négatif sur la reconstruction climatique, malgré l'addition mathématique de données que cela implique. Les oribates pourraient, quand la somme de données disponibles augmentera, donner des reconstructions plus robustes mais pour l'instant les données d'oribates sur GBIF sont trop peu nombreuses pour des reconstructions fiables.

ABSTRACT

Oribatid mites hold many qualities as palaeoecological indicators as they are numerous, ecologically various and specialized as well as resistant which makes their microfossils readily identifiable. Due to those quality and the need in paleoecology to ever improve the tools available to study the past, this study aimed at testing the potential of the underused oribatid mites as indicator for past climate reconstructions. Climate reconstruction, done through MCR (Mutual climate Range) or more recent modeling method like CRACLE, are usually achieved with plants remains or coleopteran microfossils but their remains are either hard to identify with precision and/or scarce. 46 current occurrence oribatid dataset from all over the northern hemisphere were used for climate reconstructions. This was achieved by crossing the known distributions of all species occurring in each site, based on data from the GBIF database, with the climatic data from the WorldClim database. The reconstructions obtained were compared with each sites known climate and the level of errors and their drivers were analyzed. Secondly a case study with a palaeoecological sample of oribatids and a vegetation as a verification were computed to test the methods. Overall, Oribatid mites displayed promising yet variable potential for climate reconstruction. The number of species used in a model had a negative effect on the quality of the reconstructions, despite the mathematical addition of data points. Oribatid mites might, when the amount of data available increase, display more robust reconstruction but for now GBIF oribatid mites dataset seems too scarce for consistent results in climate reconstructions.

1. INTRODUCTION

Recent scholarship presents methods used to study the recently defined Anthropocene (Crutzen, 2002; Dalby, 2013, Lewis & Maslin, 2015), underlining the necessity for a solid grasp of climate dynamics and proper tools with which to assess them. Climate change has been extensively studied through the lens of palaeoecological analysis (De Wever *et al.*, 2010) detailing, for example, that the Holocene was composed of many episodes of geographically specific climatic variations (Wanner *et al.*, 2008; IPCC, 2013). Paleoclimatology thus played and continues to play a key role in understanding climate dynamics (Pross *et al.*, 2000; Bartlein *et al.*, 2011), and multiple tools allow the study of past climates, including cores from glaciers (Masson *et al.*, 2000), from lake sediments and peat bogs (Webb, 1985). These data sources span different forms including the chemical signature of frozen bubbles in ice cores or the study of floral and faunal ecology. Depending on the indicators used, resulting information varies in scale in both space and time and are, as time, highly complementary (Bigga *et al.*, 2015). This complementarity is expected amongst biological indicators especially since their potential is derived from the ecology of each taxon or group of taxa (McGeoch, 1998). For instance, microflora remains such as pollen are extensively used to assess past climates and landscapes (Pross *et al.*, 2000) while floral macro remains facilitate the study of local patterns through time (Bigga *et al.*, 2015). Arthropods have also been used, both in archeoentomology (Bain & King, 2011; Forbes *et al.*, 2015) and palaeoentomology (Ponel *et al.*, 1999; Schelvis *et al.*, 2005), respectively studying anthropic and ecological phenomena of the past, as the chitinous remains of many Orders can withstand thousands to millions of years within sediments and still be identified to relevant taxonomic levels (Stankiewicz *et al.*, 1997; Duncan *et al.*, 1998; Elias, 2010). Arthropods also offer a known high complementarity with vegetation as bioindicators (Lafage *et al.*, 2015; Hacala *et al.*, 2020; 2023) in neoecology (*sensus* Bush, 2023). They are thus also appropriate paleoecological proxies (Coope & Lemdahl, 1996) since they are known to respond at a quicker rate than vegetation to environmental modification (Gerlach *et al.*, 2013) as many are stenothermic and have an ecology uncorrelated to vegetation (Elias, 2010; Lafage *et al.*, 2019).

Among the challenges facing paleoecology, scarce remains and difficulties of identification (Elias, 2010), can be partially met by studying preserved oribatid

mite faunas. Indeed, even if much is to discover compared to other taxa (Luoto, 2009; Behan-Pelletier & Lindo, 2023), oribatid mites have proven to be an interesting model as they are highly diverse, specialized and sensitive to climate and environmental conditions (Lehmitz, 2014; Lehmitz *et al.*, 2020) and they represent a rich suborder of acarida with over 13 000 species (Behan-Pelletier & Lindo, 2023). They are among the first animals that lived on land and fossil evidence dates back to the Devonian (Norton *et al.*, 1988). Specifically, for palaeoecological consideration, their abundance in the environment ensures their presence in the sub-fossil record (Erickson, 1988; De la Riva-Caballero *et al.*, 2010; Markkula *et al.*, 2018; Markkula & Kuhry, 2020; Schelvis, 2020). Indeed, oribatid mites are often the most abundant arthropods in their environment (Murvanidze & Kvavadze, 2010) and can reach densities of up to 425 000 ind./m² (Behan-Pelletier & Lindo, 2023). Their excellent preservation can be partially attributed to their exoskeletal sclerotization and mineralization which provides a harden cuticle (Norton & Behan-Pelletier, 2009). Erickson (1988) described five class of oribatid subfossils conservation quality, he stated that class 1 and 2 specimens, only lacking their legs but still having fine detail as setae and ventral plate intact are the most common. Indeed, identification to species level is frequent up to class 3 and to genus in class 4 as even in species where legs are used in the identification, other morphological characteristics remains on the subfossils specimen allowing specific identification. Previous studies have reached species identification of up to 80% for sub-fossil oribatids (Erickson *et al.*, 2003), highlighting their potential as palaeoecological indicators.

To assess past climates through such assemblages of arthropods, the mutual climate range (MCR) method is often used (Atkinson *et al.*, 1987; Lavoie & Arseneault, 2001; Elias, 2013; Shiyake & for Nojiriko, 2014; Fletcher *et al.*, 2019; Forbes *et al.*, 2020). This approach is centered on the premise that each species, based on its known occurrences, thrives along a spectrum of its climatic tolerance. When combined, the joint values of climates shared all species found at a given place and at a given time must coincide to the current climate of the said time and place (Atkinson *et al.*, 1987). This method is used efficiently, for instance, on beetles (Forbes *et al.*, 2020) an order whose members have highly varied ecologies and are preserved due to their chitinous hard exoskeletons in the adult stage (Elias, 2010) ensuring their preservation. More recently, new methods have been

developed based on the same logic, notably CRACLE (Climate reconstruction analysis using coexistence likelihood estimation), which improves the reconstructions by modelling species biogeography through maximum likelihood method (Harbert & Nixon, 2015).

Our study aims to test the potential of Oribatid mites for climate reconstructions as their usage as bioindicator of climates solely based on their ecology is already in usage (*e.g.* Erickson *et al.*, 2003). Our study's objectives are twofold: test the CRACLE method with known oribatid assemblages and current climate data to assess the method's ability to deliver sound climatic reconstructions. Secondly, test the method on a palaeoecological assemblage of oribatid mites from a peat core spanning two thousand years. To assess the quality of the climatic reconstruction based on the oribatid mites, vegetation from the same core was analyzed as vegetation-based reconstructions are known to be robust (Thompson *et al.*, 2012).

2. MATERIAL AND METHODS

2.1. Geographical data

The 46 datasets used to test the MCR method are from Mumladze *et al.* (2013) available as open access data sets. This includes a compilation of other published data from oribatid studies on peat bogs throughout the northern hemisphere. The original publication aimed at analyzing oribatid pattern of community composition at a large geographical scale. Dataset selection screened for assemblages with at least 10 species for sampling completeness and studies with precise locality and properly described pedology and habitat specificities for the sake of comparability. Climatic data used were mean, maximum and minimum temperatures of each month from the worldclim dataset (Fick & Hijmans, 2017), following Harbert & Nixon (2015). The most precise WorldClim available worldwide dataset was at a resolution of every 30 seconds (~1 km²). This climatic dataset is based on an average temperature calculated on a time span between 1970 and 2000. Occurrence data of each species of oribatid mites from Mumladze *et al.* (2013) were extracted from the Global Biodiversity Information Facility (GBIF) online database (GBIF.org, 2024). Only points with associated geographical coordinates

and dates from 1970 to present day were included in order to match the climate data.

2.2. The Case study: St. Pierre and Miquelon

A peat core from the St. Pierre and Miquelon archipelago, specifically from the island of St. Pierre (46.7696 E, -56.1862 N). Coring was done using a Russian corer that sampled 50 cm long semi-cylinder cores with a 52mm diameter. The whole column of peat was sampled to assess the ages of peat accumulation while the analyzed portion of the core corresponds to the last 2000 years only, based on C14 dating. Each sample of peat used for oribatid, corresponded to a 1 cm slice of the core for a mean volume of 6.33 ± 1.6 ml. 1cm every 3cm were processed through the core. Samples were sorted by hand under a x40 magnification. Oribatids sub fossil remains were conserved in a 70% ethanol solution. Identification was done using Behan-Pelletier & Lindo (2003) and morphological comparison with the Canadian National Collection of Insects & Arachnids at the Agriculture and Agri-Food Canada in Ottawa. Identification was done under microscopic magnification (x400) in lactic acid (70%) and specimens too dark for identification were left in the same solution for a few hours to make them more translucent and ease the identification (Krantz & Walter, 2009). The climatic projection based on paleo-remains of oribatids was subdivided into six temporal zones based on the analysis of the diagram of repartitions of species over time. The sampled habitat is an Atlantic bog with vegetation indicative of bog habitat like *Rubus chamaemorus*, *Sarracenia purpurea* or *Drosera rotundifolia* (Payette & Rochefort, 2001) found only under poor and acidic conditions along with species associated with a richer inland peat bog considered a minerotrophic poor fen like



Figure 37 St. Pierre case study sites with example (left) of the landscape surrounding the sites (Photographer: Pascaline Caudal) and (right) the peat bog where the peat core was sampled (Photographer: Patrick Hacala).

Juniperus communis (Damman & Dowhan, 1981; Glaser, 1992; Ayotte & Rochefort, 2019). The surrounding site is characterized by a landscape composed of both anthropogenic areas as well as forests and subarctic heathlands (Fig. 37).

Time zonation throughout the peat core was done through a CONISS (Constrained Incremental Sum of Squares) cluster analysis based on a method and using a Bray-Curtis distance matrix. The number of zonation were chosen based on the main pattern observed within the studied assemblages (Fig. 38). Since the analysis focuses on oribatid mites, the zonation undertaken according to the repartition of the core's oribatid and the vegetation subdivision was done following the oribatid mite's one as well for comparability

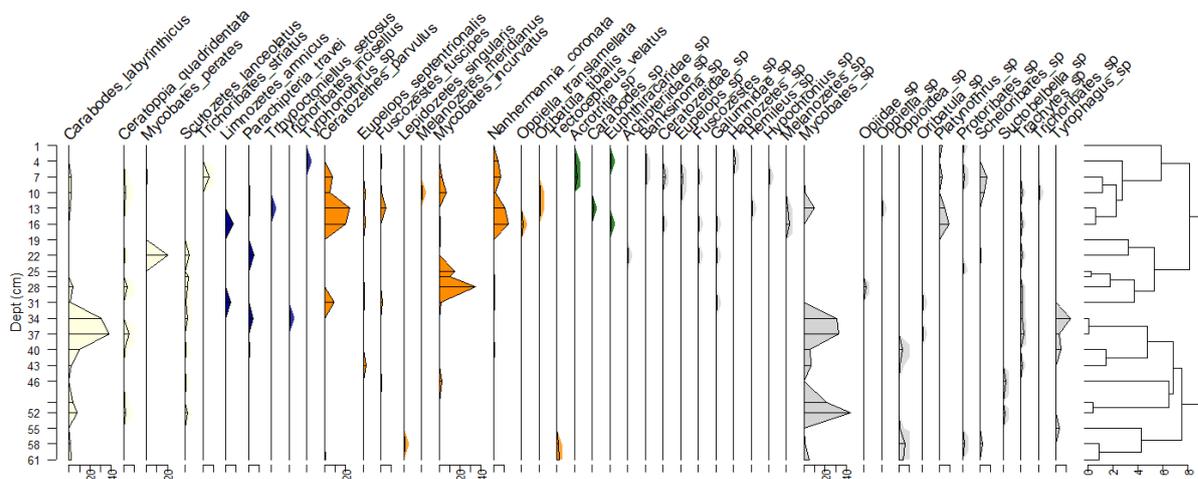


Figure 38 Oribatid mites abundance through the peat core. In yellow the xerophilic species, in blue the aquatic, semi-aquatic and hygrophilous species, in orange, the mesophilic species, in green the species associated with forests and in grey the species without an associated ecology. The CONISS dendrogram is represented on the right of the diagram.

The dates associated to those times zones in the core (Tab. 2) were dated by three radiocarbon analyses performed by the Laboratoire de Radiochronologie of the Centre d'études Nordiques (CEN), Université Laval (Québec, Canada). These three radiocarbon dates obtained on plant macrofossils were distributed between 30 and 89 cm to which the date of the top of the core was added. Each ^{14}C date was calibrated to calendar years BP (=1950) using the calibration data set IntCal20 (Reimer *et al.*, 2020) (Tab. 2). In order to build an age/depth curve, a Bayesian approach was used. This specific method was first developed by Lanos in RenCurve application (2004), now implemented in the new version of ChronoModel (Lanos & Dufresne, 2019; 2022; Lanos *et al.*, in prep). The estimation of the curve itself is

based on a penalized cubic spline function. The numerical calculation is performed using MCMC (Metropolis-Hastings algorithm) techniques (Gilks *et al.*, 1997) implemented in ChronoModel. The construction of the age-depth curve required 3,000,000 iterations to obtain an accurate estimate of the mean curve, its error envelope, the posterior irreducible variances (over time and depth) and the smoothing parameter (Lanos *et al.*, 2019).

Climate reconstructions on each assemblage follows the process described in the data analysis section, using the species identified in each zone as the indicator assemblages. The species *Limnozetes amnicus* (Behan-Pelletier, 1989) was removed from the analysis for there is no data of repartition for this species in the GBIF database used.

Table 2 Example of macrofossils both, leaves and seeds, from an analysis performed by the Centre d'étude nordique (Québec, Canada) on samples from the peat core of Saint-Pierre (ZS1).

Time zone	Dept (cm)	Date (MAP Cal. BP)
Z1	0-10	Actual - 237
Z2	10-18	237-585
Z3	18-21	585-715
Z4	21-31	715-1143
Z5	31-45	1143-1724
Z6	45-31	1724-2352

2.3. Data analysis

Climate inferences from oribatid mites were assessed following Harbert & Baryames (2020) through weighted MCR) method from the CRACLE package (Harbert & Baryames, 2020). Spatial autocorrelation of the deviation from the observed temperatures for Mean, Max and Min values were estimated for each month using Moran's test with the spdep package (Bivand *et al.*, 2015). The weighted matrix used for the tests was calculated using an Euclidian distance matrix based on sites coordinates.

Each assemblage from the 46 datasets from Mumladze *et al.* (2013) was first tested and compared to the real climate associated to each sampling point based on an extraction from the climatic raster from the WorldClim database (Fick &

Hijmans, 2017) of maximum, mean and minimum temperatures. A second reconstruction was done after removing problematic species. This was completed by removing each species from each assemblage which, once removed, decreased the overall net differences between the reconstruction and the known climate. This was done because some species can affect the reconstruction due to their specific ecologies (e.g. aquatic beetles decrease the quality the temperature of reconstruction, Fletcher *et al.*, 2019) or poorly known worldwide repartition (Atkinson *et al.*, 1987; Alfimov & Berman, 2009). The influence on the quality of the dataset (number of species contacted and number of associated biogeographic data) was tested through GLMM (=Generalized Linear Mixed Model) with a Gamma distribution with a log link error following Zuur *et al.* (2009) to assess which variable might affect the quality of the reconstruction. The mixed model was used to specify sites and month as random variable with month nested in sites variables.

**Reconstruction errors ~ Number of points + Number of species +
(Month | Site) + (1 | Site)**

All the data analyses were conducted using the free software R-3.6.2 (R Development Core Team, 2021).

3. RESULTS

Of the 46 original data sets comprising 409 species, 295 remained after the removal of species with no known biogeographic data on GBIF, resulting in over 85 000 occurrence points.

3.1. Model improvement through species screening

Amongst the 98 species that were removed to improve the reconstructions, the pattern was not consistent (Fig. 39). Some species, such as *Pergalumna nervosa* (see Fig. 40 for known repartition) was removed 19 times from the 20 sites in which it was present. Twenty-nine other species were removed from the calculation as they had a negative effect on the reconstruction 100% of the times they were present within a site assemblage. Those 29 species that always had a negative effect occurred in 1 to 7 sites.

ORIBATID MITES AS BIOINDICATOR OF PAST CLIMATES

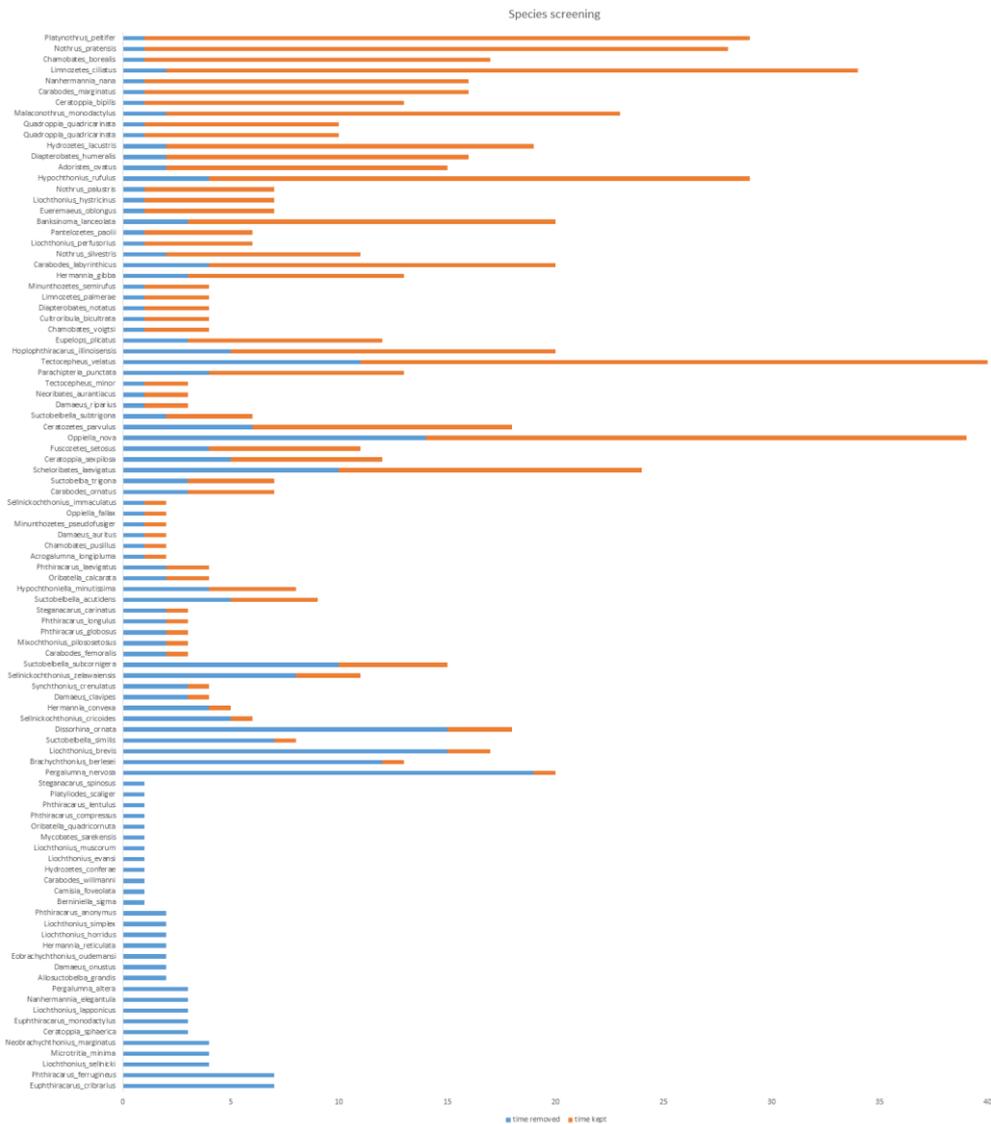


Figure 39 List and occurrences of species that were removed for the reconstruction. In blue the number of sites from which the species was removed, in orange the number of sites in which the species was kept.

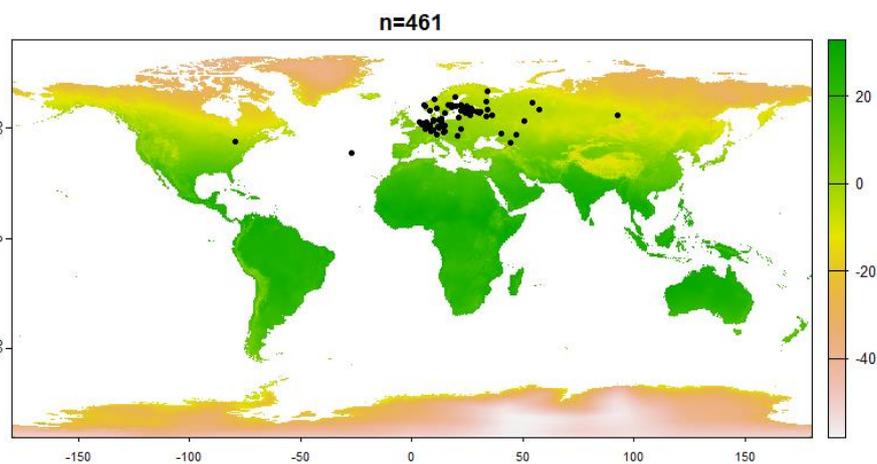


Figure 40 Worldwide repartition of Pergalumna nervosa projected a maximum temperature raster.

3.2. Climatic reconstructions test with known conditions

The resulting corrected temperatures values curves can be divided in four categories: (1) poor reconstruction, $n_{\text{site}} = 15$ (e.g. Fig. 41.a); (2) intermediate, $n_{\text{site}} = 16$ (e.g. Fig. 41.b); (3) improved reconstruction, $n_{\text{site}} = 12$ (e.g. Fig. 41.c); (4) "miscellaneous", $n_{\text{site}} = 3$ (e.g. Fig. 41.d). Curves for all sites are in appendix 3.

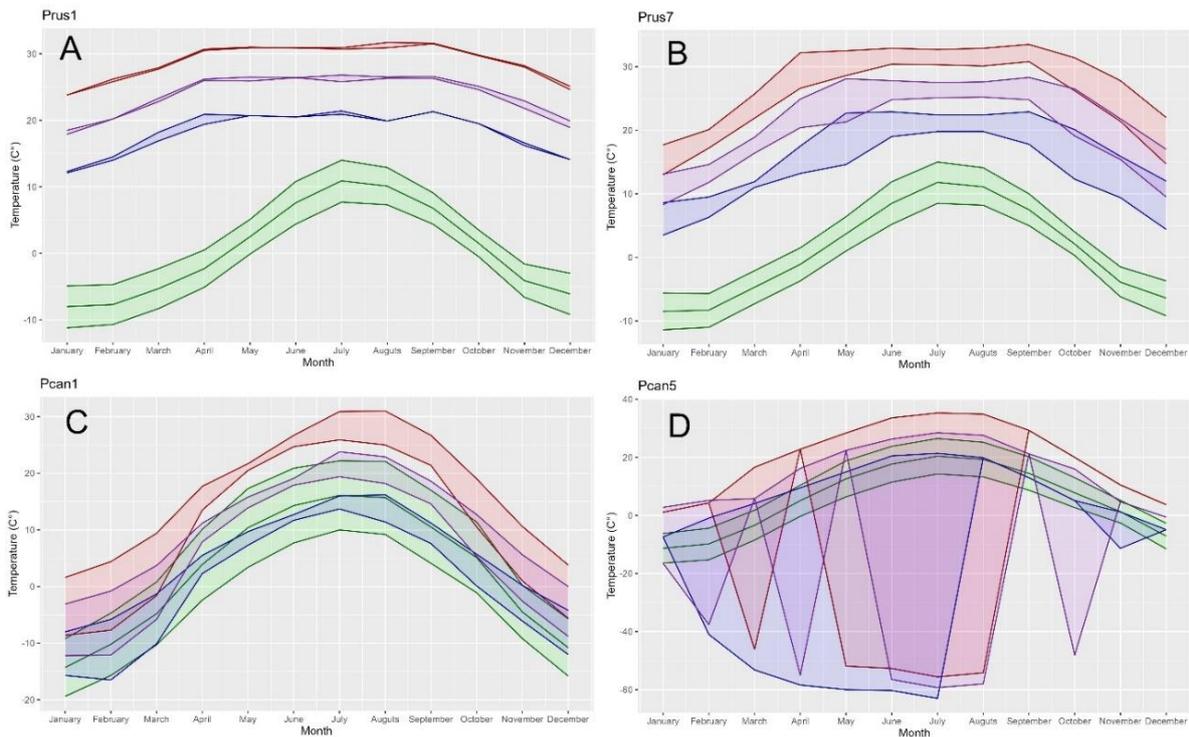


Figure 41 Climatic reconstructions based on oribatid mite's assemblages for each month. In green the known temperature of the studied site, the upper and lower line being maximum and minimum temperatures while the middle line being the median temperature. In red, the reconstructed intervals of maximum temperature. In purple, the intervals of reconstructed median temperature. In blue, the intervals of reconstructed minimal temperatures. A: an example of poor temperature reconstruction with the Prus1 site; B: an example of intermediate temperature reconstruction with the Prus7 site; C: an example of improved temperature reconstruction with the Pcan1 site; C: an example of miscellaneous temperature reconstruction with the site of Pcan5.

Overall, there was an overestimation of temperature, particularly for summer months, in all sites except the "miscellaneous" ones. The "poor reconstruction" category was characterized by highly overestimated temperature and a flat curve. This induces a great error for winter reconstructions. The "intermediate" category still overestimates the temperature but the curve follows the seasonal variation of the observed temperature, smoothing the error. The "improved" category display

reconstructions that often overlaps with the observed winter temperatures. Furthermore, the summer reconstruction of minimal temperatures are also within the range of observed temperatures. Yet, the maximal reconstructed temperatures remained overestimated. The “miscellaneous” category comprises odd and unique pattern results that resemble no other reconstructions.

3.3. Analysis of the test reconstructions

No significant spatial autocorrelations were observed for any month and any temperature (Tab. 3).

Table 3 Spatial Autocorrelation test values. For every month, the autocorrelation between the reconstruction errors and the site locations were tested for the errors of mean, maximum and minimum temperatures.

Month	Mean Temperatur Δ obs -predicted		Max Temperatur Δ obs -predicted		Min Temperatur Δ obs -predicted	
	Moran I statistic	p-value	Moran I statistic	p-value	Moran I statistic	p-value
January	0.045	0.48	0.11	0.45	-0.16	0.56
February	-0.65	0.74	0.07	0.47	-0.24	0.60
March	-0.17	0.57	-0.51	0.69	-1.04	0.85
April	-0.14	0.55	0.11	0.45	-0.80	0.79
May	0.18	0.43	-0.26	0.60	0.02	0.49
June	-0.50	0.69	-0.48	0.68	-1.67	0.95
July	-2.15	0.98	-0.24	0.59	-0.84	0.78
August	-0.41	0.66	0.15	0.44	-0.34	0.63
September	-0.37	0.64	-0.32	0.62	-1.37	0.91
October	0.41	0.34	-0.77	0.78	-0.44	0.67
November	-0.32	0.63	-0.40	0.66	0.03	0.49
December	0.14	0.44	-0.24	0.59	0.11	0.46

The variables impacting the deviation from the observed temperatures displayed the same patterns for the three temperatures modelled: mean (Fig. 32), max (Fig. 43) and min (Fig. 44). The number of points within the biogeographical data had a positive impact on the reconstruction by significantly decreasing the differences between the observed and reconstructed temperatures (Mean: $R=-0.0000151$ $p=7.08e-05$; max: $R=-1.609e-05$ $p=1.24e-9$; min: $R=-1.213e-5$ $p=1e-04$). However, the number of species within the community had a negative impact on the reconstruction as it increases the differences between the observed and predicted temperature (Mean: $R=0.0093618$ $p=3.65e-09$; Max: $R=0.01$ $p=1.58e-12$; Min: $R=0.001$ $p=1.45e-08$).

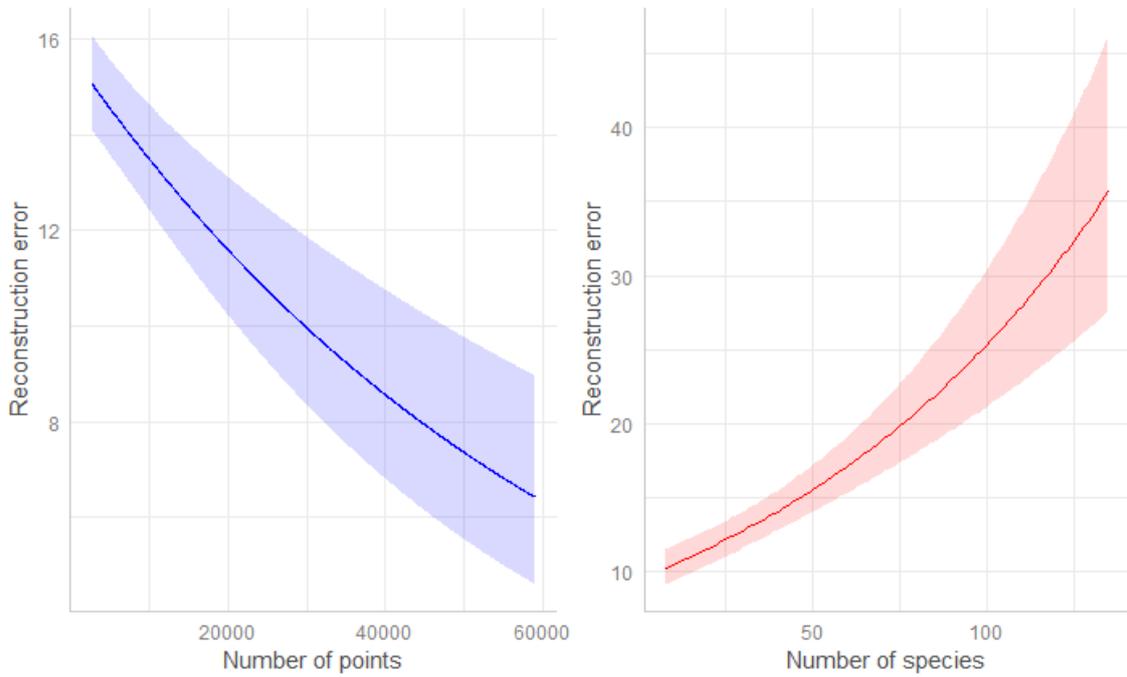


Figure 42 Fitted Gamma regression models showing the effect of explanatory variables on the delta between reconstructed and observed mean temperatures for the number of points (left) and the number of species (right).

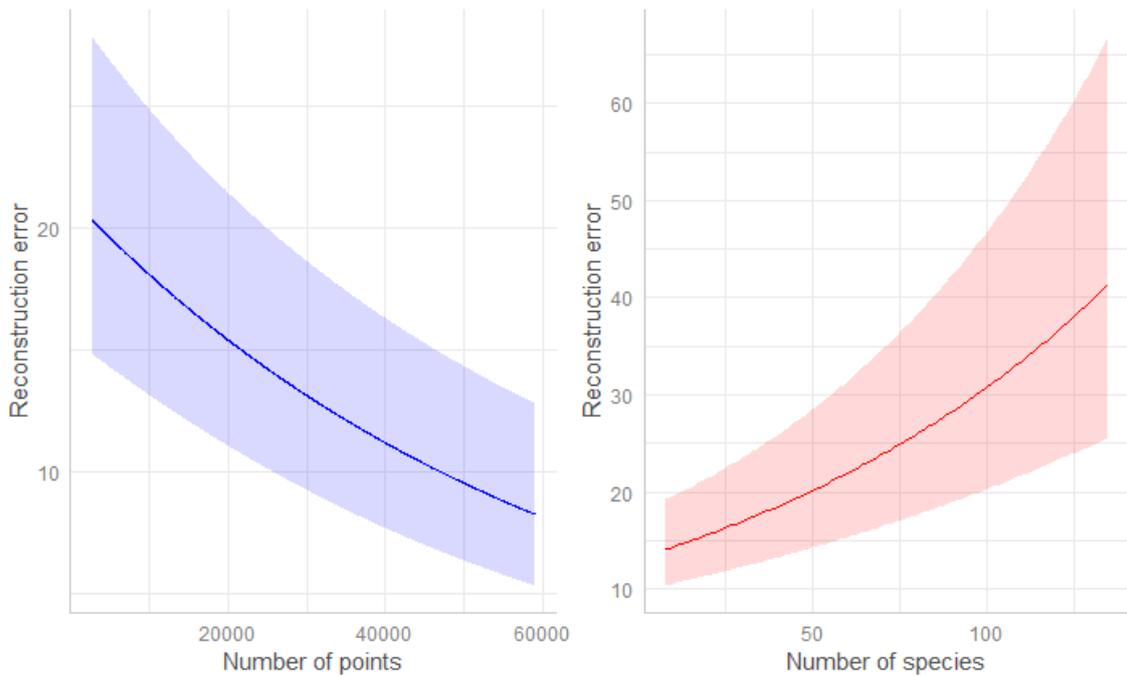


Figure 43 Fitted Gamma regression models showing the effect of explanatory variables on the delta between reconstructed and observed maximum temperatures for the number of points (left) and the number of species (right).

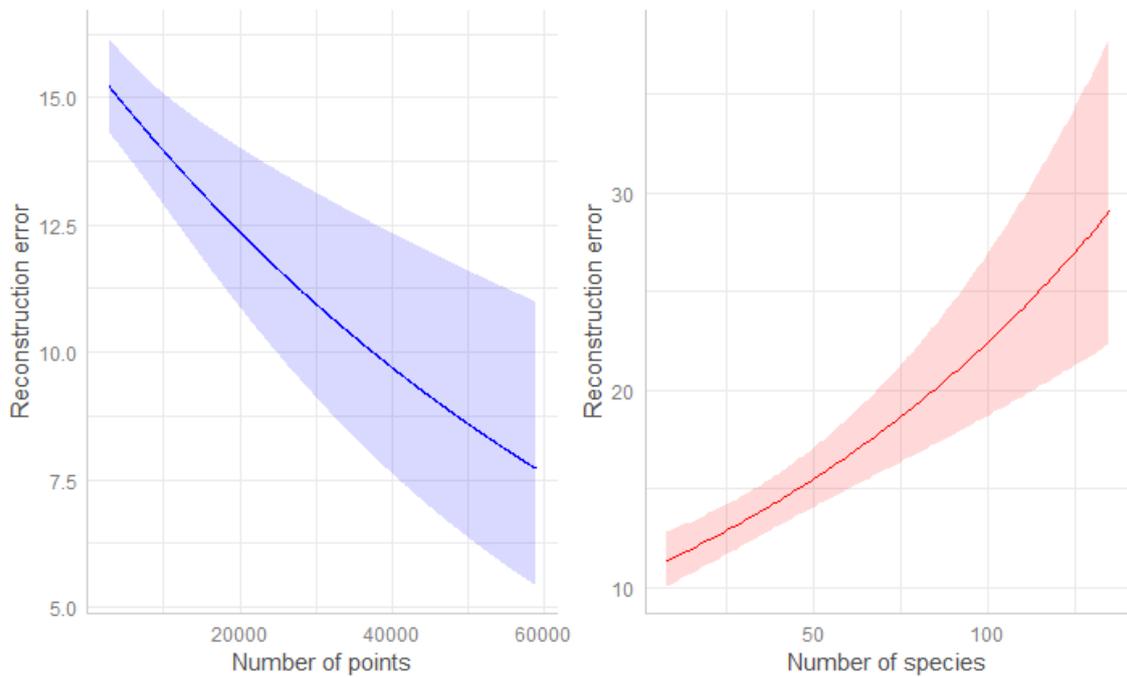


Figure 44 Fitted Gamma regression models showing the effect of explanatory variables on the delta between reconstructed and observed minimum temperatures for the number of points (left) and the number of species (right).

3.4. The Case Study

The oribatid assemblage used for then Saint-Pierre & Miquelon case study comprises 18 species. The six temporal zone divisions contained between five and 12 species and the number of biogeographic points from 873 to 7676 (Tab. 4). Vegetation assemblages had between five and 14 species which resulted in a number of points between 509107 and 1130629.

The curves from the oribatid case study (Fig. 45) can be associated with the “intermediate” or “improved” categories as the curvature of the reconstructions seems to follow the global pattern of seasonal temperatures. The temperature values are rather similar throughout the timeline with only zones 3 and 4 that have lower winter temperatures that can reach -24.9 C° for Zone 3 and -19.2 C° for zone 4 while the others are situated around minimums of -15 C° . When compared to the vegetation data (Fig. 46), the temperature reconstructions matched both in terms of curve behavior and values. The only exception was that vegetation climatic reconstructions do not display the same decrease in temperature in zones 3 & 4 as their 6 curves are highly similar.

ORIBATID MITES AS BIOINDICATOR OF PAST CLIMATES

Table 4 Species by time zone for oribatid mites and vegetation. The richness and number of points associated to the assemblages of each time zone is specified.

Species		z1	z2	z3	z4	z5	z6
<i>Ceratoppia quadridentata</i>	(Haller, 1882)	x	x	x	x	x	x
<i>Mycobates incurvatus</i>	(Hammer, 1952)	x	x	x	x	x	
<i>Parachipteria travei</i>	(Nevin, 1976)	x	x	x		x	
<i>Carabodes labyrinthicus</i>	(Michael, 1879)	x	x		x	x	x
<i>Eupelops septentrionalis</i>	(Trägårdh, 1910)	x	x		x	x	
<i>Fuscozetes fuscipes</i>	(C.L. Koch, 1844)	x	x		x	x	
<i>Nanhermannia coronata</i>	(Berlese, 1913)	x	x		x	x	
<i>Ceratozetes parvulus</i>	(Sellnick, 1922)	x	x		x		x
<i>Oribatula tibialis</i>	(Nicolet, 1855)	x	x				
<i>Mycobates perates</i>	(Behan-Pelletier, 1994)	x		x			
<i>Melanozetes meridianus</i>	(Sellnick, 1928)	x					
<i>Trichoribates striatus</i>	(Hammer, 1952)	x					
<i>Oppiella translamellata</i>	(Willmann, 1923)		x				
<i>Trhypochthonius setosus</i>	(Hammer, 1952)		x				
<i>Scutozetes lanceolatus</i>	(Hammer, 1952)			x	x	x	x
<i>Trichoribates incisellus</i>	(Kramer, 1897)					x	
<i>Lepidozetes singularis</i>	(Berlese, 1910)						x
<i>Tectocepheus velatus</i>	(Michael, 1880)						x
Richness		12	11	5	8	9	6
number of points		4048	7676	873	1985	2261	4297
<i>Sphagnum fuscum</i>	(Klinggräff, 1872)				x	x	x
<i>Chamaedaphne calyculata</i>	(Moench, 1794)			x	x	x	x
<i>Empetrum nigrum</i>	(Linnaeus, 1753)			x	x	x	x
<i>Andromeda glaucophylla</i>	(Link, 1821)			x	x		x
<i>Sphagnum papillosum</i>	(Lindberg, 1873)			x	x		x
<i>Rhododendron groenlandicum</i>	(Kron & Judd 1990)				x	x	x
<i>Vaccinium vitis-idaea</i>	(Linnaeus, 1753)						x
<i>Rhododendron canadense</i>	(Torrey, 1841)						x
<i>Vaccinium oxycoccos</i>	(Linnaeus, 1753)			x		x	x
<i>Sphagnum tenerum</i>	(Sullivant, 1856)					x	
<i>Picea mariana</i>	(Britton, 2010)	x	x	x	x	x	x
<i>Juncus effusus</i> var. <i>conglomeratus</i>	(Bosch, 1850)				x	x	
<i>Carex aquatilis</i>	(Wahlenb., 1803)				x		
<i>Sphagnum rubellum</i>	(Wilson, 1855)			x			
<i>Sphagnum flavicomans</i>	(Warnstorf, 1911)			x			
<i>Sphagnum magellanicum</i>	(Bridel, 1798)			x			
<i>Trichophorum caespitosum</i>	(Hartman, 1849)			x			
<i>Carex canadense</i>	(Dewey, 1866)			x			
<i>Sphagnum affine</i>	(Renauld & Cardot, 1885)			x			
<i>Abies</i> cf. <i>balsamea</i>	(Mill., 1768)	x	x	x	x	x	x
<i>Sanguisorba</i> cf. <i>canadensis</i>	(Linnaeus, 1753)				x		
<i>Typha</i> cf. <i>latifolia</i>	(Linnaeus, 1753)	x	x	x	x	x	x
<i>Myrica gale</i>	(Linnaeus, 1753)	x	x	x	x	x	x
<i>Pinus</i> cf. <i>strobus</i>	(Linnaeus, 1753)	x	x	x	x	x	x
Richness		5	5	16	14	12	14
number of points		509107	509107	967374	704190	778143	1130629

ORIBATID MITES AS BIOINDICATOR OF PAST CLIMATES

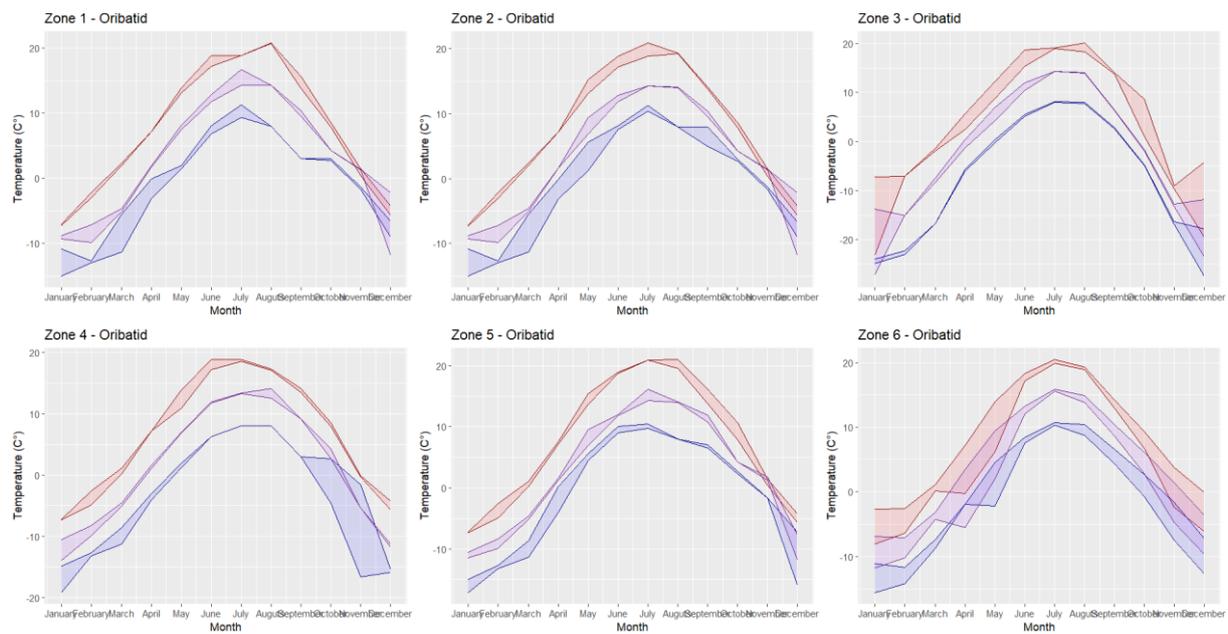


Figure 45 Temperature reconstruction based on the oribatid assemblages for each month and for each time zone. In red the interval of maximum temperatures, in purple the interval of mean temperature and in bleu the interval of minimum temperatures.

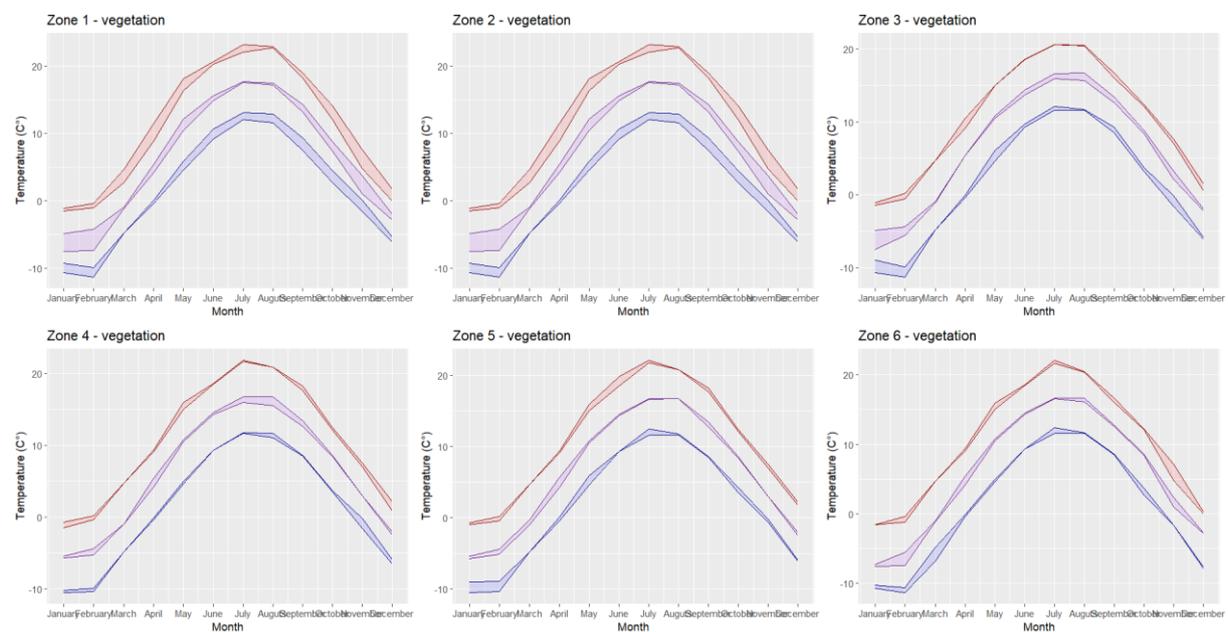


Figure 46 Temperature reconstruction based on the vegetation assemblages for each month and for each time zone. In red the interval of maximum temperatures, in purple the interval of mean temperature and in bleu the interval of minimum temperatures.

4. DISCUSSION

4.1. Reconstruction testing

The primary result of this study is how the climatic reconstruction spanning the last two thousand years deviates from the present-day climate and how many species appears to be linked to those deviations. Several species decrease the model reconstruction with various degrees of regularity (e.g. *Pergalumna nervosa* observed 20 times and having a negative effect in 19 of those sites or *Tectocephus velatus* which was observed on 40 sites and had a negative effect 11 times). Those negative effects, while having an apparent additive behavior, must be more complex as after species with net negative effects were removed, a negative effect of the number of species remains. Therefore, some negative effect may result from interaction between species that will need further analysis in the future. The remaining errors, the ones in the corrected reconstruction model were explained by the number of points and species. The number of points having a positive effect was expected as it increases the data upon which the model creates the reconstructions. On the other hand, the negative effect of the number of species is more surprising. Indeed, within the literature the same method of reconstruction for vegetation displayed a positive effect on the number of species (Thompson *et al.*, 2012). One explanation could be due to poorly documented or understood repartition of some oribatid species. Knowledge gaps within the subarctic region have been highlighted specifically for Canadian subarctic peatlands (Warner & Asada, 2006; Young *et al.*, 2012; DeWaard *et al.*, 2019). This lack of detailed knowledge of species at their northern limits would increase the bias associated to climate reconstruction in cold areas (Atkinson, 1987; Alfimov & Bernan, 2009). Another possible problem could be due to the lack of knowledge of oribatid distribution in the GBIF database. Such incomplete data could create or increase problems previously stated and diminish the analytical capacity of the use of the MCR method. Also, following Alfimov and Berman 2009 who advised the use of global data of species repartition to avoid the known regional biases in previous MCR studies, one could question the effect of the strong bias towards European oribatid data in the GBIF database. This might create a temperate bias in reconstructions based on GBIF oribatid datasets when working with non-European climate reconstructions. Likewise, it was proposed that errors within the systematics (e.g. two species under the same name that have contrasting ecology)

may lead to errors in MCR reconstruction (Fletcher *et al.*, 2019). Even though no species in this study are synonyms, allopatric population may hide several species (e.g. Ivanov *et al.* 2021, 2023), a complexity relevant to the issue at hand. Reciprocally, a spatial variation of ecological tolerance within one species could interfere with the reconstruction premises. Such variation are described in other arachnids (Duffey, 2005; Monsimet, 2021) and, if present in oribatid mites, may be responsible for climate reconstruction errors.

Another explanation for the cold temperature reconstruction may reside in the relationship of Oribatida to the cold. Indeed, Cold tolerance and avoidance is known in beetles to create a threshold for minimum temperature reconstruction as, below a certain point, the cold is no longer a filter as it is avoided (Fletcher *et al.*, 2019). Oribatids are known for remarkable cold tolerance (Coulson & Birkemoe, 2000; Coulson *et al.*, 2023). This cold tolerance capacity involves supercooling, which they achieve by the evacuation of gut contents and by the accumulation of colligative antifreeze. By doing so they withstand temperatures of -30C° (Cannon & Block, 1988; Sømme, 1979).

A potential source of error could be the result of an important premise of the MCR method which necessitates that the species under consideration reflect the air temperature (Alfimov & Berman, 2009). This premise of MCR can be broken for instance by using aquatic species than do not reflect air temperature (Fletcher *et al.*, 2019). Indeed, many oribatids are semi-aquatic to aquatic (Behan-Pelletier & Lindo, 2023) and this could cause such an error. However, we reject this explanation as only a few species are aquatic or semi-aquatic within the dataset used and that they are not over represented among the species discarded for their negative effects.

4.2. Case study

Within the case study, a remarkably stable temperature for both oribatid mites and vegetation was observed when considering the known climatic variation of the time period (Wanner *et al.*, 2008). The known colder mesoclimate in the peat bog (Rydin *et al.*, 2013) might provide an explanation for colder reconstructions errors but its absence in the Mumladze *et al.* (2013) dataset, all from peat bogs, rules it out. Since the zonation selected through the timeline is based upon oribatid assemblages, it could be considered that oribatid mites assemblages' variations

through time might be uncorrelated from climatic changes through time. Indeed, Oribatid mites shown no latitudinal gradient at the northern hemisphere scale (Mumladze *et al.*, 2013) which is essentially a climatic gradient (but see Maraun *et al.*, 2007). When they do respond at a large-scale latitudinal gradient, it is not the latitude itself but other environmental variable correlated to it that shape the assemblages like precipitation or soil organic matters (Caruso *et al.*, 2019). Concurring with the precipitation gradient previously cited and that oribatid mites are known to be great indicators of hydrology (Bokhorst *et al.*, 2008; Kardol *et al.*, 2011; Lehmitz *et al.*, 2020; Barreto *et al.*, 2021), it should be considered here that the zonation used here might not be a climatic temporality as much as and hydrological one. Following this logic, the temporal zone might encompass climatic variations, colder and warmer periods which cancelled out each other in an always moderate climatic reconstruction. This idea is strengthened by the ecological profile of the oribatid mites that characterized those zonation thresholds as the clustering follows hydrological preferences (see chapter 3 for oribatid repartition through time). Furthermore, having broader, longer hydrological time zones, and by not following short climatic variations, this could be linked to peat bogs having a reservoir function and therefore a hydrological inertia. Likewise, in order to have a comparable data site, the vegetation temporal zonation, was based on the oribatid mite's zonation. It should be noted that if the same exercise was based on plant clusters through the core, the zonation would have been different (see chapter 3 for plant assemblages clustering). Perhaps, as the vegetation is a known fruitful indicator of past climates (Harbert & Baryames, 2020), a temporal zonation based on the vegetation could give more logical results.

4.3. Conclusion

Climatic reconstructions using oribatid mites seems to remains a goal for the future of the discipline. In order to decipher what element of the quality of data used or the intrinsic ecology of the oribatid mites is at fault remains to be seen. We can look forward to an improved biogeography of oribatids where the number of points of occurrences will catch up to that of the vegetation and where samples are taken homogeneously across the world. At the moment, some perspectives are achievable. If it can be managed to find a way to identify which curves category ("poor", "intermediate" or "improved") one has reconstructed, a correction factor could be computed following Atkinson's MCR correction for ground beetles (1987)

but in a nonlinear, seasonally dependent fashion in order to meet the behavior of the curves reconstructed in our analyses. In order to explore the hydrological indicators over time hypothesis, it would be interesting to try the same reconstruction methods but with precipitation data instead of temperature data in order to assess if oribatids are better predictors of variation of hydrology over time. If this appears to be true, it would highlight an interesting means for oribatids to complement vegetation in reconstructions of past climates. Finally, this case study analysis could be improved by using vegetation induced temporal zonation. This could shed light on the patterns observed here and help understand the potential of oribatids for the reconstruction of past environments.

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B. Atlantic subarctic peat bogs ecology through a two millennia dynamic, a transdisciplinary multi-taxon approach.

Axel Hacala^{1,*}, Elia Roulé², Valerie Behan-Pelletier³, Marie-Eve St-Pierre⁴, Najat Bhiry⁴, Allison Bain⁵, Julien Pétillon^{1,6}, Dominique Marguerie¹

¹ UMR CNRS 6553 Ecobio, Université de Rennes, 263 Avenue du Gal Leclerc, CS 74205, 35042, Rennes Cedex, France

² Université de Franche Comté, Laboratoire Chrono-environnement, 16 route de Gray, Besançon, France

³ Invertebrate Biodiversity Program, Research Branch, Agriculture and Agri-Food Canada, K.W. Neatby Bldg., Ottawa, Ontario, Canada.

⁴ Département de géographie and Centre d'études nordiques, Université Laval, Québec, Québec, Canada

⁵ CELAT Research Centre, Université Laval, Québec, Canada

⁶ Institute for Coastal and Marine Research, Nelson Mandela University, Port Elizabeth, South Africa

*Corresponding author: axel.hacala@gmail.com, +33 6 16 50 76 52

RESUME :

Les deux derniers millénaires de l'Holocène récent ont été une période riche en variations tant sur le plan climatique qu'anthropique. Dans le contexte géographique de la côte Atlantique nord-est du Canada, la période climatique étudiée était connue pour être particulièrement variable et peu étudiée. Cette étude visait à mieux comprendre à la fois l'histoire environnementale locale de l'archipel de Saint-Pierre et Miquelon et à renforcer la compréhension de la dynamique climatique de la région. Pour ce faire, les restes biologiques de plusieurs indicateurs ont été extraits des carottes de tourbe. La comparaison des restes sub-fossiles d'acariens oribatides, des macrofossiles de végétation et du pollen a fourni, sur une période de deux millénaires d'accumulation de tourbe, des aperçus sur la dynamique des tourbières et le contexte climatique de l'archipel. Plusieurs variations liées au climat et à l'hydrologie locale, ainsi qu'à des événements d'incendie, naturels et éventuellement d'origine humaine, ont été

observées. Ces dynamiques étaient associées à des patterns écologiques spécifiques des oribatides ainsi qu'au développement de la végétation, tant des plantes vasculaires que des sphaignes à l'échelle locale, et croisées avec l'échelle plus large des réponses du pollen. Cette approche multi-taxon a permis une compréhension plus robuste et précise des modèles en jeu. Ce qui peut être conclu de cette étude est que l'habitat de tourbière était déjà et est resté une tourbière océanique ombrotrophe au cours de la période étudiée. De plus, les modèles climatiques observés ici correspondaient aux variations historiques régionales spécifiques, contribuant ainsi à renforcer cette histoire climatique et à éclairer le cas précédemment non étudié de Saint-Pierre et Miquelon.

ABSTRACT:

The last two millennia of the late Holocene was a period rich in variation both in climatic and anthropogenic considerations. In the geographical context of the northeastern Atlantic coast of Canada, the studied climatic period was known to be especially variable and understudied. This study aimed at a better understanding of both the local environmental history of the archipelago of Saint-Pierre and Miquelon and strengthen the understanding of the climate dynamics of the region. To achieve this, the biological remains of several indicators were extracted from peat cores. The comparison of oribatid mite subfossils, vegetation macrofossils, and pollen provided, through the span of two millennia of peat accumulation, insights into the peat bog dynamics and climatic context of the archipelago. Several variations related to climate and local hydrology, as well as fire events, both natural and possibly human-made, were observed. These dynamics were associated with oribatid specific ecological patterns as well as vegetation development of both vascular plants and sphagnum at a local scale and crossed with the pollen's broader scale of responses. This multi-taxa approach allowed for both a more robust and precise understanding of the patterns at stake. What could be concluded from this study is that the peat bog habitat was already and remained an ombrotrophic oceanic bog over the span of the studied period. Also, the climatic patterns observed here matched the specific regional historical variations, participating in strengthening that climatic history and shedding light on the previously unstudied case of Saint-Pierre and Miquelon.

1. INTRODUCTION

Within the Anthropocene, a period of worldwide changes, both climatic and habitats wise (Venter *et al.*, 2016), it appears crucial to ever improve our understanding of habitat dynamics. Paleoecology provides such information as it allows to study how habitats, species and climates changed over the course of time. Actual ecology only has the knowledge from the length of Science History to work with and stable long term experiences are too rare in order to provide an acute understanding of what was or to predict what might be (Pardi & Smith, 2012).

In order to understand such dynamics peat bogs are among the best habitats to study for they are of high conservation value and natural history book (Payette & Rochefort, 2001). Peat bogs are formed by accumulation of organic matter within a context of high hydrology (Rydin *et al.*, 2013). Those conditions combining stratifications of matter over time and low degradation of various remains allows cores of peat to tell the tales of the bog itself but also of its surrounding landscapes through the remains more mobile like pollens (Rydin *et al.*, 2013). This dependence on hydrology drove their conservation states as, for instance, 80% of Europe peatland surfaces were lost to drainage (Rydin *et al.*, 2013), mostly for agriculture purposes (Bonn *et al.*, 2016). Those remains are therefore at risk with the ever growing number of lost peat bogs (Rydin *et al.*, 2013), highlighting the urgency to both protect those environments and the information they retain.

Yet, as much as paleoecology opens a window on the past it suffers from drawbacks. Methodologically, paleoecology is bound to cues left from scarce remains which temper the possible drawn conclusions (Efremov, 1940; 1953, but see Fernandez-Jalvo, 2011). A possible angle to strengthen those conclusions is to multiply the studied model. Such an approach, aiming at the complementarity of the models, is widely used in both current ecology (Hacala *et al.*, 2020) and paleoecology (Panagiotakopulu *et al.*, 2020). This methodology relies on the complementarity of the models, in current ecology it often means un-correlated responses to one phenomenon between models in order to encapsulate the complexity of the studied objects (Hacala *et al.*, 2024). Here in paleoecology, redundancy between models is not an issue as it can strengthen the patterns (Blundell & Barber, 2005; Mazei *et al.*, 2020).

The models used here are pollen, vegetation macrofossils (hereafter referred to as macrofossils) and Oribatid mites sub-fossils. Pollen are one of the most used remains in paleoecology (De Wever *et al.*, 2010) as they can be found in great numbers which gives robust answers (Birks & Line, 1992) and gives an idea of broad ecological phenomenon as they provide an overview of the surrounding vegetation at a landscape scale and further (Sugita, 1994). On the other hand, the pollens can't be readily identified to the species level for every taxa and therefore doesn't give precise answer on the observed patterns (Williams & Shuman, 2008) as well, the broad scale of potential sources of pollen make it hard to decipher between local and landscape patterns (Birks & Birks, 2000). The macrofossils of vegetation and Oribatid mites offer complementary responses to pollen as they are bound to local patterns (Elias, 2010) and to each other as arthropods and vegetation are known complementary indicators (Hacala *et al.*, 2019; 2024).

All three methods, although having specificities than can highlight complementarities, strengthen each other as they all assess vegetation assemblages within a site. Vegetation being the most used model to assess ecological patterns (Kuiper *et al.*, 2014; Robroek *et al.*, 2015) there is numerous information that can be drawn by the unraveled vegetation patterns, may it be climatic (Chevalier *et al.*, 2020) or habitats wise (Blaus *et al.*, 2023). The last methods use Oribatid mites as ecological bioindicators. Oribatids are recognized as indicator taxa in peat bogs, both for actual ecology (Lehmitz *et al.*, 2020; Behan-Pelletier & Lindo, 2023) and paleoecology (Schelvis, 1990). Oribatids are a known complementary model taxa to vegetation (Lehmitz *et al.* 2020). As they are great indicators of moisture (Lehmitz *et al.*, 2020) they have been used to strengthen patterns observed from vegetation in paleoecological context (Schelvis & Geel, 1989). In a paleoecological context they provide interesting information as a percentage of subfossil as high as 87% can be identified to the species level (Schelvis, 2020). Furthermore, as Oribatid can reach concentrations of individuals as high as 400 000 individuals per square meters (Behan-Pelletier & Lindo, 2023) they are found in respectable quantities in paleo-deposit, providing an opportunity to observe rather robust patterns. On the other hand, Oribatid mites are still an under-studied taxa which lead to vast gaps of knowledge (*e.g.* only 40% of north-American Oribatid fauna is estimated to have been found, Behan-Pelletier & Lindo, 2023). This lack of information could reduce some of the possible conclusions

drawn from these assemblages. Yet such a multi taxa study offers the opportunity to provide hindsight on the lesser known specie's ecology as Oribatid and known vegetation species are crossed.

This study aims at understanding the local ecological patterns that characterize the two last millennia within sub-arctic coastal Atlantic peat bogs. This habitat, as previously discussed, has its perk ecologically and conservation wise but the specificity of Atlantic bogs (Damman & Dowhan, 1981; Glaser, 1992) crossed with the sub-arctic enclave driven by cold northern sea current in a meridional site (Aubert De la Rüe, 1970) motivates the need for information. The time scale of two thousand years was selected as it encompasses known broad climatic variation as the little ice age or the medieval thermic anomaly (Cronin *et al.*, 2003) and a rich human history (Native North American cultures and European colonization) (Marchand *et al.*, 2023). Those large drivers within a peculiar geographical context harboring odd climatic specificity could have led to unique responses. This study could provide hindsight at a fine scale on habitat dynamics, improve general knowledge of such patterns, increase knowledge of understudied habitats and sharpen paleoecological tools through its multitaxa approaches. The main objectives of the study are therefore to unravel the natural history of the Saint-Pierre & Miquelon archipelago and highlight the complementarity of the indicators used to achieve this goal.

2. MATERIAL AND METHODS

2.1. Site description

Peat bogs were sampled on the archipelago of Saint-Pierre and Miquelon (Fig. 47) and specifically on the island of Saint-Pierre (46.7696 E, -56.1862 N) during the summer 2021. The mean temperature of the archipelago is 5.5 °C, with a maximum in August of 15.7 °C and a January minimum of -2.97 °C (mean values calculated from 1933 to 1987, Muller *et al.*, 2012). The sampled habitat was an Atlantic bog which is characterized by a vegetation dominated by bog specialist, adapted to the poor and acidic conditions but with the added occurrence of poor minerotrophic species (Damman & Dowhan, 1981; Glaser, 1992; Ayotte & Rochefort, 2019). The site is characterized by a landscape context composed of both anthropogenic areas as well as forest and subarctic heathlands surrounding the bog.



Figure 47 Map of the Saint-Pierre & Miquelon archipelago with, on the right, the Burrin peninsula of the Newfoundland territory. The red dot being the sampling site on the Saint-Pierre Island.

2.2. Soil sampling

Peat coring was done using a Russian corer that sampled 50 cm long semi-cylinder cores with a 52mm diameter. The whole column of peat was sampled to assess the ages of peat accumulation while the portion of the core choose to be analyzed was selected to corresponds to the last 2000 years only, based on C14 dating.

2.3. Chrono-sequence modeling

The ZS1 core was dated by three radiocarbon analyses performed by the Laboratoire de Radiochronologie of the Centre d'études Nordiques (CEN), Université Laval (Québec, Canada). These three radiocarbon dates obtained on plant macrofossils were distributed between 30 and 89 cm to which the date of the top of the core was added. Each ^{14}C date was calibrated to calendar years B.P. using the calibration data set IntCal20 (Reimer *et al.*, 2020) (Tab. 5).

Table 5 Radiocarbon dates and calibrated age of the ZS1 core, Saint-Pierre

Laboratory codes number	Depth (cm)	Material dated	Date (14C yr B.P.)	Age (cal. yr B.P.) (95 %)
UCIAMS-263148 ULA-10500	30-31	macrofossils	1185 ± 15 BP	1175-1061 AD
UCIAMS-263147 ULA-10499	60-61	macrofossils	2315 ± 15 BP	2351-2331 BC
UCIAMS-263144 ULA-10498	89-90	macrofossils	3125 ± 15 BP	3388-3263 BC

For building age/depth curve, we used a Bayesian approach first developed by Lanos in RenCurve application (2004), now implemented in the new version of ChronoModel (Lanos & Dufresne, 2019; 2022; Lanos *et al.*, in prep). The Bayesian approach allows to estimate an average age-depth curve with its confidence envelop that interpolates the data and takes into account the uncertainties coming from the chronometric dates and small errors on depth measurements. Additional individual errors are respectively added on dates and depths to account for the possible presence of outlying dates and stratigraphic inversions. This Bayesian modelling therefore automatically penalizes the influence of outliers. The estimation of the curve itself is based on a penalized cubic spline function. The numerical calculation is performed using MCMC (Metropolis-Hastings algorithm) techniques (Gilks *et al.*, 1997) implemented in ChronoModel.

The construction of the age-depth curve required 1,000,000 iterations to obtain an accurate estimate of the mean curve, its error envelope, the posterior irreducible variances (over time and depth) and the smoothing parameter (Lanos *et al.*, 2019).

The age-depth curve shows a very regular accumulation of sediment over 90 cm (Fig. 48). The estimated curve with a confidence interval allows to calculate a date interval whatever the depth. The distribution is summarized as a « posterior probability density » region HPD at a given confidence level (95%). MAP (Mode *A Posteriori*) is the time value corresponding to the maximal density. Thus, an age (MAP) was assigned for each of the level studied.

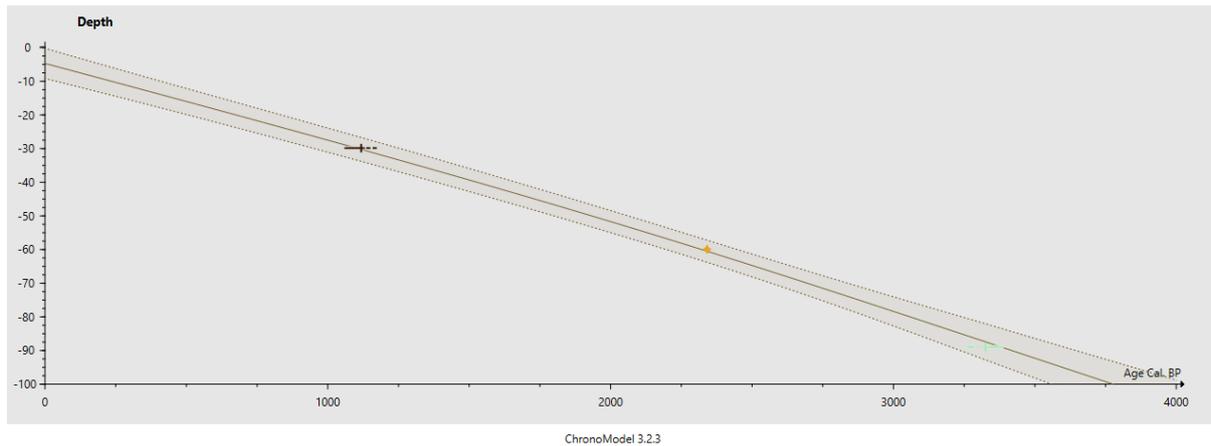


Figure 48 Age-depth curve of the ZS1 core, ChronoModel 3.2.3

2.4. Oribatid analysis

Each sample of peat used for oribatida, corresponded to a 1 cm slice of the core for a mean volume of 6.33 ± 1.6 ml. 1 cm every 3 cm were processed through the core, resulting in 22 samples. Samples were sorted by hand under a $\times 40$ magnification. Oribatids sub fossil remains were conserved in a 70% ethanol solution. Identification was done using Behan-Pelletier & Lindo (2023) and morphological comparison with the Canadian National Collection of Insects & Arachnids at the Agriculture and Agri-Food Canada in Ottawa. Identification was done under microscopic magnification ($\times 400$) in lactic acid (70%) and specimens too dark for identification were left in the same solution for a few hours to make them more translucent and ease the identification (Krantz & Walter, 2009).

2.5. Vegetation macrofossils analysis

The macrofossils analysis was performed by Marie-Eve St-Pierre and supervised by Najat Bhiry. Each sample of peat used for macrofossils corresponded to a 1 cm slice of the core for a mean volume of 6.33 ± 1.6 ml. 28 of those samples were distributed on the core. Following Bhiry & Filion (2001), the macrofossils were separated from the peat in a heated 5% solution of potassium hydroxide (KOH) and then sieved through $450\mu\text{m}$ and $180\mu\text{m}$ mesh in order to isolate macrofossils from decompositions residues. The macrofossils were sorted under $\times 40$ magnifying glass and identified with various botanical identification keys (Ayotte & Rochefort, 2019; Crow & Hellquist, 2000; Faubert, 2013; Gauthier, 2001; Lévesque *et al.*, 1988; Marie-Victorin *et al.*, 2002; Martin & Barkley, 1961; Payette, 2001; 2018) Online identification resources (Arsène, 1927; Bosseaux, 1965; Etcheberry *et al.*,

2012; Le Gallo, 1949; 1954; Le Hors, 1931) and comparison with references sample, the Louis-Marie herbarium from the Laval University in Québec. The vegetal matrix within which the macrofossils were extracted was sorted into high taxonomic categories.

2.6. Pollen analysis

The pollen analysis was done by Elia Roulé. The peat sequence was sampled every cm, before making physical-chemical pollen preparations. First, samples were sieved at 200 µm, then chloridric acid is added (10%). We added Hydrofluoric acid to remove siliceous residues, before the acetolysis to color pollen grain with sodium hydroxide, and the preservation in glycerined water (Girard, 1969). Pollen grains were identified (microscope × 40), counted using *Polycounter* 3.1.4 (Nakagawa, 1998), and identified with reference works (Arsène, 1947; Moore, 1991; Reille, 1999; Muller *et al.*, 2012; Payette, 2013; 2015; Boland, 2017).

The results have been formatted using the rioja package (Juggins & Juggins, 2019), in percentages. For more easy comparability with other methods, pollen taxa are used as raw data, without taking into account the usual methodology of using an added taxon such as *Lycopodium* to obtain relative pollen concentration (Davis, 1969). We used the total sum of square for the CONISS cluster method, which calculates the distances between pollen assemblages (Skene, 1998), to create the Local Pollinic Zones (LPZ). Beside fern spores, the total pollinic base sum includes all pollen taxa, even aquatic and hygrophilous-amphibian taxa. The taxonomic richness of pollen grains was determined without recourse to rarefaction analysis, as the grain counts are remarkably similar across all samples (ca. 300 pollen grains). Beside fern spores, the total pollinic base sum includes all pollen taxa, even aquatic and hygrophilous-amphibian taxa.

A wide variety of Ericaceae can be found in the peat bogs of the subarctic zone (*Vaccinium macrocarpon*, *V.vitis idea*, *V.oxycoccus*, *Empetrum nigrum*, *Kalmia angustifolia*, *etc.*), but also herbaceous and Cyperaceous species. Efforts have been made to identify the most precise taxonomic rank possible, although depending on morphotypes or hybridization, the degree of identification in palynology is limited to family rank (Birks *et al.*, 2023). The pollen analysis thus depicts the regional pollen rain, yet it is also highly localized at the scale of the peat bog.

2.7. *Statistical analysis*

Time zonation throughout the peat core was done through a cluster analysis based on a CONISS method and using a bray-curtis distance matrix, using the Rioja package (Juggins & Juggins, 2019). The number of zonation were chosen based on the main pattern observed within the studied assemblages.

All the data analyses were conducted using the free software R-3.6.2 (R Development Core Team, 2021).

3. RESULTS

3.1. *Peat accumulation rate*

Based on the age/depth curve obtained using ChronoModel chronological modelling software (Fig. 45), it is possible to estimate the average rate of accumulation of peat deposits in the wetland at ZS1. Analyses were carried out on a maximum sediment thickness of 89 cm (base level of plant macrofossil analyses and the depth of the earliest radiocarbon dating). MAP at this depth is 3446 before 2020 (0 cm). The average annual accumulation rate of the deposits studied is therefore 0.26 mm. This is a valid average rate for the entire sequence, given the linearity of the curve (Fig. 45). Finally, the temporal resolution of the analyses carried out on one-centimeter slices of sediment is 38.7 years.

3.2. *Sample acquired by model taxa*

20 pollen samples were read, based on a minimum identification of 500 pollen grains for better taxonomic representativeness. In all, 46 pollen taxa were identified, including 13 trees, 3 shrubs, 30 herbaceous taxa and 7 fern spore taxa.

28 Vegetation macrofossils sampled were analyzed, they comprised 1245 pieces. 21 taxa were identified to the species level while other, due to degradations or lack of criteria on the remains were attributed to higher taxonomic level from genus up to higher taxonomic grouping with an ecological interest.

22 Oribatids subfossils sampled were analyzed, they comprised 695 minimum number of individuals. Among those 408 individuals were identified to the species while the remaining subfossils were identified to the genus or the family level.

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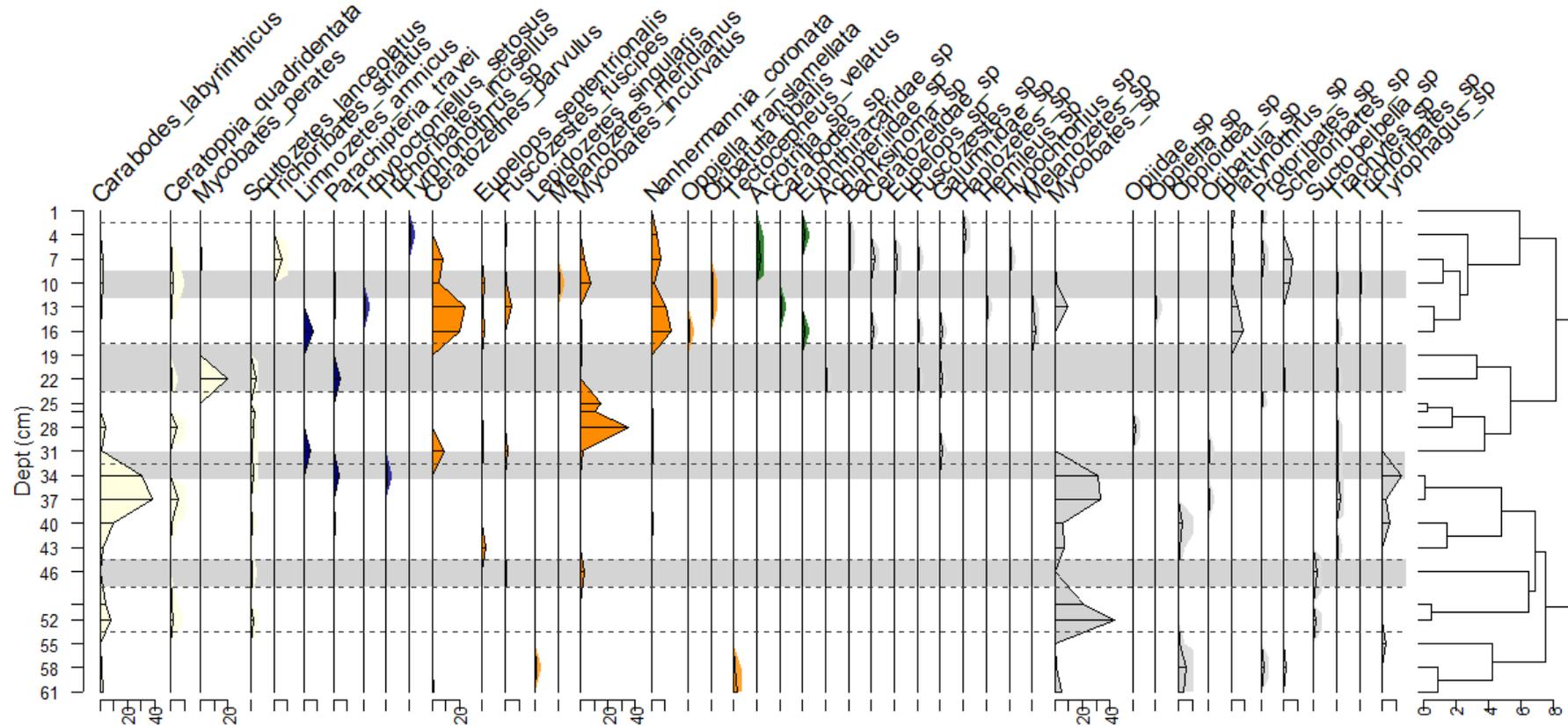


Figure 49 Oribatid mites diagram

3.3. Assemblages through time

3.3.1 Oribatids

Oribatids assemblages through time were subdivided in two principal period that subdivided themselves in a total of eight period, one of which was subdivided in two sub period, each named "O" with a number from one to eight, one being the oldest period (Fig. 49). The first main period from 2355 to 1193 BP (61 to 32 cm) appears to be overall dry and cold. The main oribatid species observed during this period are xerophilic cold resistant species. The second main period, from 1193 BP to present era (32cm to 0cm) appeared overall warmer and wetter with mesophilous and hygrophilous species characterizing the assemblages.

▪ **O1: 2355 to 2125 BP (61-55cm)**

This period encompasses the oldest fraction of the core. It contains only a few oribatid mite specimens. Three species were recovered: *Carabodes labyrinthicus*, a xerophilic species (Melekhina, 2020; 2023; Melekhina *et al.*, 2021; Behan-Pelletier & Lindo, 2023), which was present throughout the period. Two mesophilic species, *Lepidozetes singularis* (Behan-pelletier & Lindo, 2023) and *Tectocephus velatus* (Behan-Pelletier, 1997; Erickson *et al.*, 2003; Mumladze *et al.*; 2013) are observed, the first makes a brief appearance while the second was decreasing in abundance and disappears for half of the period. The two mesophile species are not observed after this period. This is despite *Tectocephus velatus* being a highly generalist species (Behan-Pelletier & Lindo, 2023), found in a wide range of habitats, including bogs (Barreto & Lindo, 2021). Popp (1962) reported it from dense, dry Sphagnum in bog, and Donaldson (1996) found it most numerous in the hummock species *Sphagnum magellanicum*. No definitive conclusion from the presence of *T. velatus* is drawn herein, although Markkula & Kuhry 2020 considered it's presence with permafrost indicators strengthened their permafrost hypothesis. *Lepidozetes singularis* is known from cold environments and has proven cold adaptation, showing super cooling to -27C to -29C depending on habitat (Sømme, 1979). *Carabodes labyrinthicus* has been considered an indicator of past permafrost in similar context (Markkula, 2014) and avoiding open water habitats (Melekhina *et al.*, 2021). However, *C. labyrinthicus* shows "remarkably wide distribution both at the global scale and at the scale of local habitats" (Prinzing *et al.*, 2004), warranting caution in its use as a bioindicator. From these observations we propose that this period was cold and dry and had the possibility of permafrosted peat

▪ **O2: 2125 to 1769 BP (55-46cm)**

In this period, a slight increase of *Carabodes labyrinthicus* abundance was observed throughout the time zone, reaching a maximum around 52cm and then steadily decreasing until the end of the period. The punctual addition of two xerophilic species: *Ceratoppia quadridentata* (Melekhina, 2023) and *Scutozetes lanceolatus* were observed, synchronous to the maximum abundance of *Carabodes labyrinthicus* at 52cm deep. A high peak of an unidentified *Mycobates* sp. was also observed in this period, reaching its maximum at 52cm deep. Species of *Mycobates* are found in dry arctic, subarctic, and alpine microhabitats. *Scutozetes lanceolatus* is found in the boreal, subarctic to low arctic (Behan-Pelletier, 2010). The increase of *Carabodes* and other xerophilic species indicate an increased dryness. In a bog this could be interpreted as a lowering of the water table due to limited precipitation or by permafrost linked palsa formation that limited access to the water, at least locally, (Payette & Rochefort, 2001). The three species are common to lichen dominated habitats (Behan-Pelletier, 1997; Hågvar *et al.*, 2014; Melekhina, 2023) which are distinctive of drier peat bog. The decrease of abundance at the end of the period could indicate a warming and/or an increase in water availability.

It could be argued that the distinction between O1 and O2 is rooted more in statistical separation due to the inherent heterogeneity of assemblages so far in the past as the species ecology remains relatively stable through the two time zones.

▪ **O3: 1769 to 1728 BP (46-45cm)**

This first event was associated with the observation of three mesophilic species: *Eupelops septentrionalis*, *Fuscozetes fuscipes* and *Mycobates incurvatus* (Barreto & Lindo, 2021). Another notable characteristic of the event was the absence of *Carabodes labyrinthicus* and other *Mycobates* sp.. However, *Scutozetes lanceolatus* was observed. The disappearance of xerophilic species and observation of mesophilic species could be linked to permafrost thawing and thermokarstic pool formation. The mesophilic species here like *Fuscozetes fuscipes* are hygrophilic mites associated with wet sub-habitats (Jacot, 1935; Madge, 1964; Melekhina *et al.*, 2021). While the three mesophilic species are also known from cold conditions (Borcard & Vaucher-von Ballmoos, 1997; Block, 1979; Sømme, 1979; Heggen, 2010; Behan-Pelletier & Lindo, 2023) the hypothesis of their presence being linked to a particularly cold event was discarded as such an event would not have ruled

out *Carabodes labyrinthicus* which is known for supercooling capacity (Sømme & Conradi-Larsen, 1977) and sub-polar habitat (Melekhina *et al.*, 2021). Event O3 we propose was a warmer event linked to wetter conditions.

▪ **O4: 1728 to 1193 BP (45-32cm)**

This period was dominated by a large number of *Carabodes labyrinthicus* that increased and hit a maximum at a depth of 37cm and then abruptly decreased. Synchronous with the *C. labyrinthicus* maximum, *Ceratoppia quadridentata* was observed. *Scutozetes lanceolatus* are present in the same time as the dominant period of *Carabodes labyrinthicus* (40-34cm) with a slight increase at the end of the period around 34 cm deep. Similarly to O2 and O3. *Mycobates sp.* abundance seems to be synchronized with that of *Carabodes labyrinthicus*. The dominance of *Carabodes labyrinthicus* in this period echoes the cold and dry conditions of O1 & O2. This was strengthened by the presence of other xerophilic species like *Ceratoppia quadridentata* and *Scutozetes lanceolatus* at the peak of *Carabodes labyrinthicus* abundance. While the unidentified species of *Mycobates* could not be associated with a specific ecology, it should be noted that it probably has an ecology resembling that of *Carabodes labyrinthicus* as their abundance mirrors one another.

▪ **O5: 1193 to 1151 BP (32-31cm)**

Analogous to O3, O5 was associated with a decrease of xerophilic species and increase of hygrophilous ones but here in greater proportions. *Carabodes labyrinthicus* displayed a sharp decrease from being the most numerous species in the whole dataset to its disappearance in a short time span. Another xerophilic species, *Scutozetes lanceolatus* remained, but in low abundance and displaying a decrease during the event. Synchronously, the observation of hygrophilous species was noted with species associated to wetter habitats: *Fuscozetes fuscipes* (Jacot, 1935; Madge, 1964; Melekhina *et al.*, 2021), *Ceratozetes parvulus* (Seniczak & Seniczak, 2021; Mumladze *et al.*, 2013), *Trichoribates incisellus* and *Parachipteria travei* (Behan-pelletier & Lindo, 2023) or semi-aquatic species such as *Limnozetes amnicus* (Larson & House, 1990; Erickson *et al.*, 2003). By contrast with other species of *Limnozetes* from northeastern North America *L. amnicus* is associated with cool running water (Behan-Pelletier, 1989). The other mesophilic species, like *Eupelops septentrionalis*, albeit not associated with aquatic habitats, are associated with peatlands (Barreto & Lindo, 2021), and therefore lean toward

wetness more than to a xerophilic dominated assemblages. The ecology of *Ceratozetes parvulus* in a mixed bog system was studied in Norway and it showed a preference for hummock over hollows among bog microhabitats (Seniczak & Seniczak, 2021). This assemblage of species, like in O3, could be associated with a brief warming event that generated pools and run-offs in the habitat, and thus overall, a greater diversity of peatland microhabitats. The greater number of species and variation in abundances may be as much linked to the amplitude of the event as to the more recent conditions of the assemblage and therefore we draw no conclusion on abundance.

▪ **O6: 1151 to 770 BP (31-22cm)**

The O6 period was complex as it was dominated by *Mycobates incurvatus*, a species first described from moss and lichen (Behan-Pelletier, 1994). It is primarily known from drier non-peatland habitats (Behan-Pelletier, 1994), it is absent from both bog and fen habitats studied by Barreto & Lindo (2021) and Barreto *et al.* (2023). This species appeared slightly in the previous event but spiked within this period with a maximum at 28 cm deep. The hydrophilic species that characterized the preceding event are still present at the beginning of the period, namely *Ceratozetes pavulus* and *Fuscozetes fuscipes*, but disappeared quickly which support drier times during this period. This was consistent with the xerophilic *Carabodes labyrinthicus* and *Ceratoppia quadridentata* also observed at the beginning of this period, yet in small abundance and up to 26cm deep, and *Scutozetes lanceolatus* also was present throughout the period. Despite their very low abundance, *Nanhermannia coronata* was present for most of the period and is a known inhabitant of raised bogs (Seniczak & Seniczak, 2023). These authors noted the wide ecological tolerance of this species for moisture, being found in different bog microhabitats such as hummocks, lawns, and the transition zone between hummock and hollow, this assemblage would indicate much drier peat habitats.

▪ **O7: 770 to 642 BP (22-19cm)**

This event was dominated by a spike of the xerophilic *Mycobates perates* a boreal species known from northeastern and northwestern North America that inhabits dry moss and lichen microhabitats (Behan-Pelletier, 1994). Two other xerophilic species are present, *Ceratoppia quadridentata* and *Scutozetes lanceolatus*. We have no explanation for the shift between the presence of *M.*

incurvatus and *M. perates*. As with O7, the overall event leans toward a drier climate at this time.

▪ **O8: 642 to -71 BP (19-1cm)**

This period was twofold, and was not statistically divided, because there are dominant species throughout the period. The first half between 19 and 11 cm is called **O8.1** and a second from 10 to 1cm is called **O8.2** with a central event between 11 and 10 cm (258 BP).

The whole **O8** was characterized by the dominance of the bog associates *Ceratozetes parvulus* and *Nanhermania coronata* (Seniczak & Seniczak, 2023; Mumladze *et al.*, 2013). This period was also unique in having species associated with forest environments within peatlands: *Acrotritia sp.*, another species of Euphthiracaridae and an unidentified *Carabodes sp.*. This association reflects the diversity of Oribatida in any peatland (Barreto & Lindo, 2021) and could infer a humid period with some growth of shrubs and trees. *Carabodes labyrinthicus*, an indicator of drier conditions, was also present during most of the period in low abundance. A heterogeneity of microhabitats could explain this cohabitation. For instance, microtopography of the bog can create pronounced local gradient of hydrology (Payette & Rochefort, 2001) and such ecological cohabitation is known for oribatid mites in peat bog habitats where dry and humid conditions exist together (Popp, 1962; Markkula & Kuhry, 2020; Barreto *et al.*, 2021). The whole period was marked with variation and was subdivided in two distinct episodes.

The first one, **O8.1**, was marked by the presence of the semi-aquatic species *Limnozetes amnicus* (Larson & House, 1990; Erickson *et al.*, 2003), the aquatic *Trhypochthoniellus setosus* (Behan-Pelletier & Lindo, 2023) and hygrophilous species like *Fuscozetes fuscipes*. The sub period was also marked by a greater abundance of the peatland dominating *Ceratozetes parvulus* and *Nanhermania coronata*. A constant presence of *Eupelops septentrionalis*, a peat bog species, also is noted. All this provides evidence for the beginning of Z5 as a warmer and wet period.

The transition between **O8.1** and **O8.2** was associated with the presence of several species for brief periods and variation in abundance of other species. The species occurring are mesophilous species: *Melanozetes meridianus*, *Mycobates incurvatus*, *Oribatula tibialis* and *Eupelops septentrionalis* as well as the hygrophilous *Parachipteria travei*, common to many peatland habitats in the boreal

and subarctic (Borcard & Vaucher-von Ballmoos, 1997; Barreto *et al.*, 2021; Behan-Pelletier & Lindo, 2023). *Oribatula tibialis* is known to resist cold and dry condition but to be sensitive to warmth (Siepel, 1996) and *Eupelops septentrionalis* which is known for cold subarctic habitats (Behan-Pelletier, 1999; Heggen, 2010) and cold adaptation with a supercooling ability of -28°C (Block, 1979). Along with the decline of hygrophilous dominant species, the E4 event is a colder and drier period.

Following this cold and dry event the hygrophilous *Ceratozetes parvulus* and *Nanhermannia coronata* increase in abundance, which could be interpreted as a warming. The hydrophilic and aquatic species of the first half of the period are absent, although the hygrophilic *Tyrphonoethrus sp.* (Behan-Pelletier & Lindo, 2023) and *Fuscozetes fuscipes* are present. Xerophilic species are more frequent, such as *Carabodes labyrinthicus*, *Ceratoppia quadridentata*, *Trichoribates striatus* and *Mycobates perates* (Behan-Pelletier & Lindo, 2023). Overall, this most recent period appears drier than the previous one but seems to be characterized by a mosaic of different conditions. As mentioned before, this pattern was most likely due to local micro gradient between micro topographic variations yet it must be considered that such variation could also have been present in the past but that older samples were less representative of the whole community and therefore blurred such patterns.

3.3.2 Macrofossils

The macrofossils assemblages through time were split in three great periods that were subdivided in ten sub periods. Each period was named “**M**” with a number from one to three, one being the oldest period and a second number for the sub period, following the same logic. The **M-I** period was not treated here, due to highly degraded materials. Only two samples at the bottom of the core were studied, at 75-76 and 88-89cm. Those two levels contained highly degraded material among which only three seed of *Chamedaphne calyculata* and one of *Andromeda glaucophylla* were identifiable, indicating the habitat was already a bog. The results for the identified macrofossils (Fig. 50) and the characterized vegetal matrix (Fig. 51) are presented together.

The detailed study focused on the upper 44cm of peat which was divided in two main zone: **M-II** from 44 to 16cm and **M-III** from 16cm to the top of the core. Within those two main zones, ten sub-period were identified.

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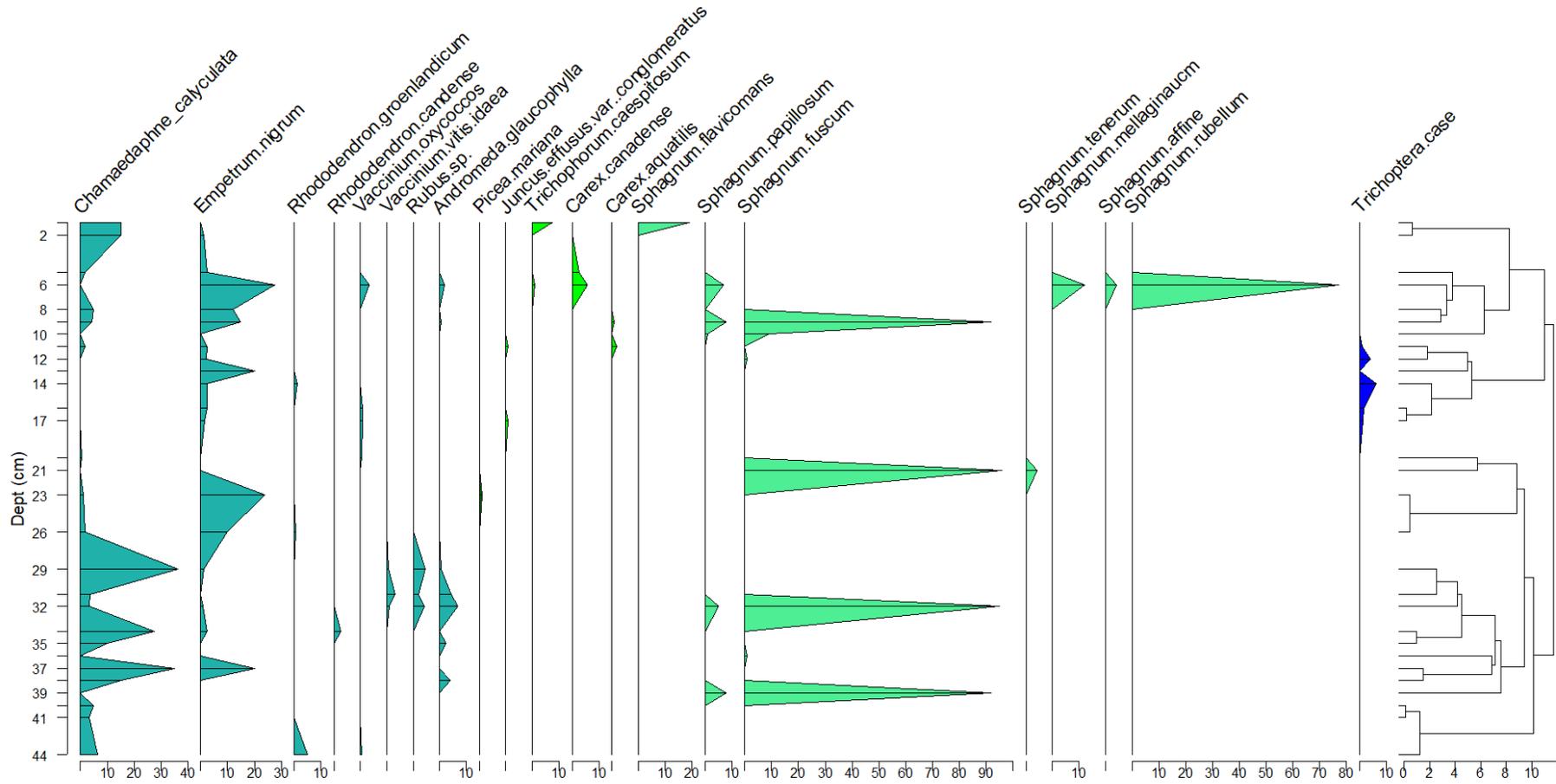


Figure 50 Vegetation macrofossils diagram

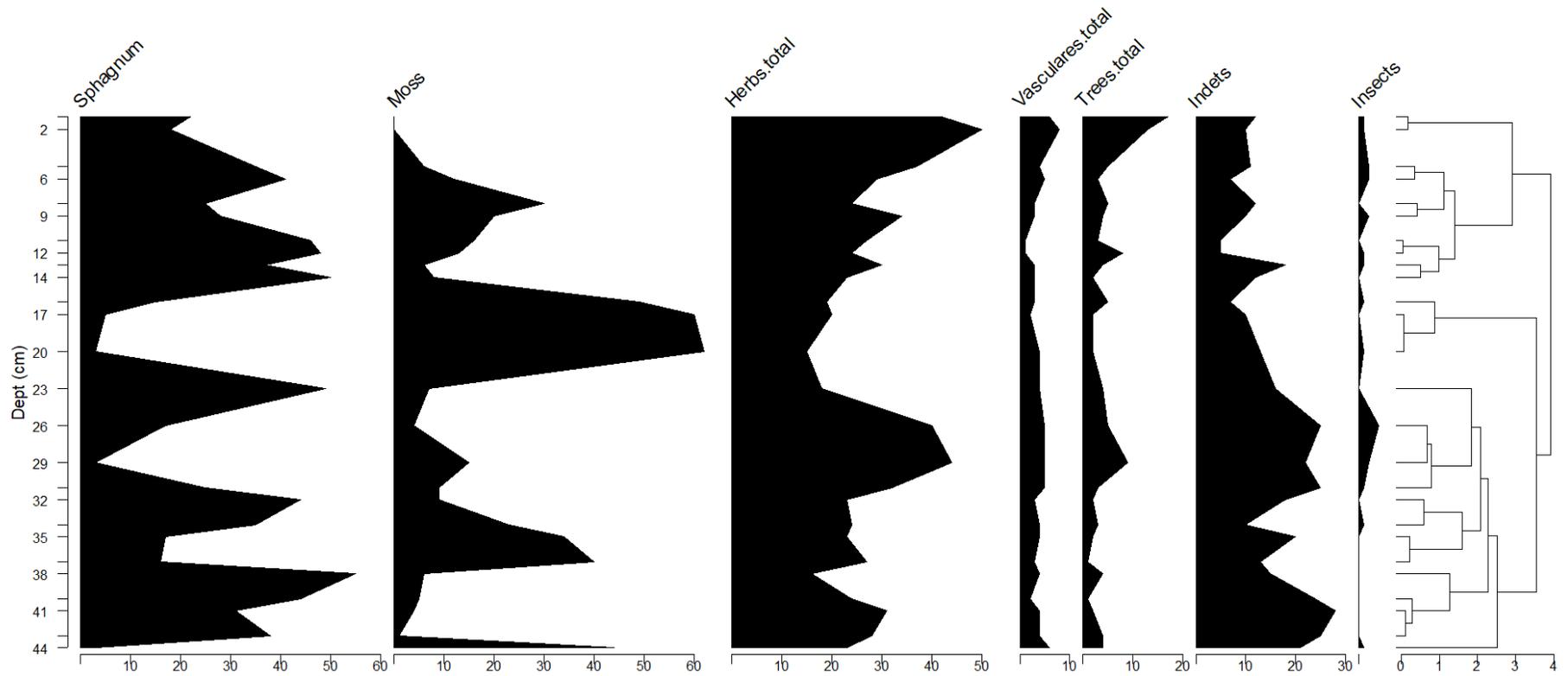


Figure 51 Vegetale matrix diagram

In the **M-II** zone, 254 macrofossils artefact from comprising 12 taxa were analyzed. Most of those were from the *Ericaceae* and all were at least tyrphophile. *Sphagnum fuscum* was the main sphagnum moss in the M-II period. Favoring the drier of ombrotrophic bog, *S. fuscum* creates hummoks (oftenly associated with *S. papillosum*), growing further away from the water table and therefore creating a drier microhabitat for the *Ericaceae* (Fleurbec, 1987; Gauthier 2001).

▪ **M-II-1: 1688 to 1566 BP (44-41 cm)**

The first sub-zone consisted of a single sample containing only seeds of *Ericaceae* (*Rhododendron groenlandicum*, *Chamaedaphne calyculata*, *Vaccinium oxycocos*). *Chamaedaphne calyculata* was known from the ombrotrophic bog and to be well-established on hummocks sphagnum, the drier part of the wet habitats (Kurmis *et al.*, 1986; Pearce *et al.*, 1988; Marie-Victorin *et al.* 2002). This species can also be typical of maritime areas with extreme temperature variations (Brown *et al.*, 1988). *Rhododendron groenlandicum*, well registered in this subzone, may have created a shrub cover on the bog, limiting the development of *Chamaedaphne calyculata*, which is very heliophilic (Marie-Victorin *et al.*, 2002). *R. groenlandicum* was amongst the main shrubs within ombrotrophic bog (Fleurbec, 1987; Payette, 2018) as well as *Vaccinium oxycoccus* also very common in sphagnum bog (Le Gallo, 1954; Marie-Victorin *et al.*, 2002). *Vaccinium oxycoccus* is also a good indicator of swamps or wetlands, which often grow on hummocks in peat bogs (Hitchcock & Cronquist, 1964) but more in mesothermic areas (Matthews, 1992a). Overall, the dominance of *Sphagnum* and the hydrophilic species indicated a relative wet period.

The small number of species encountered during this period may be associated with the taphonomic limitations.

▪ **M-II-2: 1566 to 1443 BP (41-38 cm)**

This period was marked by the presence of *Sphagnum* and low abundances of other mosses at first (41-38cm). This relative importance between sphagnum and other mosses could be interpreted as wetter times. The herbs/sphagnum fluctuation could be linked to a natural development of vegetation on a bog as the sphagnum creates a viable environment. The following decrease could be linked to an increased water table that was detrimental to herbs (Strack *et al.*, 2004) or a

less stable water table (Breeuwer *et al.*, 2009). It could also be the result of an increased temperature that favored sphagnum in the competition with herbs (Keuper *et al.*, 2010).

▪ ***M-II-m3: 1443 to 1151 BP (38-31 cm)***

In details, the abundance of *Chamaedaphne calyculata* oscillates between spikes (36 and 32cm) and disappearances, a pattern that was observed synchronously with variable abundance in *Empetrum nigrum* and inverted with the sphagnums. *Empetrum nigrum* although tolerant of a wide range of conditions, is more likely to be found in better-drained areas, on peat hummocks (Fleurbec, 1987; Gauthier, 2001; Le Gallo, 1954; Matthews, 1992b; Marie-Victorin *et al.*, 2002), away from the water table in the dryer conditions (Kurmis *et al.*, 1986; Pearce *et al.*, 1988; Breeuwer *et al.*, 2009).

Rhododendron groenlandicum and *Vaccinium oxycocos* were not observed. The absence of those two taxa favored *Andromeda glaucophylla* then *Empetrum nigrum* and *Rhododendron canadense*, indicating acidic substrate and peat hummocks (Le Gallo, 1954; Fleurbec, 1987; Marie-Victorin *et al.*, 2002). *Andromeda glaucophylla* is also a taxa that is known to develop just after fires in peat bogs, following the development of a sedge mat. As the bog dried out, or as it developed through the accumulation of sphagnum moss, it moved away from the water table. *Andromeda glaucophylla* was replaced by *Chamaedaphne calyculata* (Flinn & Wein, 1977; 1988; Taylor, 2007). The period between 38 and 31 cm was therefore drier, with a moss dominated matrix and might have seen a fire event that drove down the Ericaceae species. Some charcoals were observed.

The very end of the period was marked by the return of *Sphagnum*, indicating a return to a wetter period.

The first *Sphagnum* identified to species level here were *Sphagnum fuscum* and *Sphagnum papillosum* with *S. fuscum* being the main one in this sub-period.

▪ ***M-II-m4: 1151 to 940 (31-26 cm)***

This subzone was characterized by a global decrease of both sphagnum and other mosses. It was characterized by an increased richness events. *Chamaedaphne calyculata*, while discrete at the beginning, was the specie that displayed a spike at the end of the period (the greatest recorded in the whole

core). This dynamic is opposed to the one observed in *Andromeda glaucophylla* abundance. Those two *Ericaceae*, with *Vaccinium vitis-idea*, some rare *Empetrum nigrum* and *Rubus cf. fruticosus/idaeus* formed the woody assemblages of this sub-period. The seeds remains of *Rubus* were fragmented but according to current botanical data of the archipelago (Arsène, 1927), the probable species can be narrowed down to *Rubus idaeus* or *Rubus recurvicaulis*, associated to rather wet habitats (Le Gallo, 1954; Marie-Victorin *et al.*, 2002). This type of assemblage may correspond to lower water table that could have favored shrub development like the observed *Vaccinium* species (Hall & Shay, 1981; Carroll & Bliss, 1982; Breeuwer *et al.*, 2009). *Vaccinium* then declines after the Ericaceae stage (Tirmenstein, 1991). The *Rubus* is often associated with disturbed soils, but above all with phases of recolonization with an evolution towards shrub development (Payette, 2015; Boland, 2017).

A shared characteristic of *Vaccinium vitis-idaea*, *Empetrum nigrum* and *Chamaedaphne calyculata* is to grow preferably on dry hummocks within the peat bog (Marie-Victorin *et al.*, 2002). Adding the low quantity of *Sphagnum*, increase of *Ericaceae* and herbs all together led to conclude that the period was relatively dry after the hydrophilic short event at the end of the last period.

▪ **M-II-m5: 940 to 813 BP (26–23 cm)**

This short period was characterized at the start by a peak of *Sphagnum*. Mosses had a low development at the beginning but grew throughout the period. The steady increase of *Empetrum nigrum* associated to the spike of *Sphagnum fuscum* indicated a wet time where *Sphagnum* development allows for hummocks that benefit taxa like *Empetrum* that need the drier niche hence created (Matthews, 1992b). The wetness of the period was also highlighted by the first observation of *Sphagnum tenerum*, a hygrophilous species (Ayotte & Rochefort, 2019). Likewise, the first record of a tree species was noted with *Picea mariana*.

▪ **M-II-m6: 813 to 514 BP (23–16 cm)**

This period was marked by a strong turnover between sphagnum and moss with the highest density of moss recorded in the sequence, highlighting a relatively dry period. A few *Vaccinium oxycoccos* were observed. An early colonizer in

secondary succession, *V. oxycoccos* thrives on moist soils (Klinka *et al.*, 1989; Matthews, 1992a) indicating the relative nature of the dryness observed.

Likewise, *Juncus* were observed for the first time in the sequence. This taxon indicative of moist habitats (Marie-Victorin *et al.*, 2002) highlights a habitat mosaic with wetter niches, perhaps linked to microtopography (Payette & Rochefort, 2001).

▪ **M-III-m1: 514 to 429 BP (16–14 cm)**

188 macrofossils corresponding to 16 taxa were identified in the upper zone **M-III**. The main pattern observed here are a receding in the *Ericaceae* while an increased abundance of herbaceous led to conclude to a development toward a fen (Payette, 2001). *Empetrum nigrum* remained present, indicating dry habitat on hummocks.

The two samples that formed the first sub-period (**M-III-m1**) were characterized by an abrupt decrease of mosses and equivalent increase of *Sphagnum*, indicating an increase of wetness. *Vaccinium oxycoccos*, *Empetrum nigrum* and *Rhododendron groenlandicum* highlight a poor habitat of ombrotrophic bog (Fleurbec, 1987; Gauthier, 2001). This wetter time associated with the *Ericaceae* species appears similar in dynamics to M-II-5.

▪ **M-III-m2: 429 to 172 BP (14–8 cm)**

This period was characterized by an abundance of *Sphagnum* and fluctuating levels of mosses. It started with a spike of *Sphagnum fuscum* with some *Sphagnum papillosum*, *Carex aquatilis*, *Andromeda glaucophylla* and a cohabitation of *Empetrum nigrum* and *Chamaedaphne calyculata*. The spike of *Empetrum nigrum* could be linked with a dry event, followed by wetter conditions since *Juncus* and *Carex* were added (Payette, 2013).

Therefore, the environment was rather humid, with hygrophilous taxa. The end of this period was marked by the abrupt decrease of *Empetrum nigrum* and the discreet return of *Chamaedaphne calyculata* due to wetter conditions.

A succession was observed, starting at the beginning of the period with *Juncus effusus* var. *conglomeratus* and *Vaccinium oxycoccos* which disappeared and *Rhododendron groenlandicum* was observed briefly just before the *Empetrum*

nigrum spike. *Rhododendron groenlandicus* also thrives in sphagnum peat bogs in open environments (Gauthier, 2001). With a root system deeply rooted in the soil, *R. groenlandicus* is known to be little affected by fire (Laberge-Pelletier, 2007), which explains its brief rise, followed by *E. nigrum*, as species known to be favored post-fire. Then, just after the decrease of *Empetrum nigrum* a small amount of several species was observed, *Chamaedaphne calyculata*, *Juncus effusus* var. *conglomeratus*, *Carex aquatilis*, *Sphagnum fuscum* and *S. papillosum*. *Juncus*, species known to be particularly important in wetter conditions (Le Gallo, 1954; Payette, 2013).

▪ **M-III-m3:172 to -44 BP (8-3 cm)**

This period was marked by its richness, succession of *Sphagnum*, the dominance of *Empetrum nigrum* and the dynamics of *Chamaedaphne calyculata*.

Several indicators would lean toward a minerotrophic peat bog like *Carex canescens*, *Carex aquatilis* or *Scirpus cespitosus* (Payette, 2001).

Then a spike of *Sphagnum rubellum* accompanied by *S. magellanicum*, *S. affine* and *S. papillosum* marked an event with *Carex canescens* var. *disjuncta*, *Andromeda glaucophylla* and *Vaccinium oxycoccos*, which are synchronous to the maximum abundance of *Empetrum nigrum* and a decrease of *Chamaedaphne calyculata*. *Sphagnum rubellum* was observed and is known to be a highly hygrophilous species (Ayotte & Rochefort, 2019) which development increase with the rise of the water table (Antala *et al.*, 2022). Likewise, *S. papillosum* is known to thrive with increased precipitation (Krebs *et al.*, 2016).

It could be concluded that **M-III-m3** was a humid period which would have boosted the sphagnum production and reset the dynamics of the bog by removing, through competition, species that grow on top of hummoks. *Sphagnum* tends to increase more rapidly than others and wins competition when favored (Dorrepaal *et al.*, 2004; Keuper *et al.*, 2010). Those taxa among *Sphagnum rubellum*, *S. affine*, *S. magellanicum*, *S. rubellum* replaced *Empetrum nigrum* and *Vaccinium oxycoccos*. The context lean toward bogs or poor fens with wet hollows (Ayotte & Rochefort, 2019; Faubert, 2013).

ATLANTIC SUBARCTIC PEAT BOGS ECOLOGY THROUGH A TWO MILLENNIUM DYNAMIC

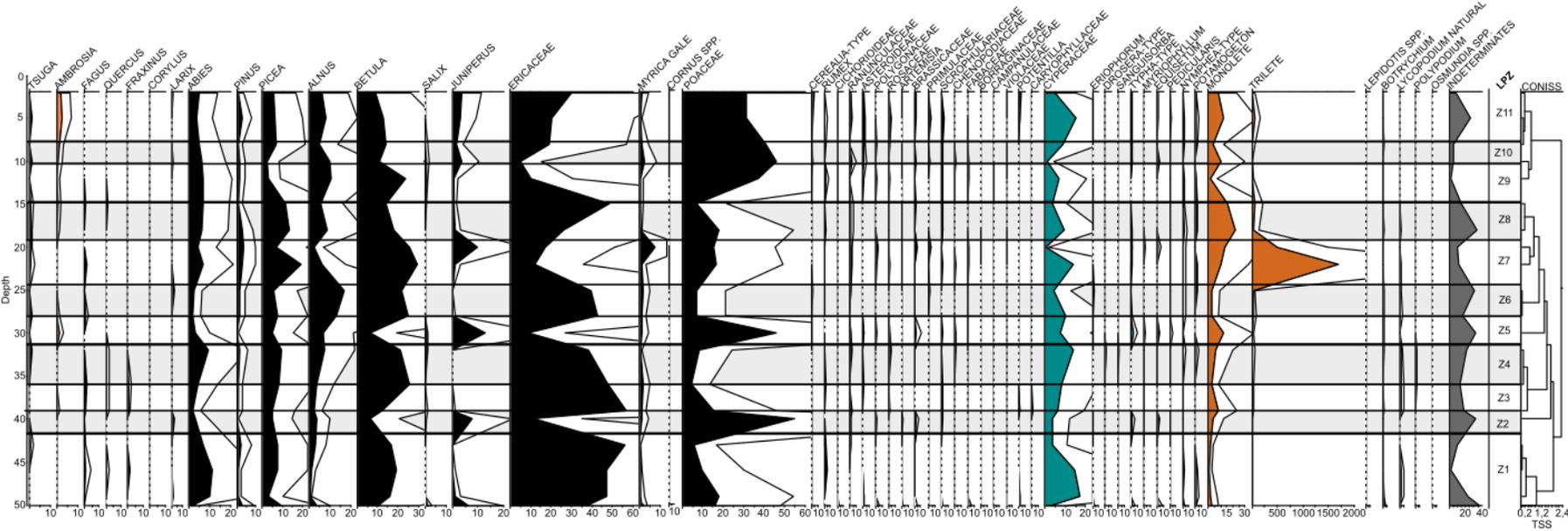


Figure 52 Pollen diagram.

▪ ***M-III-m4: -44 to -71 BP (3-0cm)***

The most recent period was characterized by a decrease in *Sphagnum* and very low abundance of other mosses.

An increasing abundance of *Chamaedaphne calyculata* and a discreet presence of *Empetrum nigrum* correspond to the pattern of Ericaceae in the subzone. *Scirpus cespitosus* indicated wetness within the period (Gauthier, 2001) but likely associated with a low water table (Strack *et al.*, 2004). The immediate environment is made up of fairly dry open peat bogs.

3.3.3 Palynology

The pollen assemblages through time were subdivided in eleven zones, each named "P" with a number from one to eleven, one being the oldest LPZ (Fig. 52).

The pollen taxa dominating were Ericaceae, Betulaceae (*Betula papyrifera*, *B. alleghaniensis*), Poaceae, *Alnus* (cf. *crispa*), Cyperaceae. More occasional *Abies balsamea*, *Juniperus communis*, *Salix uva-ursi*, etc. Furthermore, exogenous taxa have been identified in the assemblages (*Quercus*, *Corylus*, *Fraxinus*, *Tsuga*, *Ambrosia*, *Fagus*), probably from Newfoundland or elsewhere.

▪ ***P1: 1928 to 1607 BP (50-42 cm)***

The environment was largely dominated by woody taxa, including Ericaceae, birches, alders, some grasses, and Cyperaceae (Bosseaux, 1965; Matthews, 1992a; 1992b; Muller, 2010; Philippenko *et al.*, 2021). Ericaceae were the most abundant (60%), followed by *Betula*, which gradually increased and then stabilized (20%). By associating with Ericaceae, as well as *Sphagnum fuscum*, these birches can experience relatively drier conditions locally, favoring the shrubby development of meso-xerophilic taxa (Marcisz *et al.*, 2020; Keuper *et al.*, 2010). *Picea* showed a slight decrease in representation at the beginning of the zone before stabilizing at 10%. Juniper (*Juniperus*) was also present primarily at the beginning of the zone (8%) before disappearing. There appeared to be a negative relationship between the assemblage of *Juniperus-Myrica-Poaceae* and Ericaceae-*Betula*. At the beginning of the zone, the decrease in *Myrica* and *Salix* may have indicated a decrease in moisture in the environment (Cleveringa *et al.*, 2006; Roy *et al.*, 2018; Bhiry *et al.*, 2016). Balsam fir (*Abies cf. balsamea*) shown an increase

at the beginning of the sequence (+10%), contrasting with the behavior of pine (*Pinus*) and spruce (*Picea*). According to Wu *et al.* (2023), the slight increase in balsam fir may have resulted from a gradual closure of the boreal forest. Some rather mesophilic exogenous taxa (*Quercus*, *Fraxinus*), probably originated from inland to the south (Campbell *et al.*, 1999; Rousseau *et al.*, 2008; Desmet & Brouillet, 2013), were recorded. The low percentages of *Poaceae* may indicate limited open spaces (Poska *et al.*, 2004; Mazei *et al.*, 2020). Thus, the closure of the environment seems to have been accompanied by a slight drying or increased drainage. From the increased wooded pattern, it can be concluded that, on a more regional scale, the climate was rather temperate.

▪ **P2: 1607 to 1484 BP (42-39 cm)**

This new zone witnessed a very rapid decline in woody taxa, with juniper (8%) and larch (5%) being exceptions. The representation of grasses exploded to reach 60%. The diversity of herbaceous plants was affected by these changes. *Cyperaceae* were in sharp decline (15%). Conditions were therefore drier in a more open environment. *Juniperus communis* is a xero-thermophilic taxon in boreal zones (Vilčinskis *et al.*, 2016) and can thrive after fires on shallow and drained soils (Tolonen, 1985), often accompanied by other pioneer taxa such as *Artemisia*, which developed here (Roy *et al.*, 2018). Micro-charcoals have been identified just before the start of this zone 2. It is possible that a fire may have facilitated this opening of the environment and drainage (Lavoie & Sirois, 1998; Danneyrolles *et al.*, 2022).

▪ **P3: 1484 to 1360 BP (39-36 cm)**

Alnus, *Abies*, and *Picea* were gradually expanding (+5%), while *Juniperus* is less present. At the local scale, *Betula* and *Alnus* suggested sediment consolidation after a fire event, with progressive paludification (Waller & Early, 2015). *Picea*, especially *P. mariana*, is known to quickly establish itself on burned soils and can slow down the return of wetter environments, or even paludification of the bog (Viereck, 1983; Fryer, 2014; Villeneuve-Simard & Boudreau, 2016; Galka *et al.*, 2018). Additionally, the increase in thermophilic taxa like *Alnus*, accompanied by a greater diversity of herbaceous plants (*Ranunculaceae*, *Rosaceae*, *Scrophulariaceae*), may indicated environments in a more temperate context

(Brown *et al.*, 1988; Islam *et al.*, 2003; Brugger *et al.*, 2019). Exogenous taxa were more present, especially in terms of diversity (<5%), indicating stronger winds from the south (Solignac *et al.*, 2011). The increase in hydrophilic *Cyperaceae* (+10%) in this zone strengthens the interpretation of a progressive climatic improvement.

▪ **P4: 1360 to 1193 BP (36-32 cm)**

Hydrophilic-helophyte taxa continued their progression, dominated by *Cyperaceae* (20%). Taxonomic diversity was higher. Indeed, *Eriophorum*, *Sanguisorba*, *Drosera*, and other aquatic taxa (*Thalictrum*, *Pedicularis*, *Potamogeton*) were present, indicating local paludification (Payette, 2013; 2015; Waller & Early, 2015). *Potamogeton polygonifolius*, native to St-Pierre, was confined to oligo-mesotrophic running water environments, and *Potamogeton confervoides* developed more in peat bog pools with *Sparganium* (Arsène, 1947) or *Typha*-like environments, as it was observed this sequence. *Drosera* were observed and are known to be found in contexts of oligotrophic raised bogs or wet peat among pioneer taxa (Muller & Etcheberry, 2006). This event may have been favored by a rapid colder and wetter change, promoting the expansion of wetlands (Seppä & Poska, 2004). Changes also shown a greater abundance of conifers (*Abies*, *Picea*, *Pinus*), at the expense of *Betula* or *Ericaceae* in developing broadleaved-spruce communities, accompanied by the expansion of waterlogged forests (Novenko *et al.*, 2018).

▪ **P5: 1193 to 982 BP (32-27 cm)**

The environment abruptly opened up (drop in *Betula*, *Ericaceae*, *Picea*, *Abies*, *Pinus*), with the same dryness indicating assemblage as in P2 with *Juniperus* (10%). *Poaceae* (50%) once again dominated, likely indicating a context of fire, an idea strengthened by the observation of macro charcoal. A slight peak of *Ambrosia* was also notable around 1109 BP (30 cm).

▪ **P6: 982 to 855 BP (27-24 cm)**

This zone was characterized by a sharp increase in woody plants associated with the wetland, starting with the *Ericaceae*. Birch and alder were also greatly expanding while *Juniperus* disappeared. The herbaceous layer was correspondingly

declining, with grasses dropping to 10%. *Cyperaceae* were declining as well. Helophyte-aquatic taxa were less diverse and rather decreasing.

The decline of *Cyperaceae* allowed aquatic taxa to develop locally in the context of water pools near the deposition site (Mroczkowska *et al.*, 2021). Again, it was possible that fires may have temporarily opened up the environment. Hygrophilic and aquatic taxa may have escaped this disturbance with their root system in the water. *Abies* often develops after a decrease in birch or following fires in a reconquering open environment dominated by herbaceous plants (Quer, 2021). The context was quite temperate, with *Alnus* and *Abies*, thermophilic taxa, also following this trend (15%) (Van Geel, 1972; Querrec, 2014). However, rather hygrophilic taxa were becoming less present, such as *Salix*, *Larix*, *Myrica gale*, and *Cyperaceae* (Elliott-Fisk, 1988; Cleveringa *et al.*, 2006).

▪ **P7: 855 to 642 BP (24-19 cm)**

The zone was characterized by a significant increase in the percentages of *Betula* (30%), *Juniperus* at the top of the zone (10%), *Picea* (20%), and *Poaceae* (20%), while alder was decreasing. Herbaceous plants are generally declining but increasing in diversity (*Ranunculaceae*, *Polygonum*, *Brassicaceae*, *Boraginaceae*...). *Cyperaceae* were sharply increasing until experiencing a sharp drop at the top of the zone.

It was then that aquatic plants developed, and *Myrica* and *Juniperus* displayed peaks in representation. As thermophilic taxa declined, colder conditions in a more open environment were established (Laberge-Pelletier, 2007). Associated with *Artemisia*, these taxa developed on dry soils with little organic matter (Tolonen, 1985). Conditions were relatively dry on a larger scale as the peak of *Myrica* was quite significant (10%), without being correlated with *Salix* or herbaceous hygrophiles. Finally, aquatic taxa remained stable (*Nymphaea*, *Typha*-type).

▪ **P8: 642 to 472 BP (19-15 cm)**

Locally, there was a significant increase in *Ericaceae*, and in the surrounding areas, conifers followed the same trend (*Picea* at 20% and *Pinus* at 5%). This indicated a drying trend towards an "afforestation stage" (Remy *et al.*, 2019; Mazei *et al.*, 2020; Quer, 2020) on a rather regional scale. These assemblages suggested

an increase in forest cover. Accompanied by *Alnus*, hygrophilic taxa including Cyperaceae increased before decreasing at the top of the zone, along with the diversity of aquatic plants and other herbaceous species. The presence of these taxa indicated slightly more humid and mesophilic conditions (Le Gallo, 1954) on the scale of the peatland, likely with patches of ponds in depressions.

▪ **P9: 472 to 258 BP (15-10 cm)**

Exogenous taxa, mostly thermophilic, were rare in this zone, as are hygrophilic taxa. Thus, cold and dry conditions seem to prevail after 237 BP (10 cm), still during the climatic deterioration of the Little Ice Age (Grove, 2001; Viau *et al.*, 2012). Near the Saint Lawrence River, Wu *et al.* (2023) proposed the regional signature of the Little Ice Age through these same pollen taxa.

▪ **P10: 258 to 172 BP (10-8 cm)**

Ericaceae dropped drastically, going from 50% to 5%. *Picea* and *Abies* also decreased, but to a lesser extent (-5% maximum). In contrast, *Poaceae* significantly expanded. *Rumex* and *Artemisia* were part of the herbaceous assemblage. These conditions thus indicated a dry and cold climate, also impacting hygrophilic taxa, which decreased. *Betula* decreased at the top of the zone while *Juniperus* and *Picea* increased. The boreal forest remained quite open (Blondeau *et al.*, 2004).

▪ **P11: 172 to +71 BP (8-2 cm)**

At the top of the sequence, this zone hosted numerous woody plants as well as a wide diversity of herbaceous species. *Ericaceae* were predominant (30%), accompanied by *Juniperus*, *Betula*, and *Alnus*. In the herbaceous layer, *Poaceae* were abundant (30%) and *Cyperaceae* were well represented. These drier conditions may have been favored by fires indicated by micro-charcoal levels in these layers. *Ambrosia*, a taxa exotic to Saint-Pierre and Miquelon, was higher compared to the rest of the diagram (5%). *Ambrosia* is also known to be favored in anthropized environments (Basset & Terasmae, 1962) and may be a signal of the activities of Native Americans or European settlers (Basset & Crompton, 1975). Other nitrophilous and weedy taxa (*Asteraceae*, *Rumex*, *Artemisia*, *Cichorioideae*), sometimes indigenous, were on the rise (5-8%) (Summerhayes, 1928; Bosseaux,

1965; Garneau, 2000; Etcheberry *et al.*, 2010; Novenko *et al.*, 2018; Marcisz *et al.*, 2020; Mazei *et al.*, 2020). In a more open environment, pollen grains of Cerealia-type defined by Joly *et al.* (2007) may result from introductions of European cultivated cereals, such as *Poa annua*, *Hordeum jubatum*, or *Sedum acre*, for example (Arsène, 1947).

These taxa may have been favored by human activities. The first Europeans arrived in Saint-Pierre or Newfoundland during the second half of the 16th century, primarily engaged in cod fishing (Aubert de la Rüe, 1932; Allaire & Holm, 2022) before establishing themselves permanently, with subsistence agriculture on the archipelago (Etcheberry *et al.*, 2010; Losier *et al.*, 2021; Auger *et al.*, 2022). This mosaic environment with taxa from the boreal forest, as well as bogs or meadows, does not appear to be solely impacted by climate. Human activities or even animal grazing could have allowed for the expansion of herbaceous taxa, including some nitrophilous, in diversity and quantity (Rowan & Faith, 2019).

4. DISCUSSION

The peat bog dynamics through time appears to have varied between wet and dry as well as warm and cold periods. Keeping things in perspective, dryness of the bog is relative to as much a bog can get dry and remains a bog (Rydin *et al.*, 2013), it is here used to describe low water table. Likewise, warmth here is also relative as the whole climate remains subarctic locally through a cool late Holocene (Brown Macpherson, 1982; Finkenbinder *et al.*, 2022). The following discussion will follow the synthetic time division that originated from the crossed analysis of consensus between the three proxies used (Fig. 53).

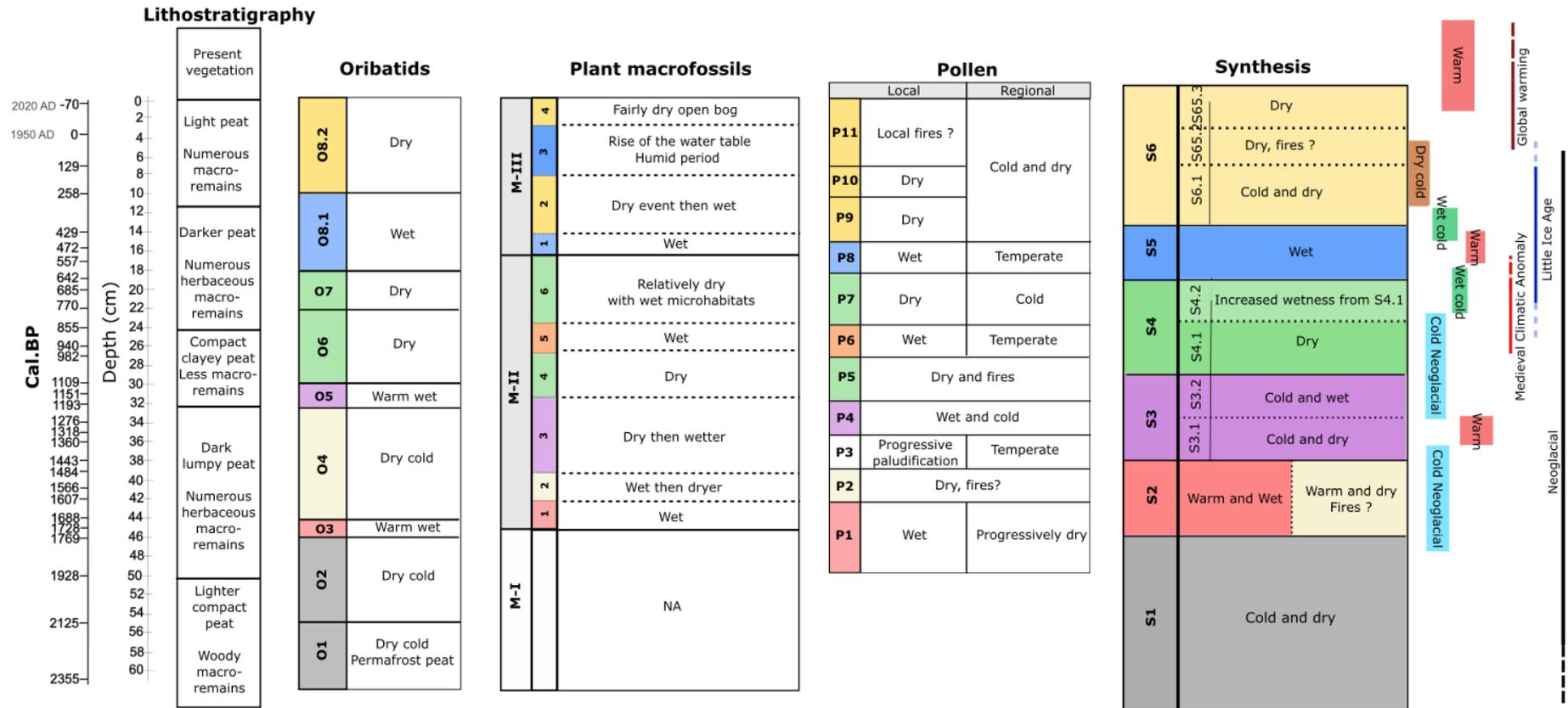


Figure 53 Synthesis of interpretations

4.1. S1: 2355 to 1728 BP cal.

The first temporal zone, the oldest of the sequence, was not covered by all model taxa as the macrofossils were too degraded and the pollen analysis didn't cover the zone below 1929 BP cal. From the only main indicator remains, the oribatida, the conclusion was that the period must have been cold and dry in Saint-Pierre as it was dominated by permafrost indicator *Carabodes labyrinthicus* (Markulla, 2014). The pollen data that overlap with the end of S1 concurred as they indicated dryness through a relatively lower amount of hygrophilous taxa. The time zone corresponds to the late neoglacial period which matches the observed response as it is described as a cooler period in the close Newfoundland region (Finkenbinder *et al.*, 2016; Sheldon *et al.*, 2016). Albeit the pollen indicates a regional temperate climate instead of a cold one as the other indicators suggest, it could be link to continental pollen signature as they can travel far (Williams, 2010) while the local climate is strongly under the influence of the sea with the cold Labrador currents (Finkenbinder *et al.*, 2022). Not much more is to be drawn from this time zone as the sampled degradation at these depths renders the samples rare and often unidentifiable.

4.2. S2: 1728 to 1566 BP cal.

This second period was characterized by a dichotomy between regional and local responses. While both appeared warm, the regional response appeared dry while locally the indicators leaned toward wet habitat. Wet habitats indication was brief within the sequence for oribatid and macrofossils. After the permafrosted bog suggested earlier, the warming here observed may have caused the apparition of thermokarstic pond (Payette & Rochefort, 2001) favoring hygrophilous species. Through the S2 period, the bottom of it coincides with the short warmer event highlighted by the Oribatid mites and macrofossil indicators. Among the oribatid it's the presence of meso-hygrophilous species and the decrease of the xerophilous permafrost indicator that led to that conclusion. The macrofossils indicators concurred with open bog species and a sphagnum dominance. Conversely, the pollen indicates a regional climatic pattern of dryness linked to a greater proportion open habitat. Therefor the rise in temperature alone associated to the creation of thermokarstic pond must be linked to the local increase hydrology. This short warmth period is coherent with regional paleoclimatic knowledge as it was

registered as a time of variable temperatures in the region (Finkenbinder *et al.*, 2022). The end of the period was associated with possible fire for there where traces of macrocharcoal in the core and pollen indicator revealing a dynamic compatible with post fire vegetation development. As the second half of the S2 period was associated with dryer condition as the small return of *Carabodes labyrinthicus*, the lowering dynamic of sphagnum in favor of other mosses in the macrofossils and the habitats opening registered in the pollen record. Such dry conditions are a known driver of natural fire in this context (Carcaillet *et al.*, 2001). The presence of *Carabodes labyrinthicus* contacted in the period might indicate that this fire event was not too intense as the species is a lichen feeder (Behan-Pelletier & Lindo, 2023) and lichen like the *Cladonia* spp. Found in the local habitats (Muller, 2010) tend to only suffer from a high level of intensity of fire (Johansson, 2006).

4.3. S3: 1484 to 1193 BP cal.

The S3 period is characterized by its cold climate as the three indicator taxa converged toward it. Nonetheless the period was subdivided into two sub-periods as they appeared to differ hydrology wise. This dichotomy was also strengthened by a consensus between the three indicators.

▪ S3.1: 1484 to 1318 BP cal.

This period appeared cold and dry locally. The oribatid mite's responses resemble the previous one with dominance of *Carabodes labyrinthicus* and strengthened by other xerophilic species. As before the possibility of permafrosted peat must be taken into account. The peak of abundance of *Carabodes labyrinthicus* was observed during this period. Likewise, the greater Ericacea vegetation strengthened this pattern in macrofossils. A dissension from the pollen here could be noted and explained by a scale sensitivity. Adding to the fact that the studied habitat is a peat bog, known to be more resilient to climatic variations (Keuper *et al.*, 2010), variations between the local indicators and the pollen are expected. Nonetheless, part of the species in the pollen register originated locally and appeared to indicate a post fire dynamic that could be linked to the S2 events. Perhaps the pollen signature was more affected by the post-fire dynamics and therefore blurred the possible response indicating climates and hydrology events.

▪ ***S3.2: 1318 to 1193 BP cal.***

This sub-period is marked by increased humidity. The oribatid assemblages showed a synchronous collapse of xerophilic species and the addition of meso-hygrophilous to hygrophilous species. The weather was presumably warm. The late macrofossils of the MII-3 concurred to the wetness hypothesis with Sphagnum returns and pollen data with many hygrophilous species. Conclusion about the temperature based solely on the presented data of the period is complex though as warmth is derived from oribatids while pollen leaned toward a colder period. The climatic data of the period correspond to the “Medieval quiet Period” (sensus Bradley *et al.*, 2016) which was characterized by warmer temperature in the Newfoundland area (Finkenbinder *et al.*, 2022) which would give reason to the oribatid interpretation.

4.4. S4: 1151 to 642 BP cal.

This period was characterized by its dryness but the dynamic state of the hydrology throughout the period led to the division in two sub-periods. In between the two subzones, a wet short period is highlighted for the vegetation, both macrofossils and pollen but not for the arthropods.

▪ ***S4.1: 1151 to 855 BP cal.***

This sub-period was deemed dry by the oribatid indicator for their assemblages was dominated by xerophilic species and the hygrophilous ones of the previous period were absent. The macrofossils correspond to Ericaceae species associated with low water table and a period dominated by mosses. Likewise, open habitats and shrub development observed in pollen records are consistent with drought. As all indicators point to a dry period, it could be proposed that the dryness expressed itself at a climate scale, with low precipitations. Indeed, the dominance of mosses instead of sphagnum rules out the increased distance from the water table that would be the result of hummock formations (Payette & Rochefort, 2001).

▪ ***S4.2 855 to 642 BP cal.***

This second sub-period is characterized by an increase in wetness, still relative but notable as many indicators of dry habitats remains. The oribatids for instance

remains indicators of dry habitats but with a turnover of species from the last sub period. The vegetation, as mentioned before, displayed a wet period at the shifting points between S4.1 and S4.2. This humidity was linked to sphagnum peak, among which the hygrophilous *Sphagnum tenerum*. Also, the pollen records contained indicators of wetness through hygrophilous plants. This wetness coincided with the beginning of the medieval climate anomaly (MCA) which was cold and wet in Newfoundland (Finkenbinder *et al.*, 2022). The second half of S4.2 being dryer is synchronous with the second half of the MCA, hence a dryer and warmer time. The cold waters of the Labrador current are no longer cooled by sea ice and cold waters that origin from the melt of arctic ice in the early MCA (Sicre *et al.*, 2014). The absence of wetness response of the oribatid mites could originated in scale of the used microhabitats as the xerophilous niches might not have been reached by the increased water table. Hygrophilous vegetation, on the other hand, was favored as it burrows deeper into the soil to find water. This difference of threshold of water table variation responses between the taxa should be tested further as if proven right would greatly enhance the complementarity of the oribatid mites and vegetation as paleoecological proxies. The variation of Oribatid assemblages, both xerophilous species (*Mycobates incurvatus* and *Mycobates perates*) might be either link to a water variation with a spectrum of water tolerance between the two assemblages or to a change in temperature with comparable wetness as the MCA went from cold to warm between the two periods.

4.5. S5: 557 to 472 BP cal.

This period was marked by an increased wetness. On the behalf of oribatid mites, several hygrophilous to semi aquatic species were observed. Likewise, the macrofossils and pollen at the local scale displayed several hygrophilous species.

This relatively short event coincided with the time just before the beginning of the Little Ice Age (LIA) which was locally described as rather warm and stable (Finkenbinder *et al.*, 2022). This warmth associated with thawing and/or increased precipitation has led to a consensus among indicators toward an increased humidity.

4.6. S6: 429 to -71 BP cal.

This last period is mainly characterized by its dryness but different assemblages' variations linked to various drivers led to the subdivision into three sub-periods. Most of the whole period is synchronous to the LIA as described for Newfoundland (Finkenbinder *et al.*, 2022). Another characteristic of this period is the richness observed gradually increasing towards the most recent periods. This pattern can be either related to taphonomy or to a habitat enrichment. Human presence increased around the sites during this period and as a result, some of the species could be linked to anthropization (Święta-Musznicka *et al.*, 2013) as suggested by some ruderal species. However, every species linked to this richer assemblage cannot be attributed to anthropization as the natural plant assemblages of coastal bogs are known to harbor some minerotrophic species (Damman & Dowan, 1981). A more parsimonious explanation for the whole increased richness in the recent strata of our sampled could reside in taphonomic degradation that lowered the samples representativity and artefact identifiability deeper in time (Efremov, 1940). Therefore the absences in the past of the species that increased the richness of the assemblages in the recent times should not be considered as an indication of enrichment as much as a lack linked to sample degradation over time. This hypothesis would concur with arboreal species of Oribatid only observed in the most recent layers even though vegetation data revealed tree cues throughout the sequence.

▪ S6.1 429 to 172 BP cal.

The whole sub-period appeared as cold and dry. Oribatid wise, the sub-zone corresponded to the transition from most recent half of O8.1 which is a wet and probably warm period, to the transition between O8.1 and O8.2. This transition is marked by a cold and dry event that led to the O8.2 dry period. The high variation of conditions indicated by oribatid assemblage concurred with climatic pattern characterizing the period, namely a highly variable period with a cold tendency (Finkenbinder *et al.*, 2022). Following the pattern, the macrofossils showed a highly variable trend with dry and wet events, following the same responses as the oribatid. As both indicators of local conditions behave similarly, it can be concluded that on a local scale, the water table of the bog has experienced high degrees of variation. The pollen data indicated a cold and dry climate, concurring

with large scale of the LIA (Bhiry *et al.*, 2016). The differences between the indicators may be either a bog effect which tends to always have indicators of relative wetness because entire habitats depend on humidity (Rydin *et al.*, 2013) or the specificity of the Newfoundland areas, subject to sea influence (Keigwin & Pickart, 1999; Finkenbinder *et al.*, 2022). Local indicators tell a different story that of the broad pollen record that would reveal the climatic effect of the LIA at a larger scale. Similarly, the variations observed here that were not reflect in the pollen could be linked to local specificities as has been pointed out in similar context (Finkenbinder *et al.*, 2022). Hydrology had a history of local responses and therefor blurred in the regional records, highlighting only the main LIA trend, dry and cold.

▪ **S6.2: 172 to 0 Bp cal.**

This sub period remains dry but was characterized by variation in assemblages that may indicate fires. Oribatid remained indicator of a dry period, not as much as they were in the transition but along de mesophilic dominating species the hydrophilic species were replaced by xerophilic ones. The macrofossils here suggest a relatively humid period while species that need dryer microhabitat and grows on hummock, like *Empetrum nigrum*, still remained and indicated the probable presence of several local micro gradients of humidity linked to peat microtopography (Payette & Rochefort, 2001). Pollen data suggested the presence of local fire. Those might be natural as the period is dry (Carcaillet *et al.*, 2001) but human activity may have been to blame since European colonization. Several battles for control of the archipelago took place during this period (Aubert De la Rüe, 1933). Such mosaics of dry and wet habitats may have been favored by fire as wet microhabitats linked to peat bog microtopography are known to be less impacted by fire and thrive after fires (Benscoter *et al.*, 2005).

▪ **S6.3 0 to -71 BP cal.**

Finally, the most recent sub-period appears as a continuity of the previous two with a general dry condition but always tempered by the presence of a few more hygrophilous species. Such ambivalent drought conditions may only be relative and driven more by the hummock's development than the climate. As hummocks of Sphagnum develop, they increase the distance to the water table and create

drier conditions locally (Payette & Rochefort, 2001). The warmth associated with the recent period of global warming (Chen *et al.*, 2021) may have triggered a greater development of sphagnum (Breeuwer *et al.*, 2008).

5. CONCLUSIONS

The late Holocene climate on the archipelago of Saint-Pierre and Miquelon, which was never studied before, appears very similar to the one documented for Newfoundland. This similarity strengthens the robustness of the conclusion drawn for the archipelago and add to regional research. This result was expectable as, on top of the proximity of the two territory, Newfoundland's climate is dictated firstly by the same sea current that surround the archipelago. This information will be precious for future local studies, whether paleoecological, archaeological or as context for neoecological work.

Concerning the bog itself, it appears to have remained stable, habitat wise, because beyond hydrological and climatic variations, the species associated with the local context observed in the core were peat bog species. Nonetheless, this stable environment (Keuper *et al.*, 2010) displayed, through the indicators, a sensitivity to environmental signals that informed our understanding of the dynamics of the understudied coastal Atlantic bog habitat.

The combination of the three indicator taxa used here showed great potential for paleoecological study. Pollen and vegetation microfossils have proved to be effective and complementary indicators as it the case in many paleoecological contexts (Birks, 2003). Here, the oribatid subfossils added a real step forward in paleo-proxies. The high preservation quality of subfossils oribatid (Erickson, 1988) and their abundance in a small amount of sediment are linked to their high abundance in nature (Behan-Pelletier & Lindo, 2023). This led to a high taxonomic resolution and robust assemblages. Here, the use of Oribatid has reinforced the local pattern observed with plant microfossils and the specificities of each have highlighted response threshold that allow us to better appreciate the pattern at play. Despite the taxonomic expertise they require (Luoto, 2009; Markkula *et al.*, 2018) Oribatid subfossils appear to have great potential for the future of paleoecology.

Even if the observed climatic patterns match to regional events, peat bogs can possibly have site-specific responses (Finkenbinder *et al.*, 2022) and, therefore, studying several sites in parallels within the archipelago would allow a broader understanding of local dynamics. Moreover, as peat accumulation on the archipelago may extend back to the early Holocene at Miquelon and Langlade. A study over a longer time span, linked to the encouraging resistance of subfossil Oribatid, could be fruitful. In the same logic adding testate amoeba among the proxies, a major known indicator of water tables dynamics (Amesbury *et al.*, 2013) would enable a more precise understanding of the peat bog dynamics across time.

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V. GENERAL DISCUSSION



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A. Objectives recall

1. SYNTHESIS OF THE RESULTS AND CONCLUSIONS

1.1. Chapter 1

Chapter one tackled the neoecological aspect of the research project and its aim was to shade light on the relationships between taxa, metrics and environmental parameters at different scale, highlighting their complementarity and respective sensitivities. The overall objective of this chapter is to both increase the knowledge on the peat bog sensitivities to environmental parameters and on the taxa used as indicators themselves, providing knowledge and improved tools at the same time.

The main results that emerge from the study is how much complementarity form multiplying taxa and metrics both uncover pattern that would not be seen otherwise and also strengthen redundant pattern. Indeed, the studied bog, albeit being comparable habitats, were nested within contrasting context. One was in a landscape were forest and heathland dominated with close proximity to human activities, while the other two were more peat bog dominated landscape but with varying amount of open water and secondary habitats.

Within the accepted and expected theory of correlation between taxonomic and functional diversity, the comparison of taxa and the variation of orders within metrics, coupled with variance partitioning highlighted specific sensitivities of the taxa studied to local and landscape factors, to hydrological and habitats cues and how those responses between sites shed light on their specificities.

1.2. Chapter 2

Chapter two had a methodological inclination as it was testing the potential of oribatid mites as indicator of past climates through climates reconstructions methods. This endeavor was motivated by the great potential of oribatid mites as palaeoecological indicators and the absences of previous work using them as model taxa for climate reconstruction. The methodology deployed to test it heavily relied on public available data as the viability test of the method needed a way to know if the reconstruction were valid. To achieve this, current assemblages of oribatid were used for reconstruction and the results compared with current climate values. The data from 46 sites from an oribatid mites study scattered all over the northern

hemisphere was used (Mumladze *et al.*, 2013) and crossed with GBIF and Worldclim database. A case study using data from this project sampling was also done and used vegetation data as a verification tool.

The main results is that oribatid mites display a variable ability to produce climates reconstruction and that the main driver of errors of reconstruction is link to some species as the model to assess the drivers of errors linked greater errors to a greater number of species albeit the positive effects of high number of points. This led to an exploration of the reasons, beyond the lack of occurrences data, of why oribatids deviated from the climate in the reconstructions. The relationship between oribatid and water appears as an interesting lead to further the study of the indicator ability of oribatid mites in climate reconstruction.

1.3. Chapter 3

Chapter 3 was a paleoecological study of Saint-Pierre's bog over the span of two millennia. This timescale was selected as it was a known period of climatic variation and human activities locally. The study reached its objectives through the crossed analysis of oribatid mite subfossils, pollen and vegetation macrofossils within a series of peat cores that were sampled in parallel and in such a close fashion that they are considered representative of one another. The usage of the three proxies with their respective sensitivity highlighted the variation in the habitats throughout the time span studied. What was observed is that the habitat itself remains the same during the whole two millennium: an ombrotrophic coastal bog with an oceanic influence. Despite this homogeneity, the climatic influences over the bog displayed striking patterns of temperature and hydrology and fire events through history and the variation of responses between indicators enlighten us about the various threshold of sensitivity of the indicators and therefor the scale of the events recorded. Overall, the climates evolution observed match the literature of the Newfoundland's late Holocene patterns that were highly specific of the period and the region. Indeed, the variability and inversion of great climatic pattern in those periods were linked to the sea current influences and the same current engulf the archipelago. The multitaxa approach was particularly interesting as the main event observed were concurring between the taxa, strengthening the robustness of the responses while the variation of responses highlights scale dependent level of variation.

B. Peat bog, a complex habitat

1. PEAT BOG, RESISTANT YET SENSITIVE

Throughout this study, we have observed peat bog responses to a large spectrum of variations, at local to landscape scale and from a current snapshot to over two millennia of events. This first aspect that can be highlighted is the peat bog resistance as one of the observed results is how the habitat, despite weathering several climatic variations, remained within the definition of the same habitat. Indeed, the vegetation observed throughout the sequence of events was and remained bog vegetation. A first token of that habitat stability is the numerous sphagnum that dominated the plant matrix of the macrofossils most of the time. Ombrotrophic peat bog are characterized by their sphagnum dominance (Rydin *et al.*, 2013) as our data suggested most of the time. As those habitats are characterized by low level of nutrients and low pH, the vegetation that inhabit them are quite specific with open bogs displaying low richness and specialized species like carnivorous plants and *Ericaceae* (Payette & Rochefort, 2001) echoing to what we observed in the cores and in the botanical relevés. The different types of peat bogs are firstly driven by their hydrology (Rydin *et al.*, 2013) and the bog here discussed are Ombrotrophic, hence the water that keeps water balance positive originate in rains, as it's etymology suggest. In our geographical context, the coastal Atlantic territory, a specific case of ombrotrophic peat bog are described, which incorporate within their species assemblages some species usually associated to poor minerotrophic habitats (Damman & Dowan, 1981; Payette & Rochefort, 2001). This pattern is precisely the one observed in our study and the proximity to the sea, which is associated to this phenomenon due to sea salt in the mist, is perfectly coherent. Indeed, the specific climate of the region, notably characterized by the great amount of fog linked to the meeting of cold and warm sea current (Lewis *et al.*, 2004) is considered a major water intake for the local bog (Damman, 1979). Those conditions that lead to our Atlantic bog, although variable through time as we observed, created a habitat that prevail through time. Such a resistance echoes the theory of peatland as a climax habitat (Klinger *et al.*, 1990; Klinger 1996). Likewise, this resistance can be linked to the colder microclimate associated to the peat bogs, a characteristic described for these habitats linked to humidity (Worrall *et al.*, 2019). Indeed, the humidity in a peat bog led to a temperature inertia that drove it to be colder from surrounding

other habitats as long as it remains wet, an effect that is increased on wooded peatlands (Nichols, 1998). Peat bogs are described to have a role of hydrological reservoir which lead to some hydrological inertia, but this property can vary greatly depending on the hydrological context (Payette & Rochefort 2001). All together making peat bog a resistance habitat to variations due to a tampon effect (Minayeva & Sirin, 2012).

Despite this resistance to changes and broad stability, the peat bogs are subject to variations in the spectrum of the habitat definition, as we observed through the studies presented here. This variability can either be from a neutral growth or, by opposition, in responses of a variability in the peat bog environment.

The first one is the natural development of a peat bog, may it be filling of an open water habitats or peat accumulation through paludification in the proper conditions (Rydin *et al.*, 2013). This usually led to a succession of peat bog habitats, starting with a fen enriched by running water that develop into a bog as the peat accumulation drives the habitats away from those water sources up to the point it became ombrotrophic, rain fed (Payette & Rochefort, 2001). Such development will not be discussed further as the objects of our study are and were ombrotrophic bogs over the whole-time span studied.

Secondly the responses of bog linked to a variation in their environment. Such variation may take various forms and be expressed at many scales. The variation may be spatial and/or temporal. Spatial variations were addressed in the first chapter as Neoecology here makes a synchronous snapshot of peat bogs in variable landscapes. The second aspect of variation, time, was addressed mostly in the third chapter where one bog dynamic was studied over time.

The spatial variation can be addressed at various scales. The dichotomy studied here was local and landscape scale. We observed on the current assemblages a response of the bog biodiversity to the variations of landscape and locale features. The local side of this results expressed themselves within the local scale with hydrological variables, notably through microtopography. Indeed, very local but strong biodiversity gradient is described in peat bogs likes to the distances to the water tables that varies within those microtopography (Payette & Rochefort, 2001).

The landscape scale can interact with the peat bog through several types of variations, the habitat matrix surrounding the peat bog habitats will have an effect, creating gradient of nutrient scarcity from the center of the peat bogs to the edges (Payette & Rochefort 2001) and act as a source of potential tyrphophile species (Vitt *et al.*, 1995). This impact is considered to be driven through the species generalist within the assemblages, and only highly tolerant generalist as the bog condition would filters the others (Desrocher & van Duinen, 2006). Similarly, the hydrology of the peat bog is highly linked to the landscape, may it be to broad topography that allows the initial paludification, the slopes that channeled the running waters that feed the peat bogs or, inversely, that drained it. The amount of nutrient available in the peat bog is also landscape dependent, the previously mentioned slopes channeling water are a vector of nutrients of minerotrophic fen (Payette & Rochefort, 2001). Likewise, the closeness to the sea lead to an enrichment of the bog through sea spray that add nutrient and temper the low pH in bog (Damman & Dowan, 1981; Payette & Rochefort, 2001), a landscape scale driver that shaped the peat bogs studied here. Lastly, landscape scale transformation that shapes peat bogs that should be noted are the anthropic linked variations. Indeed, Agriculture, forestry, peat extraction or electricity production impacted peat bog all over the world (Bonn *et al.*, 2016). Canadian peat bog are relatively un-degraded with 90% of peat bogs remaining natural, while some European country on the other hand have seen most of their peat bogs damaged, up to 85% in the Netherlands (CPG in Bonn *et al.*, 2016). Within the scope of our study the anthropic impacts, while presents, did not appeared intensives.

The temporal linked variations are more complex as they incorporate all that was cited before and more. Indeed, every spatial variation can happen through a temporal continuum and participate to the temporal scale dynamics. Other variations are more bound to temporal scale, like climatic variations as we monitored in the paleoecological section. Once again, the climatic conditions, warmth and cold as well as precipitations intensity or scarcity. Indeed, the past community variation of the bog shed light on the variations that a bog can display in front of climatic variations. Faithfull to the hydrological driven paradigm of peat bog dynamics (Payette & Rochefort, 2001; Rydin *et al.*, 2013) the pattern observed were mostly water dependent. As a constitutive element of the peat bog habitat, water is also a preponderant driver of the biodiversity within (Minayeva & Sirin,

2012). Indeed, the water direct variation can induce variations in the water table distance to the surface (Rydin & McDonald, 1985) while temperature can impact peat accumulation through sphagnum moss growth (Breeuwer *et al.* 2008) altogether inducing variation on water accessibility and therefore assemblage changes (Marie-Victorin *et al.*, 2002). Coldness of climates linked to precipitation, especially in boreal to arctic climates as studied here, will add the relationship to snow and ice to the peat bogs. Indeed, snow cover will protect vegetation of the bog in winter, strongly impacting its development (Keuper *et al.*, 2010). Similarly, the snow melt can be a substantial of the hydrology of the peat bog (Payette & Rochefort, 2001). Ice formation within the bog is also a great driver of the habitat dynamics. Indeed, the microtopography frequently discussed before as well as the presence of open water within the habitats can be linked to ice in the peat bog as pergelisol presence induces hummocks like pale as the melting creates specific pools called thermokarstic (Payette & Rochefort, 2001). Likewise, dry events, on top of affecting water tables and the whole peat bog functioning (Bonn *et al.*, 2016) can increase the probability of natural fire (Carcaillet *et al.*, 2001) even though vegetation growth increasing distance to water table and creating a dry microhabitat which is linked to cyclic fire events (Sillasoo *et al.*, 2011).

C. Bioindication, a powerful tool that still can grow through theory and usage

1. WHAT WE LEARNT ABOUT THE INDICATORS

By using several taxa as indicators, we increased our knowledges about them (Van Straalen, 1996). Indeed, each study that use a taxa as an indicator will provide new data on occurrences of the used species, observed responses to the taxa to environmental cues and therefore either strengthen or clarify known patterns or even uncover new sensitivities. In biology, this can mean a better understanding of the autecology of species, or in conservation biology, a better understanding of the status of populations. All together it's the ecological indicator tools that strengthened by their use, as the better the knowledges are on a taxon, the more information can be inferred from its observations.

Spiders were used as indicator taxa in our peat bogs. Spiders displayed sensitivity to several environmental cues and provided a fine reading of the subtle

variations between the studied habitats. The pattern of responses of the spiders was, in some aspects, faithful to what is described in the literature for the taxa. Indeed, the absences of variation of alpha diversity but strong patterns of beta diversity is a frequent pattern with spiders (Bell *et al.*, 1998; Coccia and Fariña, 2019; Hacala *et al.*, 2020). This pattern observed here as well adds a stone to the understanding of spider's responses to the environment and also broaden the known spectrum of variation for which spiders display such patterns with the landscapes feature and hydrology in bogs.

Oribatid mites were used as indicators in different ways within this study. The second chapter was almost solely aimed at increasing our knowledge of oribatids mites' potential as usage as indicators of climate reconstruction. The oribatid mites were already known indicators of climates and habitat characterization and dynamics (Polyak *et al.*, 2001; Larsen *et al.*, 2006; Erickson & Solod, 2007; Markkula, 2018; Markkula & Kuhry, 2020; Schelvis, 2020) but the specific tools of climate reconstruction, a method that allows to estimate numerically the climates based on a species assemblage. This study highlighted how the relative importance of oribatid sensitivity between climate and hydrology was inclined in such a way that the taxa potential could lean toward hydrology more than temperature. The second point about oribatid mites that was highlighted by this study was how, even if a tremendous work was done in these regards (Behan-Pelletier & Lindo, 2023), the current knowledge of global species occurrences was too limited for climate reconstructions. This result is a testimony to the need of more knowledge of those taxa, a knowledge that grows each time a study used a taxa as indicators. Under the consideration of the oribatid as paleoecological indicator, the studied shed light on the quality of the taxa as a proxy of the past. This result echoes the few works that used subfossils mites as indicators (Erickson, 1988; Erickson *et al.*, 2003; Schelvis, 2020) and is a testimony to go further.

The arthropods taxa used for those studies were an increment in general knowledge about those species as they were, for many species, not registered locally. Half the spiders in the study were not recorded in the archipelago's previous works. This could be explained as the small archipelago rely for this kind of knowledge solely on hobbyist (but competent) naturalists who work almost exclusively through hand collecting specimens, which is known to miss part of the diversity (Andersen & Arneberg, 2016). Another explanation is the taxa

themselves as spiders are not the most popular of taxa (Mammola *et al.*, 2022) while oribatid are a taxonomic challenge (Baker, 2009) tackled by so few that no data on this taxa existed before this project on the archipelago. Likewise, ground beetles and ants, despites not being used in analysis here were identified add many of them increased the local knowledges (appendix 1). This is less true for vegetation as there was a broad history of botanical study on the archipelago from the early works of Edgar Aubert De la Rüe (1933) to the recent works of naturalist like Roger Etcheberry and colleagues (2010, 2012) or the botanist Serge Muller and colleagues (2006, 2008, 2010, 2012).

Vegetation was used as indicator in several different ways within this study. The vegetation as an ecological indicator in the first chapter enlighten about the vegetation itself, which is considered more from the point a view of diversity. The combination of metrics used displayed how the bog species were primarily impacted by landscape feature, both hydrological and anthropized area in our specific context of oceanic ombrotrophic bogs.

2. WHICH INDICATOR TO PURSUE NEXT?

Several bioindicators were used within this project but as multiplicity of indicators is beneficial for ecological understanding (Samways *et al.*, 2010; Fattorini *et al.*, 2011), we will review example of other indicators that would be relevant for furthering the objectives tackled throughout the thesis. The indicator used here were chosen due to their complementarity, this is the main characteristic aimed for proposing new model taxa.

The models that were presents in paleoecology and not in Neoecology and the other way around would have been a relevant addition in both contexts. The taxa were selected for ecological complementarity. Indeed, spider, oribates and vegetation being respectively predators, detritivores and primary producers are less likely to be strongly correlated to one another. As mentioned, microfossils of spiders can be found in peat bogs (Scott, 2003) and spiders are great ecological indicators (Scott *et al.*, 2006; Pétilion & Garbutt, 2008; Cristofoli *et al.*, 2010; Hacala *et al.* 2020). Likewise, oribatid mites display a great potential in neoecology (*e.g.* Solhoy, 1979; Borcard & Vaucher-von Ballmoos, 1997; Mumladze *et al.*, 2013; Lehmitz, 2014) and should be considered for future studies in the spirit of the first chapter of this thesis. Likewise, the non-vascular vegetation, especially

Sphagnum, should be used in Neoecology. Despite being challenging to identify (Ayotte & Rochefort, 2019), they are a constitutive part of the bogs and one of the main indicators of peat bog studies (Payette & Rochefort, 2001; Rydin *et al.*, 2013). Even if some author argues for a better response from vascular plants (Laine *et al.*, 2021), the crossed usage of both sphagnum moss and vascular plants appears relevant (Lehmitz *et al.*, 2020).

Testate amoebae are used in several paleoecological studies in peat bogs as they are excellent indicators of water table levels over time (Amesbury *et al.*, 2013). The proxy used here provided information about the hydrological dynamic of the bog through time but the interactions between several environmental parameters is challenging to decipher. Adding an indicator with a specific sensitivity to water table along the other indicators would allow to discern the environmental events more precisely.

More metrics of diversity may, in the spirit of the first chapter, offer hindsight through the complementarity they display with the used metrics. For instances the phylogenetic diversity has a growing history of usage in neoecology (Faith, 1992; Rodrigues *et al.*, 2005; Cadotte *et al.*, 2013; Magura, 2016; Tucker *et al.*, 2018; Wong *et al.*, 2019; Hacala *et al.*, 2021; Ridel *et al.*, 2021) and even in paleoecology (Lamsdell *et al.*, 2017). These metrics are complementary to the taxonomic and functional diversity used here and display a particular interaction with harsh ecological conditions (Hacala *et al.*, 2021) that may find echoes in the peat bogs habitats (Rydin *et al.*, 2013).

D. From pluridisciplinarity to multidisciplinarity: reunite past and present peat-bog diversities, crossing paleoecology and neoecology to resolve ecological dynamics.

1. DEFINING THE GAP BETWEEN WHAT IS DONE AND WHAT COULD BE AIMED FOR

Firstly, the subtlety between pluridisciplinarity and multidisciplinarity objectives needs to be defined. Following the semantic of Létourneau (2008), the pluridisciplinarity is the manipulation of several disciplines next to each other within

a project but without crossing themes whereas multidisciplinary aims at a "Collective research practice seeking the connection and integration of knowledge".

This connection has been called for in the past as a lack of communication between the two disciplines has already been highlighted (Barber, 2016). Indeed, the two disciplines, albeit working on the same study model and having similar objectives (Goodenough & Webb, 2022) struggle to work together because the methods and nature of the samples used differ but also through simple lack of understanding and inertia to deviate from work habits (Rull, 2010; Davies et al., 2014). There are some interesting examples, such as the early work of Markkula (1986) comparing subfossils and current oribatid mite assemblages, using the former to contextualize the latter.

2. HOW COULD THIS GOAL BE ACHIEVED?

Many pitfalls are to be considered in order to create a bridge between paleoecology and neoecology. The first one may be the time scale. In paleoecology, temporal resolution must be kept in mind when discussing accumulation rates of remains, which can vary beyond comparability (Marguerie 2009). Rull (2014) by comparing the time scale used in both sub-discipline advocate to use the times scales that overlap between them, hence the year. The nature of the data, often qualitative in paleoecology and quantitative in neoecology could meet on common ground. Methods of randomize sub-sampling in neoecological assemblages to meet the semi-quantitative paleoecological data might be a lead to build comparisons. Likewise, this connection could be achieved by increasing the number of samples in paleoecology in order to achieve quantitative data. Such endeavor is realized with the more numerous proxies like pollens (Birks & Line, 1992). The often-unreasonable amount of work required to analyze other paleo-remains on a quantitative scale is enough to deter most of such aspirations (but see Forcino, 2012). Yet, as we observed in this project, Oribatid mites might make it possible since the amount of remains per volume of sediments is high. Neoecology may need, more than it knows, the hindsight of paleoecology (Anderson et al., 2006; Barber, 2016).

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APPENDIX 1: SPECIES LISTS

Appendix 1.1 Spider species list with functional traits

Species	Guild	Mean size (cm)	Balloning
<i>Agelenopsis utahana</i> (Chamberlin & Ivie, 1933)	Sheet web weavers	10	0
<i>Agyneta jacksoni</i> (Brændegaard, 1937)	Sheet web weavers	1.9	1
<i>Agyneta olivacea</i> (Emerton, 1882)	Sheet web weavers	2.15	1
<i>Agyneta unimaculata</i> (Emerton, 1882)	Sheet web weavers	1.8	1
<i>Aphileta misera</i> (O. Pickard-Cambridge, 1882)	Other hunters	2.1	1
<i>Araneus diadematus</i> (Clerck, 1757)	Orb web weavers	13.1	1
<i>Arctosa raptor</i> (Kulczyński, 1885)	Ground hunters	12	0
<i>Attulus striatus</i> (Emerton, 1911)	Other hunters	3.95	0
<i>Bathyphantes brevipes</i> (Emerton, 1917)	Sheet web weavers	2.95	1
<i>Bathyphantes canadensis</i> (Emerton, 1882)	Sheet web weavers	1.8	1
<i>Bathyphantes eumenis</i> (Emerton, 1917)	Sheet web weavers	2.1	1
<i>Bathyphantes pallidus</i> (Banks, 1892)	Sheet web weavers	2.35	1
<i>Carorita limnaea</i> (Crosby & Bishop, 1927)	Other hunters	1.2	0
<i>Centromerus denticulatus</i> (Emerton, 1909)	Sheet web weavers	1.65	0
<i>Centromerus longibulbus</i> (Emerton, 1882)	Sheet web weavers	2	0
<i>Ceraticelus bulbosus</i> (Emerton, 1882)	Other hunters	1.4	1
<i>Ceraticelus fissiceps</i> (Emerton, 1882)	Other hunters	1.5	1
<i>Ceratinella brunnea</i> (Emerton, 1882)	Other hunters	1.75	1
<i>Clubiona bishopi</i> (Edwards, 1958)	vegetation_hunter	3.7	1
<i>Clubiona bryantae</i> (Gertsch, 1941)	vegetation_hunter	5.8	1
<i>Clubiona gertschi</i> (Edwards, 1958)	vegetation_hunter	4.2	1
<i>Clubiona Kulczynskii</i> (Lessert, 1905)	vegetation_hunter	6.1	1
<i>Clubiona quebecana</i> (Dondale & Redner, 1976)	vegetation_hunter	4.05	1
<i>Crustulina sticta</i> (O. Pickard-Cambridge, 1861)	Space web weavers	2.5	1
<i>Cryphoeca montana</i> (Emerton, 1909)	Sheet web weavers	2.85	0
<i>Diplostyla concolor</i> (Wider, 1834)	Sheet web weavers	2.4	1
<i>Dolomedes striatus</i> (Giebel, 1869)	Ambush hunters	12.2	1
<i>Ero canionis</i> (Chamberlin & Ivie, 1935)	Specialists	2.6	0
<i>Ghelna canadensis</i> (Banks, 1897)	Other hunters	5.25	0
<i>Gnaphosa muscorum</i> (L. Koch, 1866)	Ground hunters	9.45	0
<i>Gnaphosa parvula</i> (Banks, 1896)	Ground hunters	7.4	0
<i>Gonatium crassipalpus</i> (Bryant, 1933)	Other hunters	2.25	1
<i>Grammonota capitata</i> (Emerton, 1924)	Other hunters	2.2	1
<i>Grammonota gigas</i> (Banks, 1896)	Other hunters	2.45	1
<i>Hypsosinga pygmaea</i> (Sundevall, 1831)	Orb web weavers	2.9	1
<i>Idionella rugosa</i> (Crosby, 1905)	Other hunters	2.1	0
<i>Mecynargus borealis</i> (Jackson, 1930)	Other hunters	1.4	0
<i>Mermessus entomologicus</i> (Emerton, 1911)	Other hunters	1	1
<i>Mermessus trilobatus</i> (Emerton, 1882)	Other hunters	1.7	1
<i>Micrargus longitarsus</i> (Emerton, 1882)	Other hunters	1.65	0
<i>Neoantistea agilis</i> (Keyserling, 1887)	Sheet web weavers	2.95	0
<i>Neon nelli</i> (G. W. Peckham & E. G. Peckham, 1888)	Other hunters	2.4	0

APPENDIX 1: SPECIES LISTS

<i>Neottiura bimaculata</i> (Linnaeus, 1767)	Space web weavers	3.25	1
<i>Neriere clathrata</i> (Sundevall, 1830)	Sheet web weavers	4.1	1
<i>Oreonetides flavescens</i> (O. Pickard-Cambridge, 1873)	Sheet web weavers	1.9	1
<i>Oreonetides rectangulatus</i> (Emerton, 1913)	Sheet web weavers	2.2	1
<i>Ozyptila sincera</i> (Dondale & Redner, 1975)	Ground hunters	2.75	1
<i>Pardosa fuscata</i> (Thorell, 1875)	Ground hunters	7.3	1
<i>Pardosa groenlandica</i> (Thorell, 1872)	Ground hunters	9.95	1
<i>Pardosa hyperborea</i> (Thorell, 1872)	Ground hunters	5.05	1
<i>Pardosa moesta</i> (Banks, 1892)	Ground hunters	5.35	1
<i>Pelecopsis moesta</i> (Banks, 1892)	Other hunters	1.65	1
<i>Pirata piraticus</i> (Clerck, 1757)	Ground hunters	5.85	1
<i>Piratula insularis</i> (Emerton, 1885)	Ground hunters	4.9	1
<i>Pocadicnemis americana</i> (Millidge, 1976)	Other hunters	1.9	0
<i>Robertus borealis</i> (Kaston, 1946)	Space web weavers	2.65	0
<i>Talavera minuta</i> (Banks, 1895)	Other hunters	2.35	1
<i>Tenuiphantes zebra</i> (Emerton, 1882)	Sheet web weavers	2	1
<i>Trochosa ruricola</i> (De Geer, 1778)	Ground hunters	10.5	1
<i>Trochosa terricola</i> (Thorell, 1856)	Ground hunters	9.35	1
<i>Walckenaeria digitata</i> (Emerton, 1913)	Other hunters	2.3	0
<i>Walckenaeria exigua</i> (Millidge, 1983)	Other hunters	1.6	0
<i>Walckenaeria fallax</i> (Millidge, 1983)	Other hunters	2,55	0
<i>Walckenaeria pallida</i> (Emerton, 1882)	Other hunters	2.5	0
<i>Walckenaeria tibialis</i> (Emerton, 1882)	Other hunters	1.75	0
<i>Xysticus britcheri</i> (Gertsch, 1934)	Ambush hunters	4.75	1
<i>Xysticus emertoni</i> (Keyserling, 1880)	Ambush hunters	7.1	1
<i>Xysticus triguttatus</i> (Keyserling, 1880)	Ambush hunters	3.65	1
<i>Zelotes fratris</i> (Chamberlin, 1920)	Ground hunters	6.55	0

Appendix 1.2 Spider species list contacted in secondary habitats

Species	Langlade	Miquelon	Saint-Pierre	Unique to secondary habitats
<i>Agelenopsis utahana</i> (Chamberlin & Ivie, 1933)	1	1	1	
<i>Agyneta jacksoni</i> (Braendegaard, 1937)	0	0	1	
<i>Agyneta olivacea</i> (Emerton, 1882)	1	0	0	
<i>Allomengea dentisetis</i> (Grube, 1861)	1	0	0	X
<i>Aphileta misera</i> (O. Pickard-Cambridge, 1882)	1	1	0	
<i>Arctosa raptor</i> (Kulczyński, 1885)	1	0	0	
<i>Bathyphantes brevipes</i> (Emerton, 1917)	1	0	1	
<i>Bathyphantes pallidus</i> (Banks, 1892)	1	1	0	
<i>Calobius sp.</i> (Chamberlin, 1947)	1	0	0	X
<i>Ceratinella buna</i> (Emerton, 1882)	1	0	1	

APPENDIX 1: SPECIES LISTS

<i>Clubiona bryantae</i> (Gertsch, 1941)	1	0	0	
<i>Clubiona Kulczyinskii</i> (Lessert, 1905)	0	0	1	
<i>Cryphoeca montana</i> (Emerton, 1909)	1	0	0	
<i>Cybaeopsis tibialis</i> (Emerton, 1888)	0	1	0	
<i>Diplocentria bidentata</i> (Emerton, 1882)	1	0	0	X
<i>Diplostyla concolor</i> (Wider, 1834)	1	0	1	
<i>Mermessus index</i> (Emerton, 1914)	1	1	0	X
<i>Erigone dentipalpis</i> (Wider, 1834)	0	0	1	X
<i>Gnaphosa parvula</i> (Banks, 1896)	1	0	0	
<i>Grammonota capitata</i> (Emerton, 1924)	1	0	0	
<i>Leptyphantes alpinus</i> (Emerton, 1882)	0	0	1	X
<i>Leptyphantes intricatus</i> (Emerton, 1911)	1	0	0	X
<i>Mermessus trilobatus</i> (Emerton, 1882)	0	0	1	
<i>Neoantistea magna</i> (Keyserling, 1887)	1	1	1	X
<i>Neon nelli</i> (G. W. Peckham & E. G. Peckham, 1888)	0	1	1	
<i>Neriere clathrata</i> (Sundevall, 1830)	0	0	1	
<i>Oreonetides rectangulatus</i> (Emerton, 1913)	1	1	0	
<i>Pardosa fuscua</i> (Thorell, 1875)	1	1	0	
<i>Pardosa hyperborea</i> (Thorell, 1872)	1	0	1	
<i>Pardosa moesta</i> (Banks, 1892)	1	1	1	
<i>Piratula insularis</i> (Emerton, 1885)	0	1	0	
<i>Pirata piraticus</i> (Clerck, 1757)	1	0	0	
<i>Pocadicnemis americana</i> (Millidge, 1976)	1	1	0	
<i>Scironis tarsalis</i> (Emerton, 1911)	1	0	0	X
<i>Sisicottus montanus</i> (Emerton, 1882)	1	1	1	X
<i>Tapinopa bilineata</i> (Banks, 1893)	0	0	1	X
<i>Tetragnatha extensa</i> (Linnaeus, 1758)	1	0	0	X
<i>Trochosa ruricola</i> (De Geer, 1778)	0	0	1	
<i>Trochosa terricola</i> (Thorell, 1856)	1	0	1	
<i>Tunagyna debilis</i> (Banks, 1892)	1	1	0	X
<i>Walckenaeria arctica</i> (Millidge, 1983)	0	1	0	X
<i>Walckenaeria communis</i> (Emerton, 1882)	0	1	0	X
<i>Walckenaeria spiralis</i> (Emerton, 1882)	1	0	0	X
<i>Zelotes fratris</i> (Chamberlin, 1920)	0	1	1	

APPENDIX 1: SPECIES LISTS

Appendix 1.3 Vascular plants species list with functional traits

Species	Dispersal modality				Seed mass (mg)	SLA (cm ² *g ⁻¹)	Height (cm)
	Wind	Water	Zoo	Vegetativ			
<i>Abies balsamea</i> (Mill., 1768)	1	0	0	0	7.276	196.6	50
<i>Andromeda glaucophylla</i> (Link, 1821)	0	0	1	0	0.179	86.04	40
<i>Aronia arbustifolia</i> (Pers., 1806)	0	0	1	0	1,064	146.41	53,85
<i>Betula michauxii</i> (Spach, 1841)	1	0	0	0	0.32	130	30
<i>Betula pumila</i> (Linneaus, 1767)	1	0	0	0	0.25	102.337	30
<i>Chamaedaphne calyculata</i> (Moench, 1794)	1	0	0	0	0.046	49.8	30
<i>Coptis trifolia</i> (Salisb., 1807)	1	0	1	0	0.184	227.27	3.75
<i>Cornus suestica</i> (Linneaus, 1753)	0	1	1	0	6.09	398.4	13.5
<i>Dantonina spicata</i> (Roem. & Schult. 1817)	0	1	1	0	0.519	235	18.83
<i>Drosera rotundifolia</i> (Linneaus, 1753)	0	1	0	1	0.016	397.21	3.2
<i>Empetrum nigrum</i> (Linneaus, 1753)	0	1	1	1	0.959	63.43	9.3
<i>Eriophorum gracile</i> (W.D.J.Koch, 1799)	1	1	0	1	0.311	95	42.43
<i>Eriophorum vaginatum</i> (Linneaus, 1753)	1	1	0	0	0.985	97.93	42.43
<i>Eurybia radula</i> (G.L.Nesom, 1995)	1	0	0	0	0.638	380.33	20
<i>Festuca rubra</i> (Linneaus, 1753)	1	0	1	0	0.952	47.94	35.99
<i>Gaylussacia bigeloviana</i> (Sorrie & Weakley 2007)	0	0	1	0	0.718	152.4	24.35
<i>Hypericum canadense</i> (Linneaus, 1753)	0	0	1	0	0.127	222	32.5
<i>Juniperus communis</i> (Linneaus, 1753)	0	0	1	1	68.69	81.523	10.1
<i>Kalmia angustifolia</i> (Linneaus, 1753)	0	0	0	1	0.007	2216	35
<i>Larix laricina</i> (K.Koch, 1873)	1	0	0	0	1.54	168.956	50
<i>Lycopodium annotinum</i> (Linneaus, 1753)	1	0	0	1	0	195.917	20
<i>Lycopus uniflorus</i> (Michx., 1803)	0	1	1	0	0.199	560	45
<i>Myrica gale</i> (Linneaus, 1753)	0	1	0	0	1.36	104.84	30
<i>Oclemena nemoralis</i> (Greene, 1903)	1	0	0	0	0.44	152.3	27.7
<i>Potentilla tridentata</i> (Sol. 1789)	1	1	1	0	0.2	350	10
<i>Rhododendron groenlandicum</i> (Kron & Judd 1990)	1	1	0	1	0.006	85.53	11.15
<i>Rhynchospora alba</i> (Vahl, 1805)	0	1	0	1	0.434	169.8	255

APPENDIX 1: SPECIES LISTS

<i>Rubus chamaemorus</i> (Linneaus, 1753)	0	0	1	1	7.974	149.548	5
<i>Sanguisorba canadensis</i> (Linneaus, 1753)	1	1	1	0	0.944	250	115
<i>Sarracenia purpurea</i> (Linneaus, 1753)	0	1	0	1	1.61	98.672	20
<i>Solidago uliginosa</i> (Nutt., 1834)	1	1	1	0	0.157	115.8	31.71
<i>Triadenum virginicum</i> (Ref. 1837)	1	0	0	0	0.082	200	35
<i>Trichophorum cespitosum</i> (Hartman, 1849)	0	1	0	0	0.437	37.9	23.85
<i>Vaccinium angustifolium</i> (Aiton., 1789)	0	0	1	1	0.227	135.6	18.2
<i>Vaccinium macrocarpon</i> (Aiton., 1789)	0	1	1	0	0.774	126.4	7.88
<i>Vaccinium oxycoccos</i> (Linneaus, 1753)	0	1	1	1	0.77	154.2	3.99

Appendix 1.4 Carabidae species contacted list per islands

Species	Saint-Pierre	Miquelon	Langlade
<i>Abax parallelepipedus</i> (Piller & Mitterpacher, 1783)			x
<i>Agonum affine</i> (Kirby, 1837)	x	x	x
<i>Agonum ferreum</i> (Haldeman, 1843)	x	x	x
<i>Agonum muelleri</i> (Herbst, 1784)	x		
<i>Bembidion quadralutum</i> (Notman, 1920)		x	
<i>Calathus ingratus</i> (Dejean, 1828)	x		x
<i>Carabus granulatus</i> (Linnaeus, 1758)	x	x	
<i>Cymindis cribricollis</i> (Dejean, 1831)			x
<i>Dyschirus larochei</i> (Bousquet, 1988)	x		
<i>Harpalus erythropus</i> (Dejean, 1829)	x		
<i>Harpalus somnulentus</i> (Dejean, 1829)		x	
<i>Loricera pilicornis</i> (Fabricius, 1775)	x	x	
<i>Notiophilus biguttatus</i> (Fabricius, 1779)	x		
<i>Paranchus albipes</i> (Fabricius, 1796)	x	x	x
<i>Patrobus lecontei</i> (Chaudoir, 1872)		x	
<i>Poecilus chalcites</i> (Say, 1823)	x		
<i>Pterostichus melanarius</i> (Illiger, 1798)	x		
<i>Sphaeroderus stenostomus subsp. lecontei</i> (Dejean, 1826)			x
<i>Synuchus impuctatus</i> (Say, 1823)	x	x	x
<i>Trechus apicalis</i> (Motschulsky, 1845)		x	

APPENDIX 1: SPECIES LISTS

Appendix 1.5 Ants species contacted list per islands

Species	Saint-Pierre	Miquelon	Langlade
<i>Camponotus herculeanus</i> (Linnaeus, 1758)	x	x	
<i>Formica glacialis</i> (Wheeler, 1908)	x	x	
<i>Formica neorufibarbis</i> (Emery, 1893)	x	x	
<i>Formica subaenescens</i> (Emery, 1893)	x	x	
<i>Myrmica detrinodis</i> (Emery, 1893)	x		
<i>Myrmica incompleta</i> (Provancher, 1881)		x	x
<i>Myrmica latifrons</i> (Staercke, 1927)	x	x	
<i>Myrmica rubra</i> (Linnaeus, 1758)	x	x	x
<i>Tapinoma sessile</i> (Say, 1836)		x	

Appendix 1.6 Oribatid mites identified to the species level in the palaeoecological sampled in the peat core from Saint-Pierre.

Species	
<i>Ceratoppia quadridentata</i>	(Haller, 1882)
<i>Mycobates incurvatus</i>	(Hammer, 1952)
<i>Parachipteria travei</i>	(Nevin, 1976)
<i>Carabodes labyrinthicus</i>	(Michael, 1879)
<i>Eupelops septentrionalis</i>	(Trägårdh, 1910)
<i>Fuscozetes fuscipes</i>	(C.L. Koch, 1844)
<i>Nanhermannia coronata</i>	(Berlese, 1913)
<i>Ceratozetes parvulus</i>	(Sellnick, 1922)
<i>Oribatula tibialis</i>	(Nicolet, 1855)
<i>Mycobates perates</i>	(Behan-Pelletier, 1994)
<i>Melanozetes meridianus</i>	(Sellnick, 1928)
<i>Trichoribates striatus</i>	(Hammer, 1952)
<i>Oppiella translamellata</i>	(Willmann, 1923)
<i>Trhypochthonius setosus</i>	(Hammer, 1952)
<i>Scutozetes lanceolatus</i>	(Hammer, 1952)
<i>Trichoribates incisellus</i>	(Kramer, 1897)
<i>Lepidozetes singularis</i>	(Berlese, 1910)
<i>Tectocephus velatus</i>	(Michael, 1880)

APPENDIX 2: PROJECTED WEIGHT OF TRAITS AND VARIABLES FROM THE RLQ ANALYSIS

Fig. 30A

Traits	scores
guild.Specialists.	2.36678032
guild.Space.web.weavers	1.53521444
ballo.0	0.82913204
guild.Ambush.hunters	0.51419307
guild.Other.hunters	0.42457015
guild.vegetation_hunter	-0.02527851
guild.Orb.web.weavers	-0.10288348
guild.Ground.hunters	-0.21315526
Size_mean	-0.48169751
ballo.1	-0.49874186
guild.Sheet.web.weavers	-0.94922686

Fig. 30B

Variable	scores
guild.Specialists.	3.9872854
guild.Space.web.weavers	2.0928918
guild.vegetation_hunter	0.9455649
ballo.0	0.6816273
guild.Ground.hunters	0.6299402
guild.Sheet.web.weavers	0.5317879
Size_mean	0.3409466
ballo.1	-0.4100144
guild.Other.hunters	-0.6025188
guild.Ambush.hunters	-2.5202832
guild.Orb.web.weavers	-3.3926097

Fig. 30C

Variable	scores
cov_pool	0.214784142
cov_stream	0.20661109
cov_peatbog	0.198408538
topo_min	0.19212981
topo_median	0.192115363
topo_max	0.191918232
SD_humidity	0.161130758
cov_pond	0.139014744
SD_temperature	0.138207755
cov_forest_LI	0.119578339
max_temperature	0.111002135
d_pond	0.109652306
d_forest_Ab	0.079630259
cov_Reynoutria_japonica	0.013091234
d_pool	-0.015266497
cov_humid_grassland	-0.017552473
mean_temperature	-0.024739484
topo_mean	-0.094709511
cov_ruderal	-0.11475804
cov_high_urban	-0.116682578
min_temperature	-0.137954454
mean_humidity	-0.154146944
min_Humidity	-0.158325662
todo_delta	-0.162657925
cov_sea	-0.165395329
topo_SD	-0.173396372
rugo_median	-0.183658916
rugo_max	-0.195046284
rugo_mean	-0.195243573
rugo_SD	-0.198231568
cov_shore	-0.200104131
rugo_min	-0.204340976
cov_road	-0.214549749
cov_halophile	-0.21503576
cov_forest_Ab	-0.215292205
cov_heathland	-0.215523288
cov_urban	-0.2165801

Fig. 30D

Variable	scores
mean_temperature	0.425458386
d_forest_Ab	0.370448516
cov_forest_LI	0.313855551
cov_pond	0.240806336
SD_humidity	0.145093951
rugo_max	0.139708691
topo_mean	0.118091394
d_pond	0.111774763
rugo_SD	0.091057608
SD_temperature	0.08009863
cov_heathland	0.073842358
topo_delta	0.061222105
rugo_mean	0.03240909
cov_urba	0.029826946
cov_halophile	0.029771285
cov_road	0.023861312
cov_shore	0.022440476
cov_sea	0.020013367
min_temperature	0.006903318
cov_ruderal	0.003572548
cov_high_urba	-0.00119441
cov_forest_Ab	-0.008684207
rugo_median	-0.012294084
cov_Reynoutria_japonica	-0.019564595
d_pool	-0.028904874
cov_stream	-0.038021983
rugo_min	-0.056065727
cov_pool	-0.067918544
cov_peatbog	-0.069053749
topo_SD	-0.082085852
topo_median	-0.136492119
topo_min	-0.136597633
topo_max	-0.136620718
max_temperature	-0.264375409
mean_humidity	-0.266993744
min_humidity	-0.28905533
cov_humid_grassland	-0.356566713

APPENDIX 2: PROJECTED WEIGHT OF TRAITS AND VARIABLES FROM THE RLQ ANALYSIS

Fig. 32A

Traits	scores
disp_wind	0.9529711
disp_vegetativ	0.19855529
height(cm)	-0.14920917
SLA(cm/g)	0.13242317
seed_mass (mg)	0.10238592
disp_water	-0.0404383
disp_zoo	-0.02246043

Fig. 32B

Traits	scores
seed_mass (mg)	-0.62664157
disp_vegetativ	-0.55768136
disp_zoo	-0.35683294
disp_wind	-0.01070732
SLA(cm/g)	0.14744311
disp_water	0.17129352
height(cm)	0.3432004

Fig. 32C

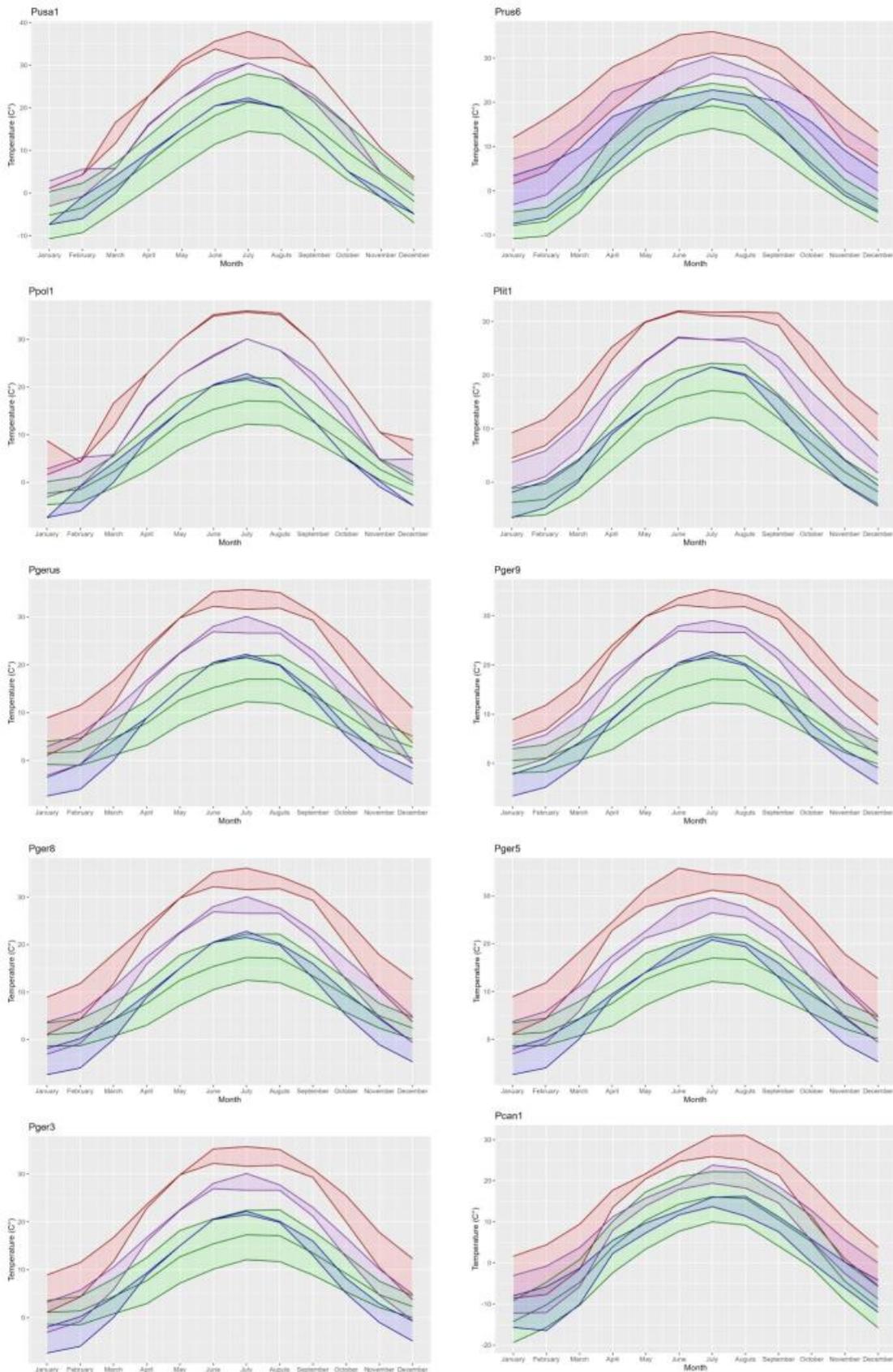
Variable	scores
cov_pool	0.237695895
cov_stream	0.230992081
cov_peatbog	0.222531435
topo_min	0.217370557
topo_median	0.217154046
topo_max	0.215882649
SD_humidity	0.215706328
cov_pond	0.214906481
SD_temperature	0.210816476
cov_forest_LL	0.210636389
max_temperature	0.209147195
d_pond	0.207181936
d_forest_Ab	0.194384081
cov_urban	0.157228684
cov_heathland	0.15284018
cov_forest_Ab	0.14502982
cov_halophile	0.112534252
cov_road	0.104995051
rugo_min	0.103817256
cov_Reynouthria_japonica	0.103762141
d_pool	0.013893385
cov_humid_grassland	0.01106119
cov_shore	-0.011034152
rugo_SD	-0.050734397
rugo_mean	-0.074890042
mean_temperature	-0.0840605
rugo_max	-0.106223951
rugo_median	-0.107384227
topo_mean	-0.121449285
cov_ruderal	-0.130680247
cov_high_urban	-0.131862424
topo_SD	-0.172871717
cov_sea	-0.173194853
topo_delta	-0.173299162
min_temperature	-0.179591252
mean_humidity	-0.182829746
min_humidity	-0.189679564

Fig. 32D

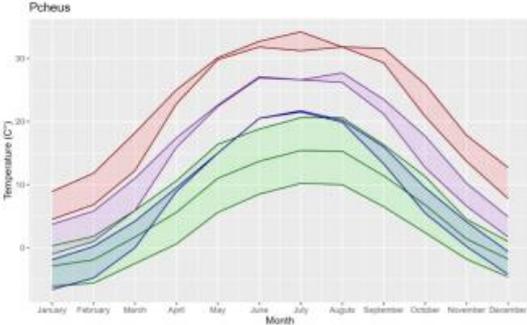
Variable	scores
topo_delta	0.232321233
cov_pool	0.206208872
rugo_mean	0.184673864
rugo_median	0.181501924
topo_max	0.17001649
topo_median	0.169217604
topo_min	0.169065067
cov_halophile	0.160547914
d_forest_Ab	0.15667934
cov_peatbog	0.153960833
cov_shore	0.150619502
rugo_SD	0.139364667
cov_sea	0.122232014
cov_pond	0.106461228
topo_mean	0.104452674
topo_SD	0.093628587
rugo_max	0.09247782
cov_urban	0.089503476
SD_temperature	0.082223628
mean_humidity	0.079593732
max_temperature	0.075510394
cov_stream	0.06754255
d_pond	0.050815513
cov_heathland	0.002543882
min_humidity	0.001928857
SD_humidity	-0.007666282
cov_road	-0.007948612
cov_forest_LL	-0.010866785
rugo_min	-0.052812901
cov_forest_Ab	-0.073201656
d_pool	-0.10570857
mean_temperature	-0.106769781
cov_humid_grassland	-0.133268074
min_temperature	-0.257959184
cov_high_urban	-0.345917319
cov_ruderal	-0.349609814
cov_Reynouthria_japonica	-0.434258011

APPENDIX 3: CLIMATE RECONSTRUCTION CURVES

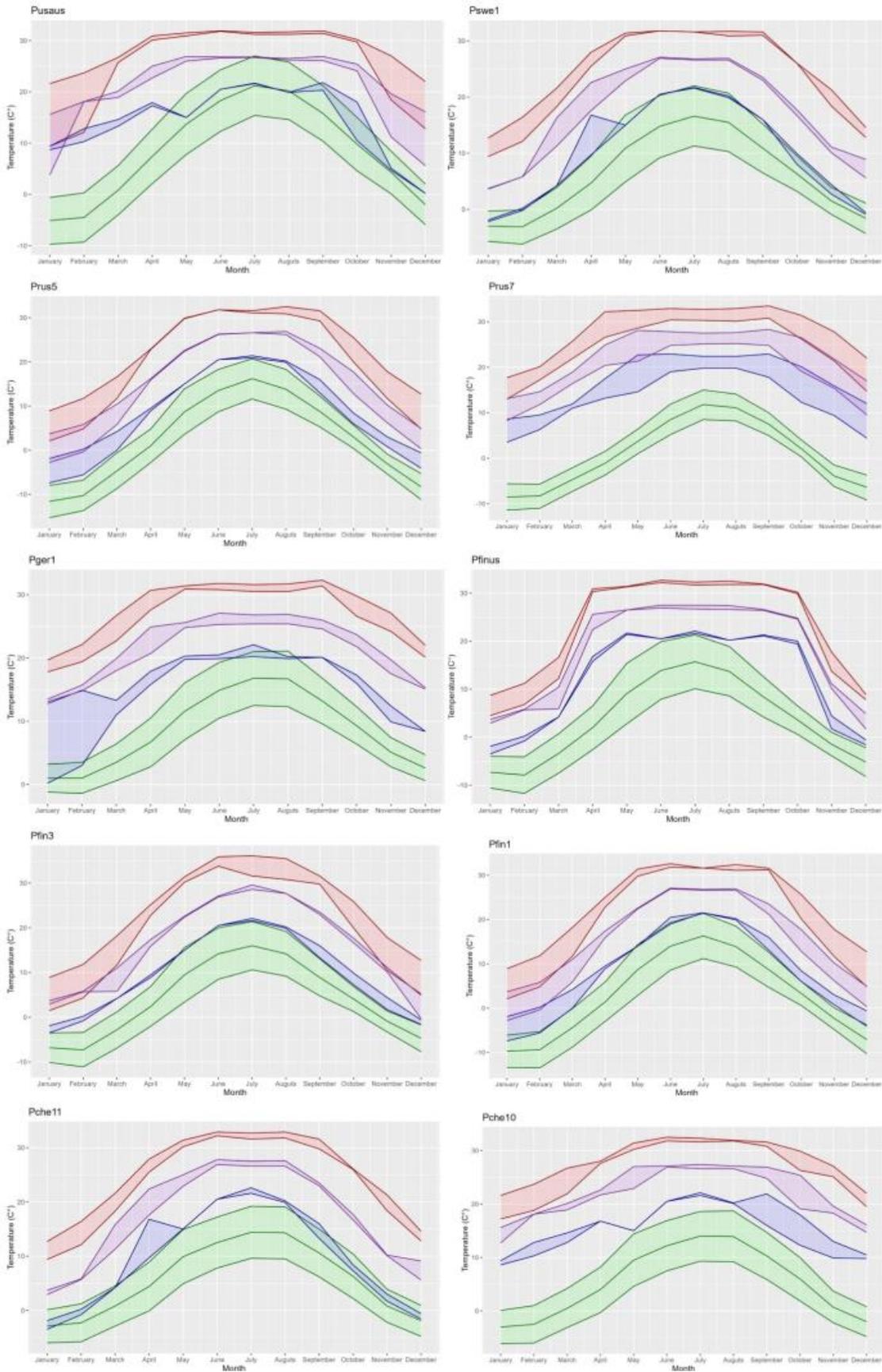
Appendix 3.1.1 Improved



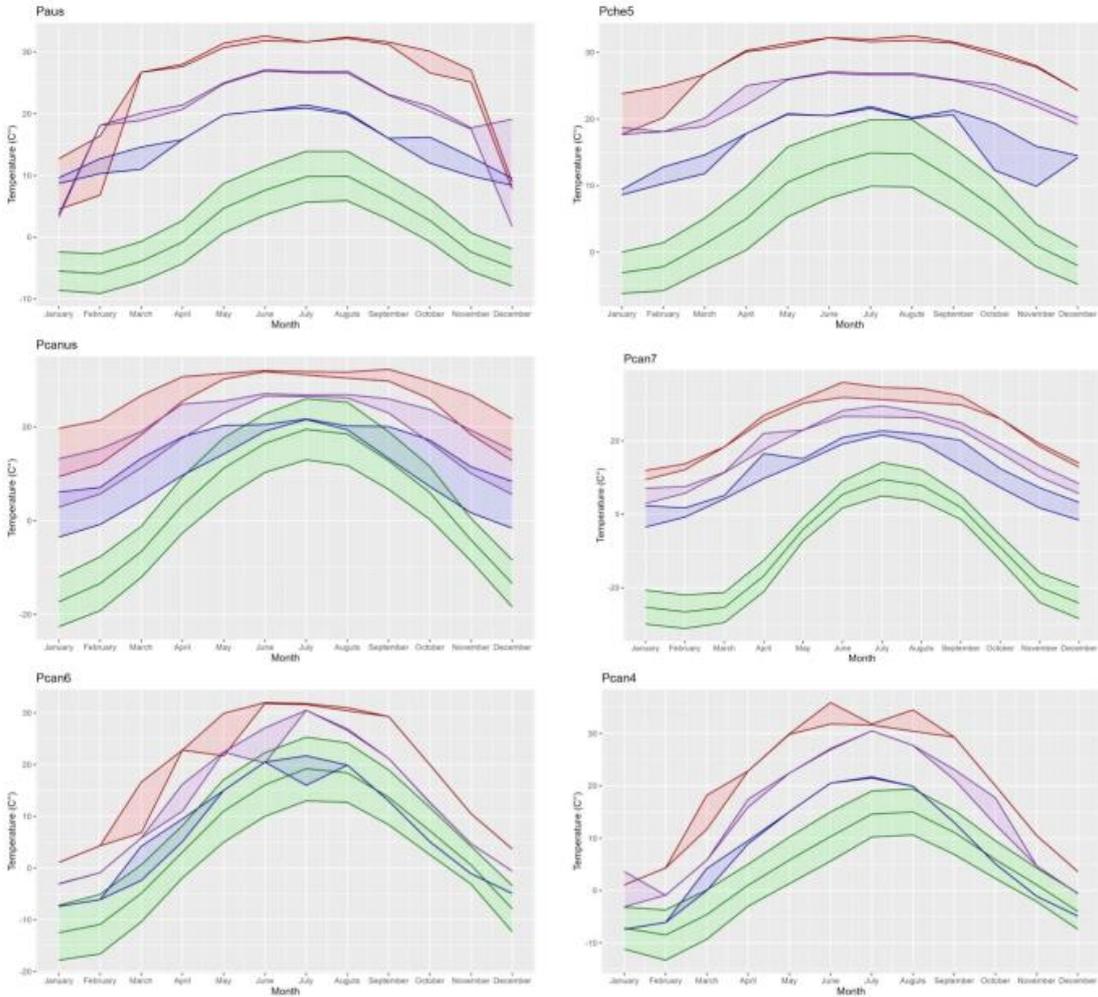
Appendix 3.1.2 Improved (continued)



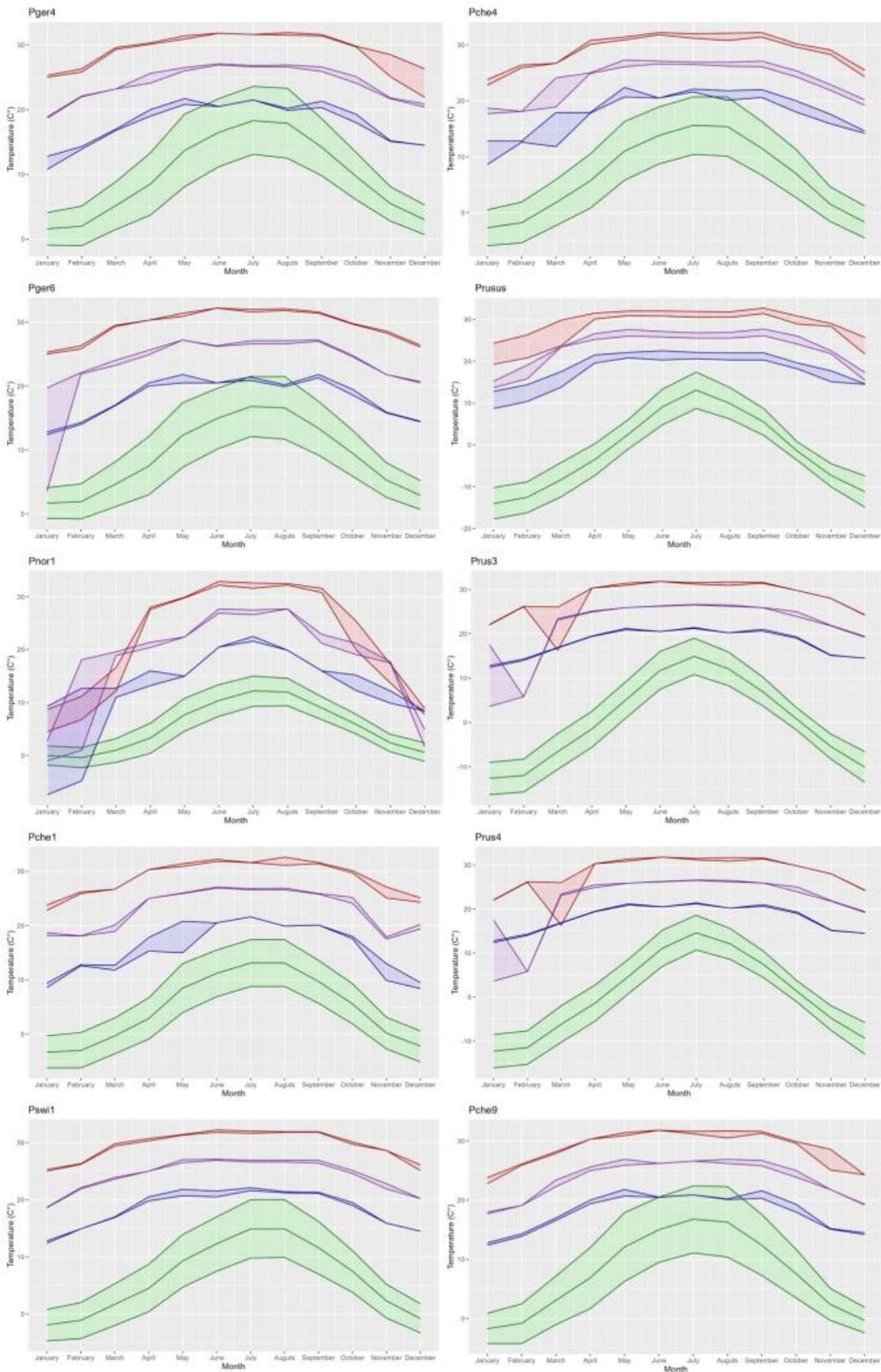
Appendix 3.2.1 Intermediate



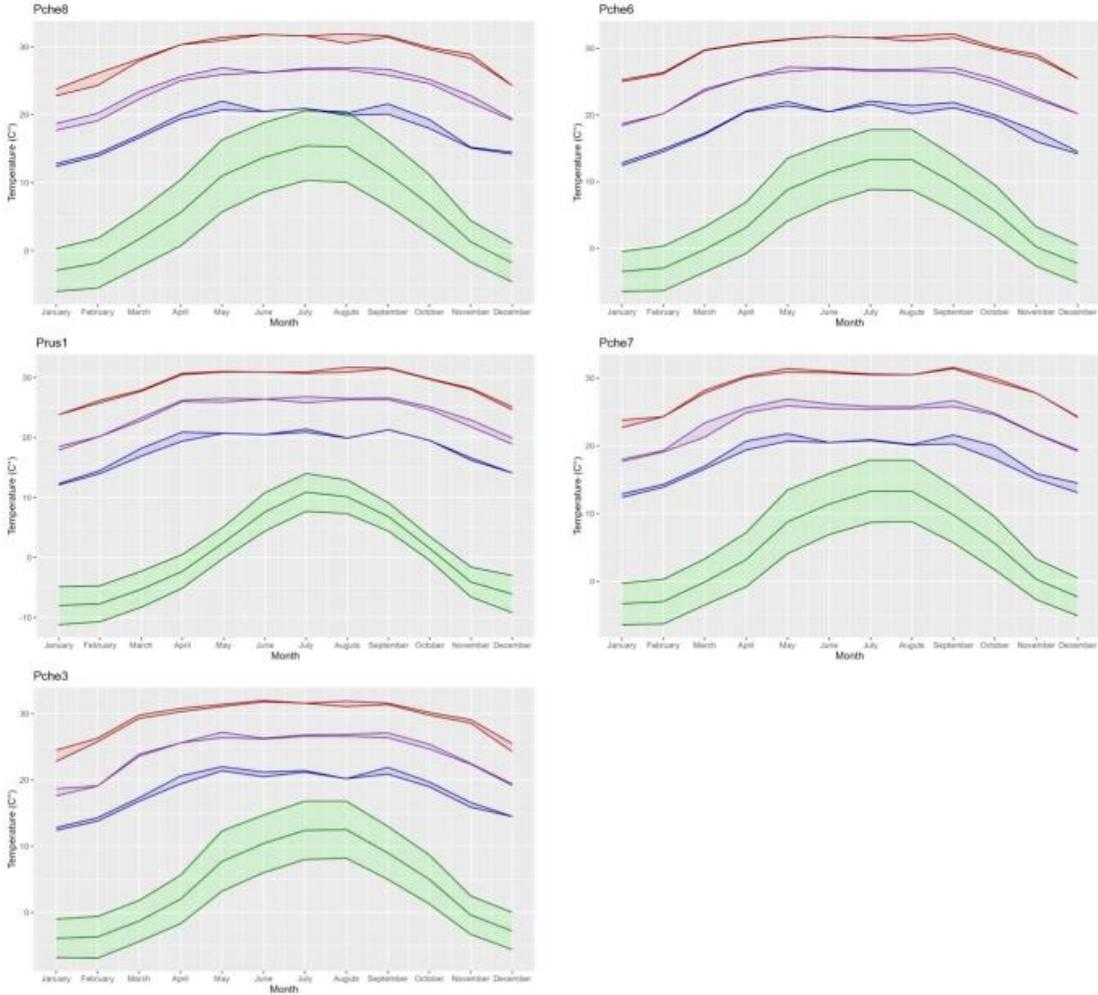
Appendix 3.2.2 Intermediate (continued)



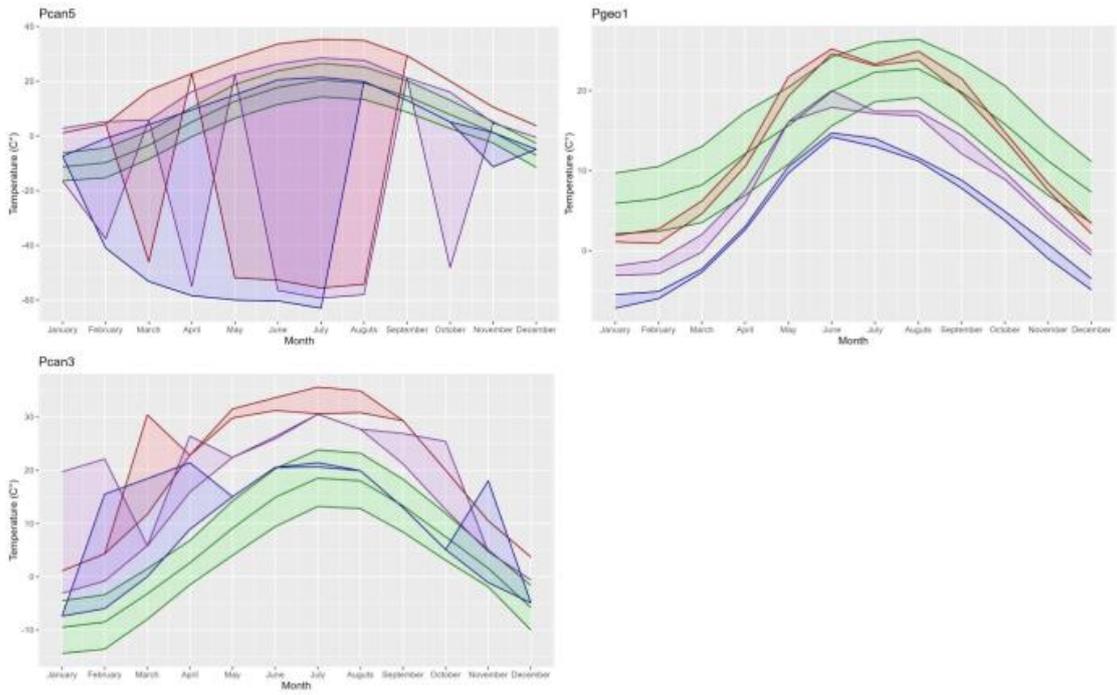
Appendix 3.3.1 Porr



Appendix 3.3.2 Porr (Continued)



Appendix 3.4 Miscellaneous



APPENDIX 4: CURRICULUM VITAE

Axel HACALA

7 route du Bouguen

29200 Brest, France

Tél. : 06 16 50 76 52

E-mail : axel.hacala@gmail.com

Né le 23/10/1991 à Saint-Pierre & Miquelon (France)



Doctorant : Conservation et dynamique des tourbières subarctiques: Les arthropodes et la végétation comme indicateurs écologiques à travers le temps sur l'archipel de Saint-Pierre et Miquelon.

• Compétences

- **Compétences naturalistes** : **Aranéologie** (taxonomie des araignées des régions tempérées/arctiques et parataxonomie des araignées tropicales), **Myrmécologie** (espèces bretonnes et Nord-Américaine), **Entomologie** (Odonata, Carabidae, Orthoptera, Syrphidae), **Oribatida** (Travail en paléoécologie sur des restes subfossiles d'oribates), **Ornithologie** (principalement pour l'avifaune d'Amérique du Nord)
- **Méthodes d'échantillonnages en écologie** : pièges Barber, D-Vac, pièges attractifs (fourmis), carottage paléoécologique, CMR (Capture Marquage Recapture), pêche électrique, relevés de végétation (quadrat et transect, phytosociologie), suivi ornithologique (IPA et sea-watching).
- **Anglais** courant et scientifique : Colloques internationaux, plusieurs séjours linguistiques, guide naturaliste pour public anglophone.
- **Informatique** : logiciels de traitements statistiques (R.), SIG (Qgis), Logiciel de bioinformatique (Geneious), logiciels de traitements d'images (Photoshop, Gimp) et programmes courants (ex : suite Office).

• Activités / Expériences professionnelles

- 2023
- **Septembre** : Intervention d'enseignement de terrain sur l'échantillonnage et l'écologie des arthropodes forestier pour les étudiants de L3 à l'Université de sciences de Brest.
 - **Juin** :
 - Vacataire d'enseignement en taxonomie, méthode et pratique en écologie pour des étudiants de Master 1 à l'Université de sciences de Brest.
 - Intervention orale durant **les journées scientifiques de l'école doctorale EGAAL 2023** sur le thème des diversités d'araignées en tourbières subarctique à différentes échelles spatiales.
 - **Mars** : Intervention orale dans le colloque **22nd International Congress of Arachnology 2023** sur le thème « Small and large spatial scales: drivers of spider diversities in sub-arctic peat bogs».
 - **Janvier & Février** :

APPENDIX 4: CURRICULUM VITAE

- Vacataire d'enseignement en taxonomie pour des étudiants de Licence 3 à l'Université de sciences de Brest (Cours Magistrale et Travaux pratiques).
 - Encadrement d'une stagiaire de L3 BOPE sur un stage de découverte des méthodes de laboratoire en écologie terrestre.
- 2022
- **Septembre** : Intervention orale dans le colloque **Congrès des sciences de la mer de Saint-Pierre et Miquelon 2022** sur le thème «Comparaison des réponses aux contextes paysagés des araignées et de la végétation des tourbières de Saint-Pierre et Miquelon».
 - **Aout** : cosignataire d'un poster issue du projet Etrezh intitulé «Assessing wetland restoration using vegetation and spiders as indicators» présenté au colloque **SER Europe**.
 - **Mars à Aout** : Encadrement d'un stagiaire de M2 sur l'analyse de communautés arthropodes.
 - **Mai** :
 - Vacataire d'enseignement en taxonomie, méthode et pratique en écologie pour des étudiants de Master 2 et de Licence 3 à l'Université de sciences de Brest.
 - Présentation d'un poster : « les liens entre les diversités des communautés végétales et facteurs locaux : exemple des tourbières de Saint-Pierre et Miquelon » au colloque **ECOVEG 2022**.
- 2021
- **Decembre** : Cosignataire d'un poster dans le colloque **BES-SFE** intitulé « Comparative of taxonomic diversity of plants and arthropods as indicators of salt-marsh restoration ».
 - **Septembre** : Cosignataire d'une intervention dans le colloque **Congrès Franco-Canadien sur sciences aquatique de Saint-Pierre et Miquelon** sur le thème « Diversité génétique chez les baleines à bosse : pourquoi s'en soucier, et qu'en sait-on à Saint-Pierre et Miquelon ? ».
 - **Août** : Intervention dans le colloque **European Congress of Arachnology** sur le thème : « Driver of spider diversities on maritime heathlands ».
 - **Juillet** : Encadrement d'un stagiaire de L3 BOPE sur un stage de découverte des méthodes en écologie terrestre, de terrain et de laboratoire.
 - **Avril** :
 - Vacataire d'enseignement en taxonomie pour des étudiants de Licence 3 à l'Université de sciences de Brest.
 - Début d'un mandat de 5 ans comme membre du conseil scientifique territorial du patrimoine naturel de Saint Pierre et Miquelon.
 - **Janvier** : cosignataire d'un poster issue du projet Etrezh intitulé « Évaluation de la restauration de zones humides en Bretagne - Indicateurs floristiques et entomologiques » présenté au colloque **REVER 11**.

- 2020
- **Septembre à octobre** : vacataire d'enseignement en taxonomie, méthode et pratique en écologie pour des étudiants de Master 2 et de Licence 3 à l'Université de sciences de Brest.
 - **Août** : Intervention sur les méthodes d'échantillonnages en écologie dans le cadre d'une école thématique organisée par **Sébastien Gallet** de l'Université de sciences de Brest.
 - **Mai à novembre** : poste de chargé d'étude environnementale sur des missions d'inventaires d'assemblages d'arthropodes et d'analyse de données pour le programme ETHREZ – laboratoire **ECOBIO**, Rennes. Inclus l'encadrement d'un stagiaire de M1 GCBio sur des méthodes de terrain en écologie terrestre, de terrain et de laboratoire.
 - **Février** : Conception et animation d'une conférence sur l'écologie des Araignées à l'Université de Science de Brest (29) pour l'association le Cercle étudiant naturaliste Brestois.
- 2019
- **Octobre à décembre** :
 - Stage à **ECOBIO** encadré par **Julien Pétilion**. Etude des métriques fonctionnelles et phylogénétiques appliquée à l'écologie des communautés d'arthropodes.
 - Intervention au colloque **RESTOBS** sur : « les arthropodes, des indicateurs de restauration ? »
- 2018
-
2019
- **Actions académiques ponctuelles** : enseignement en taxonomie des arthropodes en License 3 et Master 1 à l'Université de sciences de Brest. Travaux sur des publications scientifiques. Participation à l'encadrement d'un stage de Master 2 à l'Université de sciences de Brest. Renforcement du réseau scientifique en vue du montage d'un projet de thèse. Conception et animation de trois conférences sur la taxonomie et l'écologie des Araignées ainsi que d'une action pédagogique sur le terrain pour l'association Bretagne Vivante à Brest (29). Cosignataire d'une intervention intitulée « Evaluation of the impact of the invasion of *Baccharis halimifolia* on saltmarshes » au colloque **SFE**.
- 2017
- **Décembre** : sélectionné à l'oral pour une thèse sur l'étude d'une espèce d'araignée avec des enjeux de conservation.
 - **Avril à Septembre** – stage de M2 pour le laboratoire de **Géoarchitecture** à l'Université de sciences de Brest avec **Jérôme Sawtschuck**, **Maxime Le Roy**, **Julien Pétilion**. Etude des communautés d'arthropodes comme indicateurs de restauration sur les hautes falaises maritimes de Bretagne avec un accent sur les araignées et les fourmis.
 - **Août** – sélectionné en 4ème position pour un poste de contractuel enseignant en biologie animale dans L'UFR Sciences de Brest.
 - **Juillet** – sélectionné à l'oral pour une thèse sur l'utilisation des fourmis comme bioindicateur de restauration.
 - **Février** : Conception et animation d'une conférence sur l'écologie des Araignées à l'Université de Science de Brest (29) pour l'association le cercle étudiant naturaliste Brestois.

APPENDIX 4: CURRICULUM VITAE

- 2016
 - **Août** – guide naturaliste à la Maison de la nature et de l'environnement à Saint-Pierre et Miquelon.
 - **Juillet** – stage en organisation d'une base de données et analyses statistiques sur les populations de mammifères marins (suivi de population et analyse spatiale) de Saint-Pierre et Miquelon, réalisé pour l'association FNE Saint-Pierre et Miquelon avec **Jean-Luc Jung**.
 - **Avril à Mai** – stage de Master 1 pour le laboratoire de **Biodiversité et Gestion des Territoires** avec **Julien Pétilion** à l'Université de Rennes 1 : étude de la diversité taxonomique et fonctionnelle d'araignées le long d'un gradient d'habitat en forêt tropicale.
- 2015
 - **Juillet** (2 semaines) – relevés qualitatifs, faunistiques et floristiques pour le groupe d'étude Artelia à Saint-Pierre et Miquelon dans le cadre d'une étude d'impact.
 - **Janvier à Avril** – stage d'introduction à la recherche réalisé à l'UQAR (Université du Québec à Rimouski) dans la chaire de recherche **Biodiversité nordique** avec **Joël Betty** : étude exploratoire du régime alimentaire de la buse pattue (*Buteo lagopus*) et des communautés de micromammifères de l'île Billot en Arctique à travers l'analyse des pelotes de réjection des rapaces.
- 2013
à
2015
 - **Juillet & Aout** – guide naturaliste à la Maison de la nature et de l'environnement à Saint-Pierre et Miquelon.
- 2013
 - **Juin** – stage volontaire à l'IUEM (Institut Universitaire Européen de la Mer) Brest : assistant d'une doctorante sur le projet **MAVERIQ** : Macro-algues vertes sur les réseaux trophiques et en particulier sur la fonction de nurserie des plages de sable en Bretagne.
- 2011
 - **Mai à Aout** – Stage de BTS comme guide naturaliste pour la Maison de la nature et de l'environnement à Saint-Pierre et Miquelon.
- 2010
 - **Juillet & Aout** – stage volontaire pour l'association SPM frag'iles à Saint-Pierre et Miquelon : recensement d'une espèce exotique invasive végétale (*Fallopia japonica*). Mise en place et test de protocole de destruction.
- 2009
 - Plusieurs bénévolats pour des comptages d'oiseaux marins à St Pierre & Miquelon.

• Formations

- 2016-2017 • **Master 2** en gestion et conservation de la biodiversité à l'Université des sciences de Brest (Finistère, France).
- 2015-2016 • **Master 1** en écologie fonctionnelle, comportementale et évolutive à l'Université de Rennes 1 (Ille-et-Vilaine, France)
- 2012-2015 • **Licence** de biologie des organismes et des populations à l'UFR Science de l'Université de Brest (France) et à l'UQAR à Rimouski (Canada).
- 2010-2012 • **BTS** Gestion et protection de la nature, option Animation au LEGTA de Morlaix (Finistère).
- 2009-2010 • **Baccalauréat** scientifique, spécialité Sciences et Vie de la Terre (option art) à Saint-Pierre (Saint-Pierre et Miquelon).

• Publications

- Axel Hacala, Manuel Simon Salgueiro, Allison Bain, Dominique Marguerie, Julien Pétilion (2024) **Spider and vascular plant assemblages in subarctic peat bogs are complementary ecological indicators of variation in local and landscape factors.** *Ecological Indicators* 158(111389).
- Axel Hacala, Denis Lafage, Andréas Prinzing, Jérôme Sawtschuck, Julien Pétilion (2021) **Drivers of taxonomic, functional and phylogenetic diversities in dominant ground-dwelling arthropods of coastal heathlands.** *Oecologia*, 197(2): 511-522.
- Axel Hacala, Maxime Le Roy, Jérôme Sawtschuck, Julien Pétilion (2020) **Comparative réponses of spiders and plants to maritime heathland restoration.** *Biodiversity and Conservation*, 29(1), 229-249.
- Axel Hacala, Clément Gouraud, Wouter Deckonink, Julien Pétilion. (2021) **Relative efficiency of pitfall vs. bait trapping for capturing taxonomic and functional diversities of ant assemblages in temperate heathlands.** *Insects*, 12(4), 307.
- Stefano Mammola, ..., Axel Hacala, *et al.* (2022) **The global spread of misinformation on spiders.** *Current Biology*, 32:855-873.
- Stefano Mammola, ..., Axel Hacala, *et al.* (2022) **An expert-curated global database of online newspaper articles on spiders and spider bites.** *Scientific Data*, 9:109.

APPENDIX 4: CURRICULUM VITAE

- Stefano Mammola, Julien Pétilion, Axel Hacala, Jérémy Monsimet, Sapho-Lou Marti, Pedro Cardoso, Denis Lafage (2021) **Challenges and opportunities of species distribution modelling of terrestrial arthropods**. Diversity and Distribution, 00: 1-19.
- Axel Hacala & Clément Gouraud (2019) **Découverte de Tetramorium atratum (Schenck, 1852) dans une lande littorale de Belle-Île-en-Mer**. Invertébrés Armoricaux, 20: 53-57.
- Tristan Maury-Caudal & Axel Hacala (2023) **Première mention de Lamprodila mirifica (Mulsant, 1855) en région Pays de la Loire (Coleoptera : Buprestidae)**. Invertébrés Armoricaux, 25: 1-5.
- Kaïna Privet, Axel Hacala, Tomáš Hamřík, Greg Lamarre, Julien Pétilion (*in prep.*) **Complementary of taxon- vs. trait-based metrics to understand tropical diversity patterns – A case study using spider assemblages of neotropical forests**.
- Caudal Pascaline, Axel Hacala, Sébastien Gallet (*in prep.*) **Carabidae and vegetation responses to the specific management regime of military training areas under Natura 2000**.

• Travaux de vulgarisations, communication et d'animation

- Interview, télévisuel et radiophonique, de présentation de publication scientifique pour **SPM la 1^{er}**
- Interview pour **le Compteur Biodiversité des outre-mer** par l'UMS PAtriNat, 2023.
- Participation comme scientifique associé à un projet de **PASSAGERS DES SCIENCES** 2023.
- Interview pour **Science Ouest**, article sur les tourbières (Février 2023).
- **Fête de la science** : stands sur la découverte des araignées 2022 & 2016.
- Présentation des campagnes de terrain de thèse 2021 et 2022 respectivement au **journal télévisé de SPM la 1^{er}** et sur **l'antenne radio SPM la 1^{er}**.
- **Intervention dans les écoles de Saint-Pierre et Miquelon** (septembre 2022) (classes de 6^{ème} et terminale).
- Animation avec **la Maison de la Nature et de l'Environnement** (aout 2022) découverte des araignées avec des CP.
- Présentation au forum des anciens étudiants du **master GCBio** 2022.
- **Table ronde des métiers de l'environnement** 2022.
- **Documentaire** : « l'homme des tourbières » 2021.
- Conférences sur l'écologie des araignées pour le **CENB** 2020 & 2017.
- Animations sur l'écologie des araignées pour **Bretagne vivante** 2021, 2019, 2018 & 2017.

• Références

- **Julien Pétilion** : Professeur à l'Université de Rennes, Laboratoire ECOBIO : julien.petillon@univ-rennes.fr
- **Dominique Marguerie** : Directeur de recherche CNRS, Université de Rennes, Laboratoire ECOBIO : dominique.marguerie@univ-rennes.fr
- **Sébastien Gallet** : Enseignant-chercheur à l'Université de Bretagne Occidentale, Laboratoire Géoarchitecture : sebastien.gallet@univ-brest.fr

• Intérêts & activités

- Membre d'associations naturalistes & scientifique :
 - AAS (American Arachnological Society)
 - AsFrA (Association Française d'Aranéologie)
 - Bretagne vivante (action d'identification de *Carabidae* et de *Syrphidae*).
 - CENB (Cercle des Etudiants Naturalistes Brestois). Vice-président en 2014
 - CENR (Cercle Etudiants Naturalistes Rennais)
 - CPN (Connaitre et Protéger la Nature)
 - ESA (European Society of Arachnology)
 - FNE SPM (France nature environnement, l'antenne de Saint-Pierre et Miquelon)
 - Gretia (Groupe d'Etude des Invertébrés Armoricaains)
 - ISE (International Society of Arachnology)
 - REVER (Réseau d'Échanges et de Valorisation en Écologie de la Restauration)

Titre : Conservation et dynamique des tourbières subarctiques : les arthropodes et la végétation comme bioindicateurs à travers le temps sur l'archipel de Saint-Pierre et Miquelon (France)

Mots clés : Néoécologie, Paléoécologie, Araignées, Oribates, Macrofossile, Pollen.

Résumé : Dans une période de changements climatiques et de destructions des zones humides, l'étude des tourbières apparaît cruciale du fait de la riche biodiversité qu'elles hébergent et des archives sédimentaires et biologiques qu'elles constituent. La dynamique des tourbières peut s'étudier à travers plusieurs disciplines et sur des échelles de temps variées. Afin de traiter cette complexité, les qualités bioindicatrices de la végétation et des arthropodes ont été comparées. En néoécologie, nous avons étudié les effets paysagers en appliquant une approche multimétrique sur les araignées et les plantes. Nous avons observé, à travers la diversité taxonomique et fonctionnelle, alpha et bêta ainsi que les ordres de diversité de Hill, les réponses de la diversité des tourbières. Une grande complémentarité des taxons et des métriques a été mise en évidence.

En paléoécologie, le potentiel des Acariens Oribatides comme indicateurs de reconstruction climatique a été étudié. Cela a été réalisé en croisant les assemblages actuels d'oribates avec le climat actuel afin d'évaluer les erreurs de reconstruction. Cela a permis de souligner le manque de données disponibles sur les oribates pour ce genre de méthode. Enfin, nous avons étudié la dynamique des habitats et du climat au cours des deux derniers millénaires à travers l'analyse paléoécologique d'une tourbière de Saint-Pierre en croisant les oribates, les macrofossiles végétaux et le pollen. Une dynamique de variation hydrologique et climatique conformes aux spécificités régionales a été observée. Cette approche pluridisciplinaire a permis d'accroître les connaissances sur la dynamique des tourbières et d'évaluer et renforcer les indicateurs utilisés, métriques comme taxons, en fonction des hypothèses testées.

Title : Conservation and dynamics of sub-arctic peat bogs: arthropods and vegetation as ecological bioindicators over time in the archipelago of Saint-Pierre et Miquelon (France)

Keywords : Neoecology, Paleoecology, Spiders, Oribatida, Macrofossil, Pollen.

Abstract : At a time of climatic change and destruction of wetlands, studying peatbogs is essential given the rich biodiversity they harbor and the sedimentary and biological archives they constitute. Peat bog dynamics can be studied through various disciplines and time scales. To address this complexity, the bioindication quality of spiders and plants was compared. In neoecology we investigated the effects of landscape through spiders and plants comparison in a multimetrics approach. We observed through taxonomic and functional diversity, alpha and beta as well as Hill's diversity orders, the specific responses of peat bogs' diversity. A high degree of complementarity between taxa and metrics was highlighted. In paleoecology, we investigated the oribatid mites potential as potential

indicators for climate reconstruction. This was achieved by crossing current oribatid assemblages with current climate to assess the reconstruction errors, and eventually highlighted how the limited available oribatid data was a for such a method. Lastly we investigated the habitat and climate dynamics over the last two millennia through multitaxa paleoecological analysis of a peat bog in Saint-Pierre crossing oribatid mites, vegetation macrofossils and pollen. This highlighted a hydrologic and climatic dynamic that match regional specificities. This pluridisciplinary approach has allowed to increase the knowledge of peat bog dynamics and to evaluate and strengthen the indicators used to this end, both taxa and metrics according to the tested hypotheses.