



Modélisation des interactions tout-partie en écologie et évolution : structure spatiale et sélection multi-niveaux

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THÈSE

Pour obtenir le grade de

DOCTEUR DE L'UNIVERSITÉ SAVOIE MONT BLANC

Spécialité : Biologie des Populations Écologie

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Présentée par

Léo LEDRU

Thèse dirigée par **Christiane GALLET** et
co-encadrée par **Jimmy GARNIER** et **Sébastien IBANEZ**

préparée au sein du **Laboratoire d'Écologie Alpine**
dans l'**École Doctorale Chimie Sciences du Vivant**

Modélisation des interactions tout-partie en écologie et évolution : structure spatiale et sélection multi-niveaux

Thèse soutenue publiquement le **7 Décembre 2021**,
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CHAPITRE I

INTRODUCTION GÉNÉRALE

Une explication historique ne repose pas sur des déductions directement tirées des lois de la nature, mais d'une séquence imprévisible d'états antécédents, dans laquelle tout changement majeur à n'importe quel stade altérerait le résultat final. Ce dernier est contingent, en ce sens qu'il est dépendant de tout ce qui s'est produit auparavant – c'est ainsi que l'histoire impose sa marque ineffaçable.

La vie est belle
Stephen Jay Gould

I.1 Préambule

Après de longues réflexions il nous paraît plus sage et pertinent de débiter cette thèse par un court récit de son historicité.

La problématique initialement envisagée était d'explorer comment la sélection naturelle pouvait s'exercer à l'échelle des écosystèmes à travers la théorie de sélection multi-niveaux. Nous utilisons pour cela une approche par modélisation. Effectivement, les mathématiques et la modélisation constituent des outils puissants en écologie et en évolution pour étudier des processus qu'il est difficile, si ce n'est impossible, d'explorer de manière empirique ([Huneman and Dutreuil, 2014](#)). Ainsi, un modèle d'écosystème primaire a été développé avec l'objectif à plus long terme de mettre en interactions plusieurs versions de cet écosystème au sein d'un méta-écosystème. Cependant, les nouveautés méthodologiques (et les réflexions conceptuelles associées) qui sont apparues lors de l'émergence de ce modèle d'écosystème primaire nous ont motivé à le valoriser avant de s'engager plus avant. Finalement, cette valorisation constitue le premier chapitre de la thèse ; et la question de la sélection au niveau de l'écosystème fait partie de ses perspectives. Un deuxième travail s'intéressant à l'émergence du mutualisme dans un système hôte-symbiote alimente la problématique initiale puisque cette émergence fait appel à plusieurs niveaux de sélection, dont le niveau supérieur correspond à un écosystème minimaliste à deux espèces. Enfin, un troisième volet explore la dynamique d'invasion d'un insecte herbivore avec une approche purement écologique et n'est donc qu'indirectement en lien avec la problématique principale. Cependant, un cadre con-

ceptuel élargi permet de l'intégrer aux réflexions issues des deux premières parties . Ces travaux forment les trois chapitres qui suivent l'introduction générale. Nous les présentons ici succinctement et montrerons ensuite dans quelle mesure ces trois travaux peuvent converger au sein d'un cadre conceptuel.

Chapitre II : Causalité réciproque entre échelles spatiales locale et globale.

Ce travail concerne l'invasion en Europe de la pyrale du buis, un insecte herbivore originaire d'Asie. Celui-ci a débuté avant la thèse, en seconde année de Master, mais la première année de thèse a été en partie consacrée à son approfondissement, notamment sur son versant théorique. La question centrale est celle de la stabilité du système pyrale-buis à l'échelle de la métacommunauté malgré son instabilité locale. Pour cela nous développons un modèle simulant l'interaction entre la pyrale et sa ressource dans un espace en deux dimensions. Les paramètres clés du modèle sont calibrés à partir de la littérature, de mesures sur le terrain et d'une manipulation en mésocosme. Nous montrons que malgré la sur-exploitation de la ressource localement, ce qui mène irrémédiablement à l'extinction locale de la pyrale, la coexistence est possible à l'échelle de la métacommunauté en fonction de la distance de dispersion de la pyrale. Cette coexistence dépend de la structure spatiale de la ressource, elle-même modulée par la dispersion de la pyrale. Ces résultats dépassent le cadre strict du système pyrale-buis et montrent dans quelle mesure un système localement instable peut être stable à travers ses interactions au sein d'une échelle spatiale supérieure.

Ce chapitre est constitué d'un papier intitulé "Spatial structure of natural boxwood and the invasive box tree moth can promote coexistence" accepté dans *Ecological Modelling* en Novembre 2021. Une partie des résultats relevant de l'écologie appliquée a été présentée oralement au colloque "Buis, enjeux, renouveau et renaissance des jardins", à Orléans en 2019. De plus, les résultats ont fait l'objet d'un poster durant le "Annual Meeting of the Ecological Society, GfÖ" de 2019, à Münster en Allemagne. Enfin, la manipulation en mésocosme réalisée pour paramétrer le modèle a également donné lieu à un projet de description de la réponse métabolique du buis (approche métabolomique) et de ses conséquences écosystémiques (activités enzymatiques du sol associé) porté par Christiane Gallet. Cette manipulation a également été le cadre d'un stage de première année de Master pour Aristide Chauveau.

Chapitre III : Causalité réciproque entre niveaux de sélection.

Cette problématique qui a émergé au cours de la thèse s'inscrit pleinement dans le cadre de la théorie de sélection multi-niveaux. Nous explorons comment une relation mutualiste entre un hôte et son symbiote peut émerger d'une relation initialement parasite en coévoluant avec la dispersion. Tout processus de choix du partenaire a été exclu, considérant que ce type de processus requiert des adaptations trop spécifiques pour expliquer une première émergence du mutualisme. Nous développons un modèle individu-centré avec un espace en deux dimensions dans lequel l'interaction hôte-symbiote détermine la fécondité de chacun des partenaires. Nous montrons que la transition du parasitisme vers le mutualisme peut se produire par la coévolution avec une dispersion locale. En effet, cette dispersion locale permet l'émergence d'une structure spatiale

avec la formation de groupes constitués de phénotypes proches. Alors que la sélection au niveau de l'individu favorise la sélection du parasitisme, la sélection au niveau du groupe favorise le mutualisme. Cependant, lorsque les conditions sont défavorables à l'évolution du mutualisme (pas de coût à la dispersion globale), la transition nécessite une compétition globale entre les hôtes qui rend les couples parasites non-viables. Cette compétition implique le niveau d'organisation de l'ensemble du paysage qui favorise également la sélection du mutualisme. Ainsi, c'est la résultante du conflit entre les pressions de sélection au niveau de l'individu, du groupe et du paysage global qui détermine si la transition du parasitisme au mutualisme est possible.

Ce chapitre est constitué d'un papier intitulé "Mutualists construct the ecological conditions that trigger the transition from parasitism" actuellement en cours de revue à Peer Community in Evolutionary Biology (retour de première revue). Les co-auteurs incluent Mathias Rohr qui a été en stage durant 6 mois dans ce projet.

Chapitre IV : Causalité réciproque entre individus, niveaux trophiques et communauté.

Ce travail, issu du modèle d'écosystème primaire développé pour la problématique initiale, explore l'effet de l'évolution de différentes stratégies d'acquisition de ressources chez les consommateurs sur le fonctionnement de la communauté. Nous développons un modèle simulant l'émergence d'une communauté formée de ressources et de consommateurs à partir de l'interaction entre les dynamiques écologique et évolutive. Une propriété importante du modèle est la dynamique évolutive de la stratégie d'acquisition des ressources des consommateurs (Adaptive Foraging, noté AF dans la suite du document). La littérature montre que l'AF joue un rôle important dans le fonctionnement des écosystèmes, notamment en influençant leur stabilité. Cependant, les modèles suggérant ce lien ne considèrent ni la dynamique évolutive de l'AF, ni l'émergence de la communauté, ce qui rend impossible l'étude de certaines interactions comme le lien entre AF et diversité. En incluant la dynamique évolutive de l'AF, ainsi que la diversification des ressources et des consommateurs, notre modèle permet l'étude des interactions au sein de la triade AF-diversité-stabilité dans un contexte éco-évolutif. Le premier résultat est une évolution par sélection naturelle de l'AF dépendante des conditions. Ensuite, nous montrons que l'évolution de l'AF se traduit par un effet positif sur la diversité de l'ensemble de la communauté ressources et consommateurs. Cependant, l'effet sur la stabilité est plus contrasté puisque les trois types de perturbations que nous utilisons ont des effets différents : l'AF a un effet négatif sur la stabilité face à des changements progressifs, et un effet positif lorsque le changement est brutal. Par ailleurs, l'effet de l'AF sur la stabilité peut être direct ou indirect via son effet sur la diversité.

Ce chapitre est constitué d'un papier prochainement soumis intitulé "The evolution of adaptive foraging mitigates the Biodiversity Ecosystem Functioning relationships". Parmi les co-auteurs figure Océane Guillot qui a été en stage durant 6 mois au sein de ce projet. Les résultats de ce chapitre ont été présentés oralement au colloque international "Annual Meeting of the Ecological Society, GfÖ" de 2019, à Münster en Allemagne, ainsi qu'au colloque du groupement de recherche TheoMoDive la même année.

I.2 Des interactions entre niveaux d'organisation à la pensée dialectique

I.2.1 Niveaux d'organisation

Dans l'ensemble de cette thèse, nous considérons plusieurs niveaux d'organisation différents partageant des interactions causales multidirectionnelles. Nous détaillerons ces interactions entre niveaux dans les introductions respectives de chacun des travaux. Ainsi, dans la première partie nous pouvons différencier deux niveaux d'organisation au sein du système plante-herbivore : la communauté locale et la metacommunauté constituée de toutes les communautés locales présentes dans le paysage global. Dans la deuxième partie, les niveaux d'organisations sont multiples au sein du système hôte-symbiote : l'organisme (symbiote ou hôte), le couple symbiote-hôte, le groupe formé de plusieurs couples symbiote-hôte, et enfin l'ensemble des organismes à l'échelle du paysage dans lequel s'organise une compétition densité dépendante. Enfin, dans la dernière partie, nous distinguerons trois niveaux d'organisation : l'individu (ressource et consommateur avec leur stratégie de consommation), le niveau trophique (deux niveaux : ressources et consommateurs), et la communauté ressources-consommateurs. Dans ces trois parties, les différents niveaux d'organisation interagissent entre eux. De plus, les interactions peuvent avoir des directions multiples, c'est-à-dire que le niveau d'organisation A peut avoir une relation causale vers le niveau d'organisation B, mais celui-ci peut aussi avoir une relation causale vers le niveau A, induisant un processus de bouclage, ou de causalité réciproque ([Svensson, 2018](#)).

I.2.2 La vision mécaniste

La vision mécaniste découle de Descartes, qui en 1637 dans "Discours de la méthode" décrit toutes choses dans l'univers, y compris les êtres vivants, à travers la métaphore de la machine. Cette métaphore n'a rapidement plus été considérée comme telle et est devenue une approche épistémique ([Biasetti, 2020](#)), c'est-à-dire une description du monde à adopter pour accéder à des connaissances sur ce monde. Cependant, la vision mécaniste implique des postulats discutables :

- le postulat d'aliénation, *sensu* [Levins and Lewontin \(1985\)](#) : toute chose est vue comme étant composée de sous-éléments distincts dont les propriétés sont indépendantes du tout dont ils font partie ;
- le postulat de réductionnisme : il existe des éléments fondamentaux dont les propriétés causent les propriétés des tous complexes dont ces éléments font partie ;
- le postulat de déterminisme : la connaissance des propriétés des éléments fondamentaux permet de prédire les propriétés des tous complexes dont ils font partie.

Cette vision mécaniste et réductionniste (Figure I.1a et b) est à l'origine, entre autres, dans le domaine de la biologie de la vision gène-centrée (Gould, 2002). En ce qui concerne son application au développement des organismes (qui ne sera pas détaillé plus avant) nous signalons simplement les critiques qui ont émergé notamment à cause des interactions complexes et multidirectionnelles "gène-environnement", dans lesquelles l'organisme prend une place centrale, remettant en question les deux premiers postulats, et a fortiori le troisième (Griffiths and Gray, 1994; Griffiths and Tabery, 2013; Levins and Lewontin, 1985; Oyama et al., 2001).

Dans le domaine de l'évolution, la vision gène-centrée (Dawkins, 1976, 1982) a également fait l'objet de critiques en raison des multiples relations causales entre différents niveaux d'organisations (Okasha, 2006; Sober and Lewontin, 1982; Sober and Wilson, 1999). En effet, bien que les gènes soient une structure biologique nécessaire à l'évolution, le niveau d'organisation sur lequel s'effectue la sélection, *le niveau de sélection*, n'est pas limité à ces gènes (Lewontin, 1970). C'est ainsi le deuxième postulat qui est questionné : en effet, si la sélection ne s'effectue pas uniquement au niveau des gènes alors les propriétés des tous (les organismes, les espèces, les communautés) dont font partie les gènes ne découlent pas exclusivement des propriétés des gènes. Cette alternative est portée par la théorie de sélection multi-niveaux (Okasha, 2006; Pievani, 2014). Le niveau du gène n'est pas renié, mais il n'est plus considéré comme unique.

L'approche mécaniste, incluant le réductionnisme, présente d'autres inconsistances dans un contexte écologique. Levins and Lewontin (1980) propose de considérer l'exemple simple d'une proie et d'un prédateur en interaction (Figure I.2). Le système ainsi formé va atteindre un équilibre en suivant une spirale dans l'espace à deux dimensions dont les axes correspondent aux densités respectives de la proie et du prédateur. Dans cet espace le mouvement du système est parfaitement prévisible. Cependant, les densités respectives de la proie et du prédateur oscillent, de telle sorte qu'étant donné seulement la densité du prédateur, par exemple, il n'est pas possible de prédire son augmentation ou sa réduction au pas de temps suivant. Ainsi, alors même que la trajectoire du système est monotone et déterministe en considérant sa distance à l'équilibre, les trajectoires de ses deux sous-éléments ne le sont pas. Le refus du deuxième postulat de la vision mécaniste est dans ce cas illustré par la non prédictibilité du comportement du système à partir du comportement des sous-éléments. De plus, le comportement de chacun des sous-éléments dépend de l'interaction qu'ils entretiennent et n'est pas donc pas prédictible uniquement à partir de leurs équations respectives : le premier postulat de la vision mécaniste est également réfuté.

Cependant, cette critique de la vision mécaniste réductionniste ne constitue en rien une justification d'une vision idéaliste holistique. Cette dernière peut faire l'objet des mêmes réserves que l'approche réductionniste, en considérant un niveau fondamental différent. Revenons à des considérations évolutives pour illustrer cela, et notamment à la controverse nourrie concernant la sélection de groupe (Borrello, 2010). En effet, avant la période charnière des années 1960-1970, la vision holistique considérant que la sélection était forcément bénéfique pour l'espèce, le groupe ou la communauté dominait la littérature. Les travaux de Wynne-Edwards (1962) sur la dispersion et la reproduction animale pour le bien de l'espèce en sont une bonne illustration. Dans la décennie 1960-1970 cette vision a été vivement critiquée (Williams, 1966), ce qui a conduit à une vision réductionniste opposée (Dawkins, 1976). Cette évolution peut être schématiquement

résumée en qualifiant la sélection de groupe pré-1960 de vision idéaliste holistique et la vision gène-centrée qui a suivi de vision mécaniste réductionniste (Biasetti, 2020; Levins and Lewontin, 1980, 1985).

Notre présentation de la vision réductionniste s’est concentrée sur ces limites, l’objectif étant d’expliquer notre démarche qui a consisté à aller au-delà. Néanmoins, elle demeure une puissante heuristique qui a permis de nombreuses avancées.

La citation qui suit illustre les verrous inhérents à l’approche réductionniste lorsque les sujets d’étude sont des systèmes biologiques complexes :

”Cities are laid siege to, and most surrender, but a few hold out indefinitely. The army sweeps around these, leaving behind some of its troops, who settle down to a long and frustrating encirclement. This has certainly been the case in biology, where the extraordinary progress made in molecular studies has been the consequence of a straightforward reductionist program, while the understanding of embryonic development and of the functioning of the central nervous system have remained in a rudimentary state” (Levins and Lewontin, 1985).

Nous rejoignons cette réflexion, la compréhension des systèmes complexes issus de la biologie - espèces, communautés, métacommunautés - font partie des cités qui résisteront toujours au siège du réductionnisme (ou de l’holisme idéaliste), ce qui justifie le besoin de développer des approches différentes.

I.2.3 La vision dialectique

Comme alternative, ou dans une moindre mesure comme complément à la vision mécaniste là où elle est inopérante, la vision dialectique peut être proposée (Figure I.1c). Celle-ci ne constitue pas une véritable méthodologie, mais elle repose sur des principes devant prévenir tout raisonnement de tomber dans les pièges du réductionnisme (Biasetti, 2020; Levins and Lewontin, 1985).

Levins and Lewontin (1985) définissent quatre principes.

- principe 1 : ”un tout est une relation de parties hétérogènes qui n’ont pas d’existence indépendante préalable en tant que parties”
- principe 2 : ”en général, les propriétés des parties n’ont pas d’existence préalable mais sont acquises en étant des parties d’un tout particulier”
- principe 3 : ”l’interpénétration des parties et des ensembles est une conséquence de l’interchangeabilité du sujet et de l’objet, de la cause et de l’effet”
- principe 4 : ”le changement est une caractéristique de tous les systèmes et de tous les aspects de tous les systèmes”

La vision dialectique est un concept ayant une longue histoire, bien au-delà de l’écologie et l’évolution, développée entre autres par Hegel (”Science de la logique”, 1812), Engels (”Dialectique de la nature”, publication posthume en 1925) et Marx (”Le Capital”, 1867). De ce fait, nous ne prétendons pas ici saisir la pensée dialectique dans toute sa complexité, notamment concernant ses composantes sociales et sociétales, mais

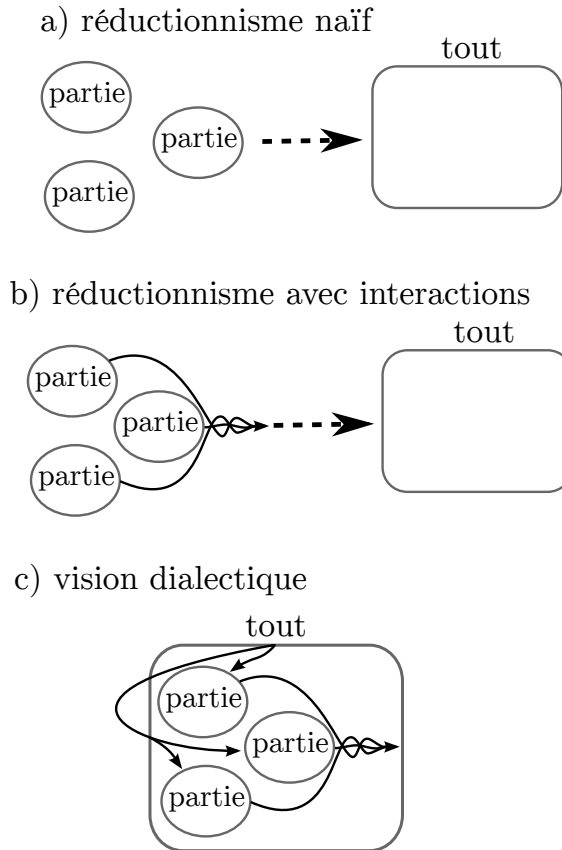


Figure I.1 – Représentation schématique de trois visions différentes : a) un réductionnisme naïf où on considère que l'ensemble des propriétés de chaque partie indépendante génère le tout, b) un réductionnisme où on considère que l'ensemble des propriétés des parties et l'ensemble des interactions entre elles génèrent le tout, c) la vision dialectique où les parties et le tout constituent un système complexe d'interactions multidirectionnelles. Les flèches en trait plein symbolisent les interactions. Alors que dans la vision réductionniste ces interactions ne sont qu'entre les parties, dans la vision dialectique il existe également des interactions du tout sur les parties formant ainsi une causalité réciproque.

nous cherchons à explorer dans quelles mesures celle-ci peut guider les questions et les méthodologies associées, en écologie et en évolution.

La tendance en écologie et en évolution semble déjà s'orienter vers une approche dialectique en abandonnant progressivement le réductionnisme, voir (Svensson, 2018) en évolution, ou l'intérêt grandissant pour la notion de systèmes complexes en écologie (Jørgensen et al., 2011). Notons que cette tendance n'est pas particulièrement corrélée avec l'expression même de l'usage de la dialectique. En fait, de nombreux programmes de recherche tendent vers une approche dialectique sans pour autant expliciter le lien avec ce concept. Cependant, sa priorité historique, par rapport à celui de "systèmes complexes" par exemple, justifie à notre avis son usage.

Le profond débat sur la relation entre complexité et diversité des écosystèmes, et plus largement le fonctionnement des écosystèmes, "Biodiversity Ecosystem Functioning" (Loreau and De Mazancourt, 2013), repose sur l'usage de modèles de plus en plus en accord avec une vision dialectique, notamment avec l'apparition des modèles éco-évolutifs

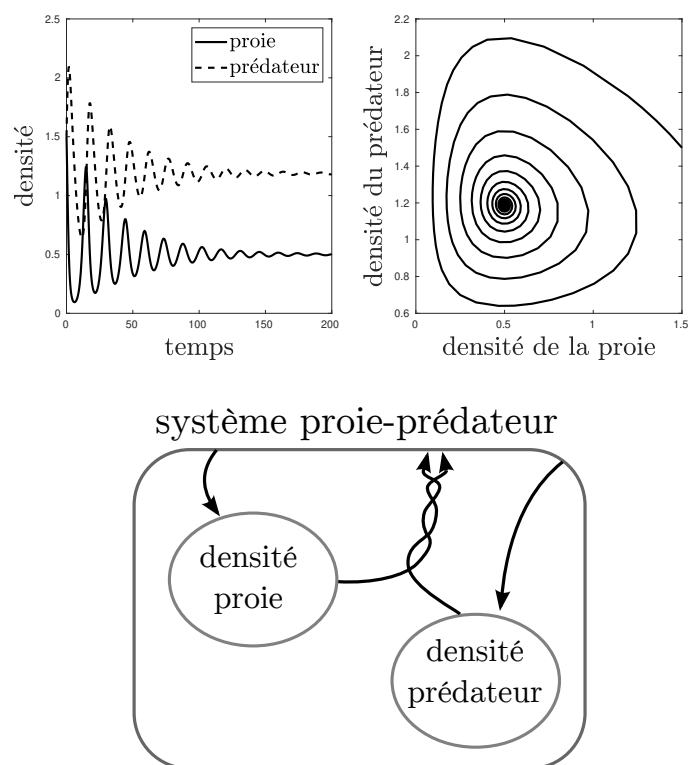


Figure I.2 – Le système simple proie-prédateur de Lotka-Volterra comme exemple des limitations d’une vision purement réductionniste. Les densités de chaque partie du système (la proie et le prédateur) oscillent à cause de l’interaction entre elles, de sorte qu’en prenant chaque partie indépendamment il est impossible de prédire sa densité à l’intervalle de temps suivant. Pourtant le tout, formé de l’interaction entre les parties, suit une trajectoire en spirale prédictible car définie par un unique vecteur en chaque point de l’espace.

en remplacement de modèles purement écologiques ([Fussmann et al., 2007](#); [Landi et al., 2018](#); [Thuiller et al., 2013](#)).

Un constat similaire caractérise le débat, tout aussi profond, concernant l’évolution de la coopération - incluant l’altruisme, par exemple le don de nourriture intra-spécifique chez des chauves-souris ([Denault and McFarlane, 1995](#)), et le mutualisme, par exemple les bénéfices mutuels inter-spécifiques entre des acacias et des fourmis ([Janzen, 1966](#)). On l’a dit, par le passé, le débat a abandonné la vision idéaliste holistique (sélection au bénéfice de l’espèce) pour une vision mécaniste réductionniste (sélection au bénéfice du gène égoïste). Il nous semble que la tendance évolue à présent vers une approche multi-niveaux, en accord avec une vision dialectique, mettant l’accent sur les différents niveaux d’organisation sur laquelle la sélection naturelle peut agir et les causalités réciproques entre eux ([Okasha, 2006](#); [Sober and Wilson, 1999](#)). De plus, cette approche multi-niveaux dans le cadre de l’évolution de la coopération est intimement liée à la structure spatiale, qui elle-même peut résulter de processus écologiques. La causalité réciproque entre processus évolutifs et processus écologiques est ainsi de plus en plus prise en compte, et de fait utilise des modèles éco-évolutifs ([Lion and Van Baalen, 2008](#); [Pepper and Smuts, 2002](#)).

Enfin, dans un cadre purement écologique, le développement du concept de métacommunauté,

et des modèles associés, naît d'une volonté de considérer différentes échelles spatiales en interactions, et potentiellement avec une causalité réciproque ([Hanski and Gilpin, 1991](#); [Wilson, 1992](#)).

Des modèles qui seront abordés dans ce travail de thèse, deux catégories de complexité se dégagent : celle venant du couplage de processus écologiques et de processus évolutifs, et celle consécutive à la présence de plusieurs échelles spatiales, sachant que les deux peuvent s'entremêler. Une approche réductionniste consisterait à étudier les interactions entre les parties constitutives de ces complexités pour accéder à une compréhension du tout, en négligeant le fait que le tout à son tour peut entrer en interaction avec les parties. Nous distinguons ainsi deux types d'interactions : les interactions entre les parties qui génèrent le tout, et les interactions réciproques du tout vers les parties. Alors que l'approche réductionniste se focalise uniquement sur les premières, la vision dialectique défend que toutes les interactions doivent être considérées également, formant une causalité réciproque entre les parties et le tout.

Bien que l'approche dichotomique entre les parties et le tout propre au réductionnisme puisse être riche d'enseignements, la vision dialectique suppose que d'autres enseignements seraient inaccessibles par cette méthode et que la préservation de la complexité est indispensable à l'approfondissement de notre connaissance de ces objets complexes. C'est pourquoi dès lors que des programmes de recherche s'intéressent à la préservation de la complexité de leur modèles d'études, on peut considérer qu'ils s'inscrivent dans une vision dialectique, sans pour autant l'explicitier. Cela revient donc à s'intéresser non seulement aux interactions entre les parties, mais également à la causalité réciproque du tout sur les parties.

I.3 Dépasser la dichotomie entre les parties et le tout par la causalité réciproque

Nous allons maintenant détailler les deux types de complexité présentes dans cette thèse, à savoir le couplage entre dynamiques écologique et évolutive et la présence de multiples échelles spatiales. Le chapitre II explore la complexité émanant de la présence de plusieurs échelles spatiales. Le chapitre III s'intéresse à la causalité réciproque entre niveaux de sélection, qui émerge de la complexité de multiples échelles spatiales. Enfin, le chapitre IV inclut la complexité issue du couplage entre une dynamique écologique et une dynamique évolutive à travers la causalité réciproque entre individus, niveaux trophiques et communauté.

I.3.1 Causalité réciproque entre échelles spatiales locale-globale

Le concept de metacommunauté ([Hanski and Gilpin, 1991](#); [Wilson, 1992](#)) constitue un bon exemple de système écologique pour lequel les interactions entre échelles spatiales sont cruciales (Figure I.3). Une metacommunauté est un assemblage de multiples communautés reliées par des processus de migrations, le tout formant la metacommunauté. Cela implique donc deux échelles spatiales distinctes formant une structure spatiale : l'échelle locale de la communauté, et l'échelle globale de la metacommunauté. Une vision réductionniste proposerait de considérer les communautés comme bien distinctes les

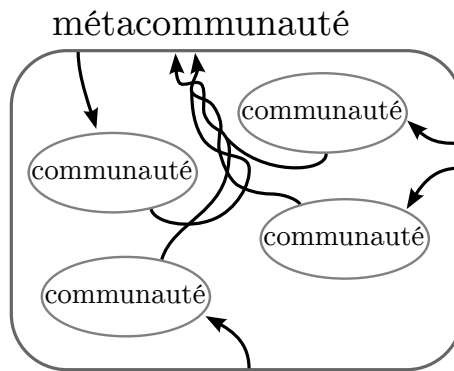


Figure I.3 – Une représentation dialectique du concept de métacommunauté. Le tout, la métacommunauté, émerge des interactions entre toutes les parties, les communautés, qui elles-même subissent l'effet du tout selon une causalité réciproque. Idéalement la représentation des communautés comme des parties différenciées ne devrait même pas être possible. La vision dialectique atteint donc ses limites pratiques mais demeure une méthode heuristique. Dans les faits la vision mécaniste s'impose pour modéliser des systèmes complexes. Ainsi, pour modéliser une métacommunauté nous sommes contraints de considérer des communautés en interactions et non pas un ensemble flou d'interactions complexes.

unes des autres, et les propriétés de la métacommunauté comme totalement résultantes et prédictibles par les propriétés des communautés.

La première faiblesse de cette approche réside dans le fait de considérer les communautés comme des sous-parties distinctes. Effectivement, à cause de migrations d'organismes et de flux abiotiques, l'identité de chacune des communautés est une propriété floue car en perpétuelle évolution. Par exemple, en considérant deux communautés au sein d'une métacommunauté entretenant des interactions tellement fortes qu'elles sont pratiquement toujours similaires dans leur composition en espèces et leurs propriétés abiotiques, il devient problématique de les considérer comme deux sous-parties distinctes de la métacommunauté. Si on réduit progressivement les interactions entre ces deux communautés, à partir de quelle intensité limite d'interaction, ou à partir de quel degré de dissimilarité, considère-t-on qu'elles forment à présent deux sous-parties distinctes ? La solution à cette question semble résider dans le choix d'un seuil arbitraire. L'alternative proposée par la vision dialectique est de considérer que les communautés n'ont pas d'existence indépendamment de leurs interactions au sein de la métacommunauté. Ainsi, les communautés n'ont pas de propriétés intrinsèques, mais des propriétés résultant de leurs interactions avec le reste du système.

La seconde faiblesse de l'approche réductionniste est de considérer que les propriétés de la métacommunauté sont accessibles par la connaissance des propriétés des communautés, autrement dit que le tout est égal à l'ensemble des parties. Nous pouvons questionner cette considération en imaginant une métacommunauté composée de communautés similaires dont les dynamiques locales mènent à l'extinction des espèces les composant. L'étude de chacune des sous-parties, les communautés, mènerait à la conclusion logique que la métacommunauté court vers son extinction. Cependant, dès lors que l'on considère les interactions entre les communautés, et la capacité de recolonisation de communautés éteintes par des communautés encore actives, la conclusion réductionniste ne tient plus.

Une métacommunauté persistante peut être composée de communautés instables ([Amarasekare, 2008](#); [Holyoak et al., 2005](#)). Un degré de subtilité supplémentaire est franchi en considérant qu’une métacommunauté constituée de communautés dont les abondances des espèces oscillent peut présenter des abondances globales monotones à partir du moment où les dynamiques des communautés sont désynchronisées ([Amarasekare, 2008](#)).

I.3.2 Causalité réciproque entre niveaux de sélection

La causalité réciproque entre échelles spatiales est également cruciale en évolution. Effectivement, la présence de plusieurs échelles spatiales différenciées, et donc d’une structure spatiale, est un ingrédient clé de la théorie de sélection multi-niveaux ([Okasha, 2006](#)). Cette théorie propose que la sélection naturelle ne s’exerce pas uniquement sur les organismes, mais que d’autres niveaux sont à considérer. La sélection résultante dépend des forces de sélection sur les différents niveaux en jeu. La présence d’une structure spatiale permet l’émergence de niveaux de sélection supérieurs à l’organisme (le groupe, la communauté, voire l’écosystème), ainsi que des niveaux inférieurs comme suggéré pour l’émergence de la vie multicellulaire ([Hochberg et al., 2008](#); [Szathmáry and Smith, 1995](#); [Van Gestel and Tarnita, 2017](#)).

Pour qu’un niveau d’organisation donné puisse être considéré comme un niveau de sélection il doit satisfaire aux trois critères de l’évolution par sélection naturelle ([Lewontin, 1970](#)) : variabilité, hérédité, sélection. Pour tous les niveaux d’organisation supérieurs à l’individu, l’hérédité est souvent considérée comme le critère le plus problématique afin de les considérer comme des niveaux de sélection. Nous évitons ici d’entrer dans des considérations qui pourraient à elles seules constituer l’intégralité d’une thèse, mais une alternative est de considérer que l’hérédité est une sous-composante du concept de persistance ([Bouchard, 2014](#); [Dussault and Bouchard, 2017](#)). Ce concept de persistance apporte aussi une réponse aux questionnements sur la valeur sélective de niveaux d’organisations supérieurs dont il est difficile de considérer un processus de reproduction ; la reproduction est vue comme une composante de la valeur sélective et la persistance en est une seconde ([Bouchard, 2008, 2011](#)). Une thématique parallèle, étroitement liée à la structure spatiale, est la question de l’individualité ([Buss, 1987](#); [Pradeu, 2016](#)). Effectivement, dès lors que l’on considère que des niveaux d’organisation supérieurs à l’organisme constituent des niveaux de sélection il est tentant de les considérer comme des organismes eux-mêmes, ou des “superorganismes” ([Wilson and Sober, 1994](#)). Cette discussion, susceptible d’engendrer des digressions importantes, peut être temporairement close en acceptant la définition de l’individualité selon ([Huneman, 2014a,b](#)). Dans ce scénario, accepter qu’un tout forme un individu est fondé sur la force des interactions entre les sous-parties.

Un exemple de sélection multi-niveaux assez simple et fondé sur la structure spatiale est donné par le “structured demes model” introduit par ([Wilson, 1977](#)). Ce modèle considère l’existence de “trait-group” c’est-à-dire des groupes dont les limites sont déterminées par l’interaction entre les individus. Les individus interagissent au sein des groupes durant une phase de dynamique intra-groupe, puis suit une phase de dispersion globale où les groupes sont reconstitués aléatoirement à partir du stock total, et de nouveau reprend la dynamique intra-groupe jusqu’à la prochaine dispersion (Figure I.4).

(Wilson, 1976) utilise ce modèle pour décrire l'évolution de communautés plante - vers de terre. Ce modèle considère deux types de plantes A et B en interaction avec des vers de terre. Les deux plantes profitent de la présence de vers de la même manière (la densité de vers détermine leur capacité de charge), tandis que les vers ne profitent que de la présence de la plante A (leur capacité de charge est déterminée par le ratio des densités de A sur B). Le "structured demes model" considère que les groupes sont les communautés plantes-vers qui ont une phase de dynamique interne et une phase de dispersion globale. De plus, nous ajoutons au modèle initial un coût métabolique pour les plantes de type A, nous considérons ainsi que leur action positive sur les vers est une interaction mutualiste impliquant un coût pour les plantes. Les résultats de

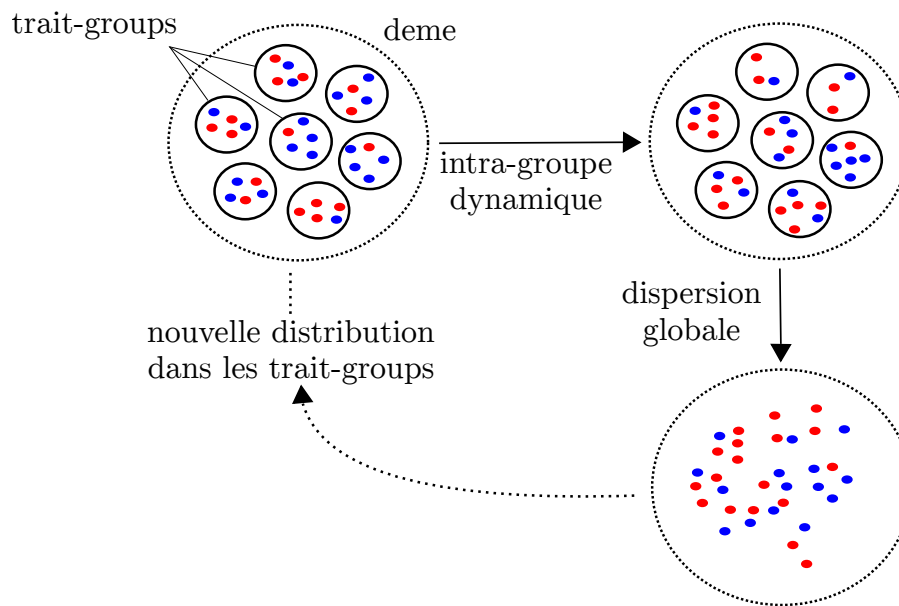


Figure I.4 – Représentation schématique du "structured deme model" (Wilson, 1977). La structure spatiale réside dans la considération de groupes à composition différente (en terme de traits des individus). Une dynamique interne aux groupes se met en place, entrecoupée d'évènements de dispersion globale. Lors de la dispersion globale les groupes sont reformés en redistribuant aléatoirement les différents individus au sein de nouveaux groupes. Ce modèle considère donc deux niveaux de sélection, le niveau des individus lors de la dynamique intra-groupe, et le niveau du groupe grâce à la dispersion globale.

ce modèle montrent qu'en absence de structure spatiale (initialement tous les groupes ont des compositions similaires en termes de densités de chaque type de plantes), la sélection ne s'effectue qu'au niveau des individus au sein des groupes, et défavorise ainsi la plante de type A qui paie un coût métabolique (Figure I.4 haut-gauche). En revanche, la structure spatiale (variabilité initiale dans la composition des groupes) induit une bien plus forte densité des plantes de type A comparée à la densité de celle de type B, alors qu'en conditions initiales le type B est cinq fois plus abondant (Figure I.4 haut-droite). Cette dynamique va de pair avec une forte augmentation de la densité en vers de terre qui profitent de la présence des plantes de type A. Cette dynamique s'explique par le fait que, malgré la contre-sélection des individus du type A au sein de chaque communauté, les communautés qui comportent initialement une plus large proportion de type A voient leur densités fortement augmenter grâce à l'interaction

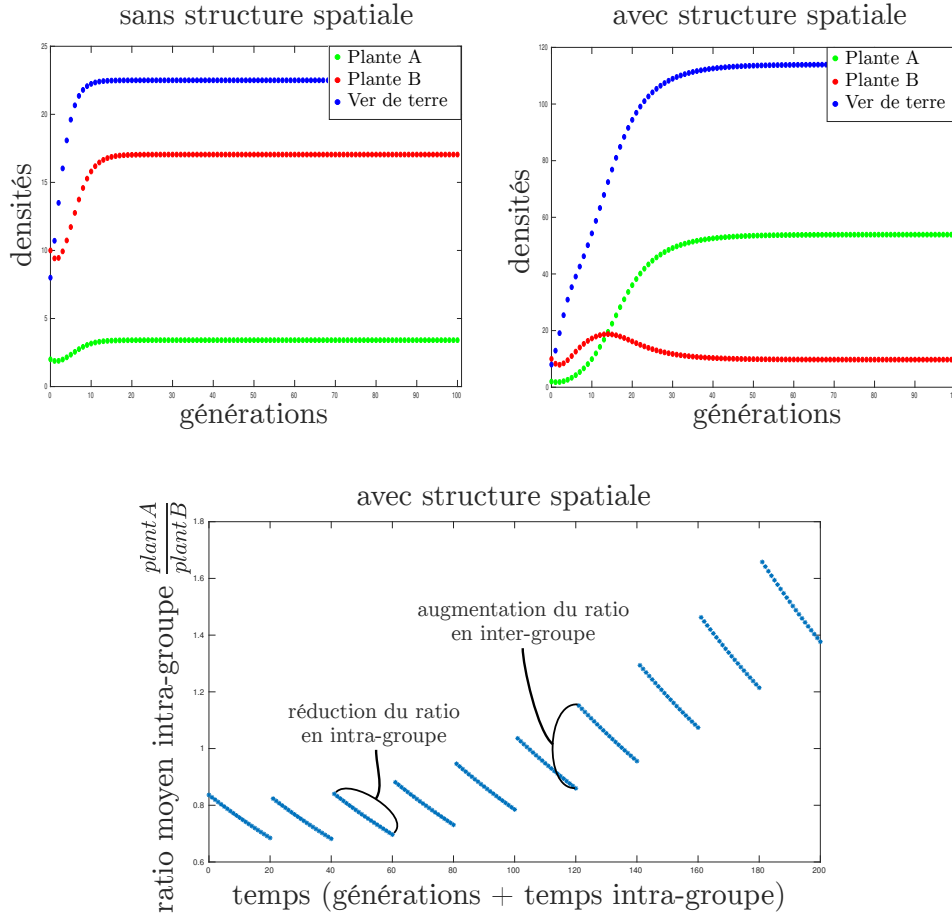


Figure I.5 – Adaptation personnelle des résultats de (Wilson, 1976) en ajoutant un coût métabolique pour les plantes de type A (mutualistes). Les deux panels du haut montrent les densités globales des deux types de plantes et des vers de terre en fonction de la présence ou absence d’une structure spatiale. Le panel du bas montre la dynamique du ratio entre les densités des plantes de type A et de type B dans une situation avec structure spatiale. La dynamique inclut les dynamiques internes aux groupes ainsi que les générations de dispersion globale.

mutualiste entre le type A et les vers de terre. Ces communautés plus productives sont donc une source de plantes de type A - bien qu’au sein de la communauté la proportion de type A diminue durant la dynamique interne (Figure I.4 bas). Il s’agit en fait d’une version écologique du paradoxe statistique de Simpson (Simpson, 1951), dans lequel une tendance apparaît dans plusieurs groupes de données mais disparaît ou s’inverse lorsque les groupes sont combinés. Dans notre cas, malgré une tendance à la diminution de la proportion des plantes mutualistes (type A) dans chaque groupe, la tendance globale en combinant tous les groupes est à l’augmentation de la proportion en plantes mutualistes. Ce qui s’explique par la plus forte productivité des groupes ayant initialement une plus grande proportion de plantes mutualistes.

Bien qu’initialement (Wilson, 1976) s’intéresse à la sélection au niveau de la communauté sans considérer l’interaction mutualiste (pas de coût mutualiste du type A) notre

ajout d'un coût métabolique du type A illustre le conflit entre le niveau de sélection de l'individu et le niveau de la communauté. D'ailleurs, la théorie de sélection multi-niveaux, et le rôle fondamental de la structure spatiale, ont été largement développés grâce à des études sur l'évolution de la coopération.

Un second exemple, relatif à l'évolution de la consommation restreinte (une forme de coopération) permet de décrire une situation dans laquelle la structure spatiale prend une forme plus explicite que dans le "structured deme model". [Pepper \(2007\)](#); [Pepper and Smuts \(2002\)](#) proposent un modèle composé de ressources structurées en dèmes dans un paysage en deux dimensions et des consommateurs en quête de ressources qui peuvent se déplacer dans ce paysage. Tandis que les ressources suivent une croissance logistique, l'énergie des consommateurs dépend de leur consommation de ressources. Ainsi, lorsqu'un consommateur occupe une position de l'espace où une ressource est disponible, il la consomme. Si un consommateur ne trouve aucune ressource durant une période de temps trop longue, il meurt. Deux phénotypes coexistent chez les consommateurs, un phénotype gourmand et un phénotype modéré. Un consommateur gourmand extrait 99% de la biomasse de la ressource qu'il utilise, tandis qu'un consommateur modéré n'en extrait que 50%. Cette consommation restreinte correspond à une coopération puisque les consommateurs modérés laissent un avantage compétitif aux gourmands à leur détriment.

Le résultat majeur de ces travaux met en évidence le lien entre l'intensité de la structure spatiale et la nature du phénotype avantageux. Lorsque la structure spatiale est faible (les dèmes de ressources sont grands et/ou proches dans le paysage) le phénotype gourmand se fixe dans la population de consommateurs ; lorsque la structure spatiale se renforce, les deux phénotypes peuvent coexister ; et si la structure spatiale devient suffisante (petits dèmes et assez éloignés dans le paysage) le phénotype modéré se fixe (Figure I.6). En fait, à l'échelle locale du dème le phénotype gourmand est le plus compétitif et est sélectionné. Cependant, il existe un risque de sur-exploitation du dème lorsqu'il y a trop de consommateurs gourmands dans un dème, ceux-ci se retrouvent alors obligés d'émigrer vers un autre dème, avec le risque de mortalité accrue associé. Ainsi, à l'échelle globale du paysage, si la structure spatiale est suffisamment forte, c'est le phénotype modéré qui est sélectionné. Finalement, pour être en mesure de prédire la trajectoire évolutive du système, c'est bien l'interaction entre les deux échelles spatiales qui doit être prise en compte. Dans ([Pepper, 2007](#); [Pepper and Smuts, 2002](#)), la structure spatiale est fixée a priori par l'expérimentateur. Cependant, pour explorer si la structure spatiale peut émerger de la dynamique des consommateurs nous ajoutons un processus de mortalité aux ressources, d'autant plus fort qu'elles sont fortement exploitées. Afin que l'espace contienne toujours des ressources nous considérons que les ressources qui "meurent" se régénèrent après un certain temps. De plus, nous ajoutons un processus de mutation qui va conduire à l'émergence du phénotype modéré à partir de consommateurs initialement gourmands (et inversement). Ainsi, en considérant un état initial où les ressources sont uniformément réparties dans l'espace - c'est-à-dire sans structure spatiale - le phénotype gourmand est sélectionné. Mais l'abondance de consommateurs gourmands va créer des "trous" de ressources dans l'espace, et ainsi favoriser la sélection du phénotype modéré. Autrement dit, l'échelle spatiale globale émerge de l'échelle spatiale locale, et la causalité réciproque entre les deux détermine la trajectoire évolutive (Figure I.7).

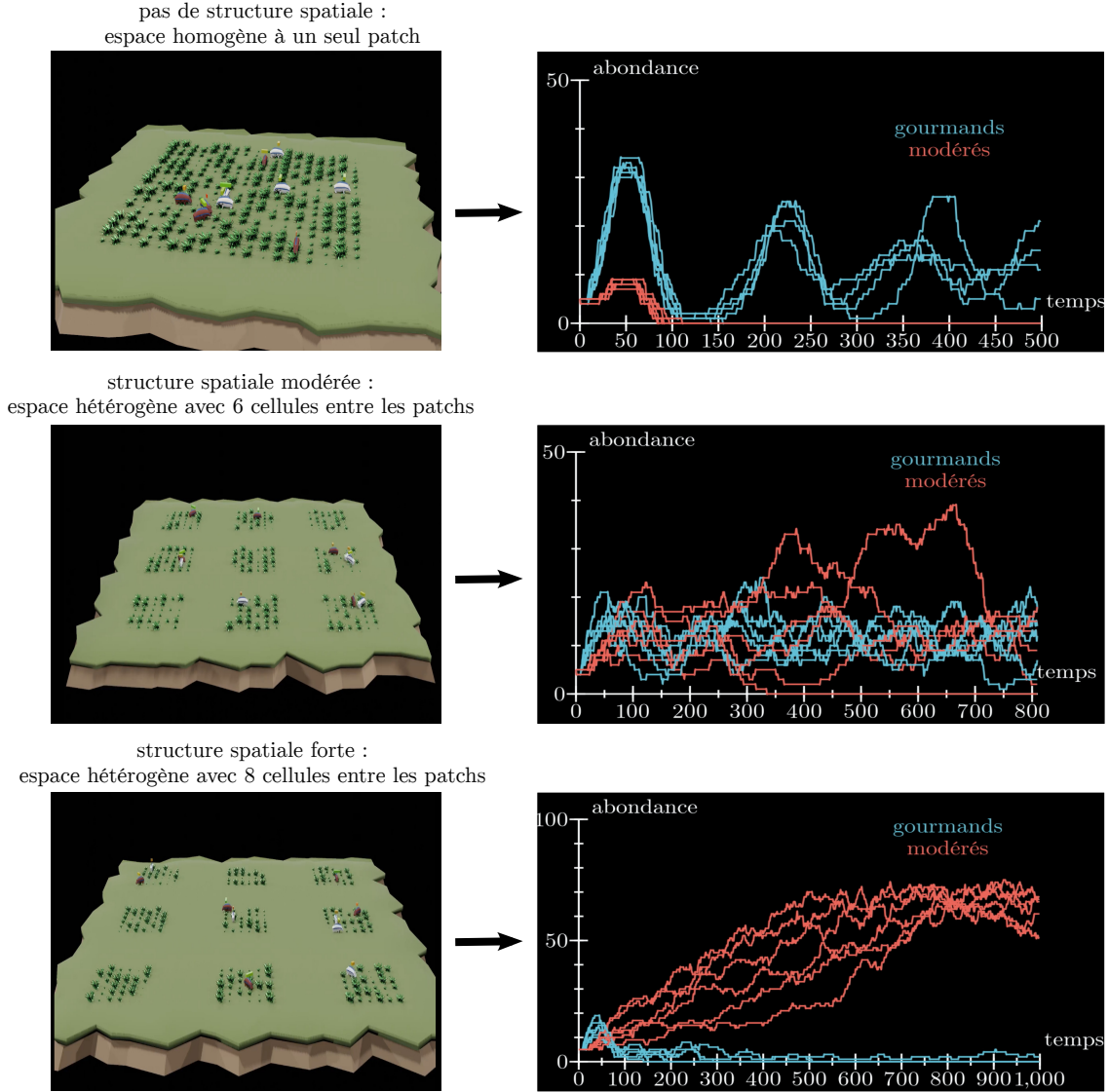


Figure I.6 – Adaptation personnelle des résultats principaux issus du modèle de (Pepper and Smuts, 2002). Les panels de gauche sont une représentation de l'espace selon trois intensités de structure spatiale. La structure spatiale est dictée par la distribution des ressources (les plantes) dans l'espace. Les consommateurs gourmands sont blancs et les consommateurs modérés sont rouges. Initialement 5 agents de chaque type sont distribués dans l'espace. Les panels de droite montrent les dynamiques démographiques de cinq simulations pour chaque intensité de structure spatiale. Une version animée de ces résultats, développée dans le cadre d'une présentation de vulgarisation scientifique, est disponible en suivant ce lien : https://youtu.be/v_zI6WKxFFc

I.3.3 Causalité réciproque écologie-évolution

Le second type de complexité que nous explorons dans cette thèse est celui résultant de la causalité réciproque entre les dynamiques écologique et évolutive. Ces deux dynamiques ont souvent été considérées comme indépendantes car se référant à des échelles de temps différentes. Les deux ont donné naissance à des travaux fondateurs tels que, pour la dynamique évolutive les travaux des modèles de génétique (Fisher, 1919; Haldane,

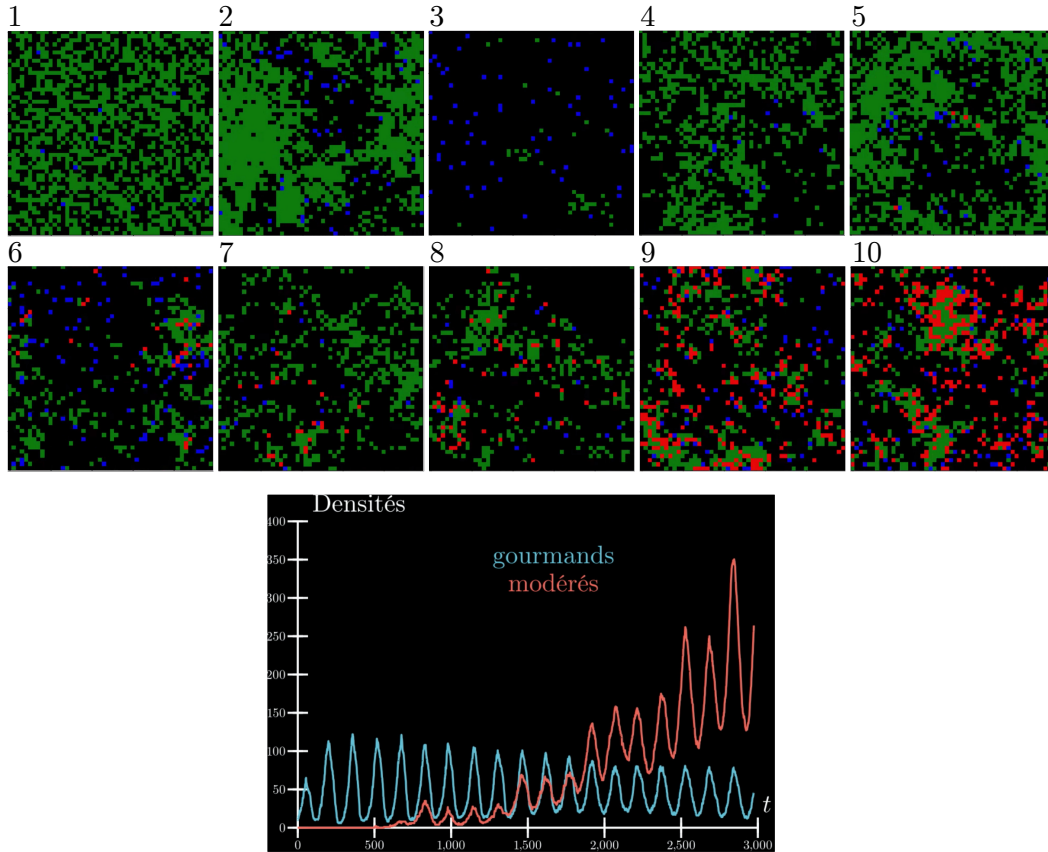


Figure I.7 – Émergence du phénotype modéré suivant l'émergence de la structure spatiale provoqué par l'ajout 1) de mutations chez les consommateurs, 2) de disparition temporaire de ressources (mortalité). Les panels numérotés de 1 à 10 montrent la dynamique spatiale pour dix pas de temps différents (de $t = 0$ à $t = 3000$). Les ressources sont en vert, les consommateurs gourmands en bleu, les consommateurs modérés en rouge, enfin en noir les ressources qui se régénèrent. Une version animée de ces résultats est disponible en suivant ce lien : https://youtu.be/v_zI6WKxFFc

1931; Wright, 1931), et pour la dynamique écologique, le modèle proie-prédateur de (Rosenzweig and MacArthur, 1963).

Plus fondamentalement, cette séparation entre écologie et évolution prend racine dans une vision externaliste du processus d'évolution par sélection naturelle. L'externalisme admet que les gènes sont le moteur de la variation à sélectionner, tandis que l'environnement, qui peut se résumer à des processus abiotiques, constitue la force extérieure qui va sélectionner parmi les variations celles qui persistent (Lewontin, 1982, 1983; Lewontin and Levins, 1997). À l'inverse, le constructivisme place l'organisme au centre du processus d'évolution, premièrement en s'affranchissant de la vision réductionniste gène-centrée dans le développement de l'organisme, et deuxièmement - ce qui nous intéresse ici - en considérant que l'organisme lui-même a un effet sur l'environnement dont résulte la force de sélection. Il existe ainsi une causalité réciproque entre l'organisme qui est sélectionné par le paysage adaptatif, résultant de l'environnement, et ce dernier qui est lui-même le résultat de l'interaction avec l'organisme (Figure I.8).

La vision constructiviste est à la base du concept de construction de niche (Laland

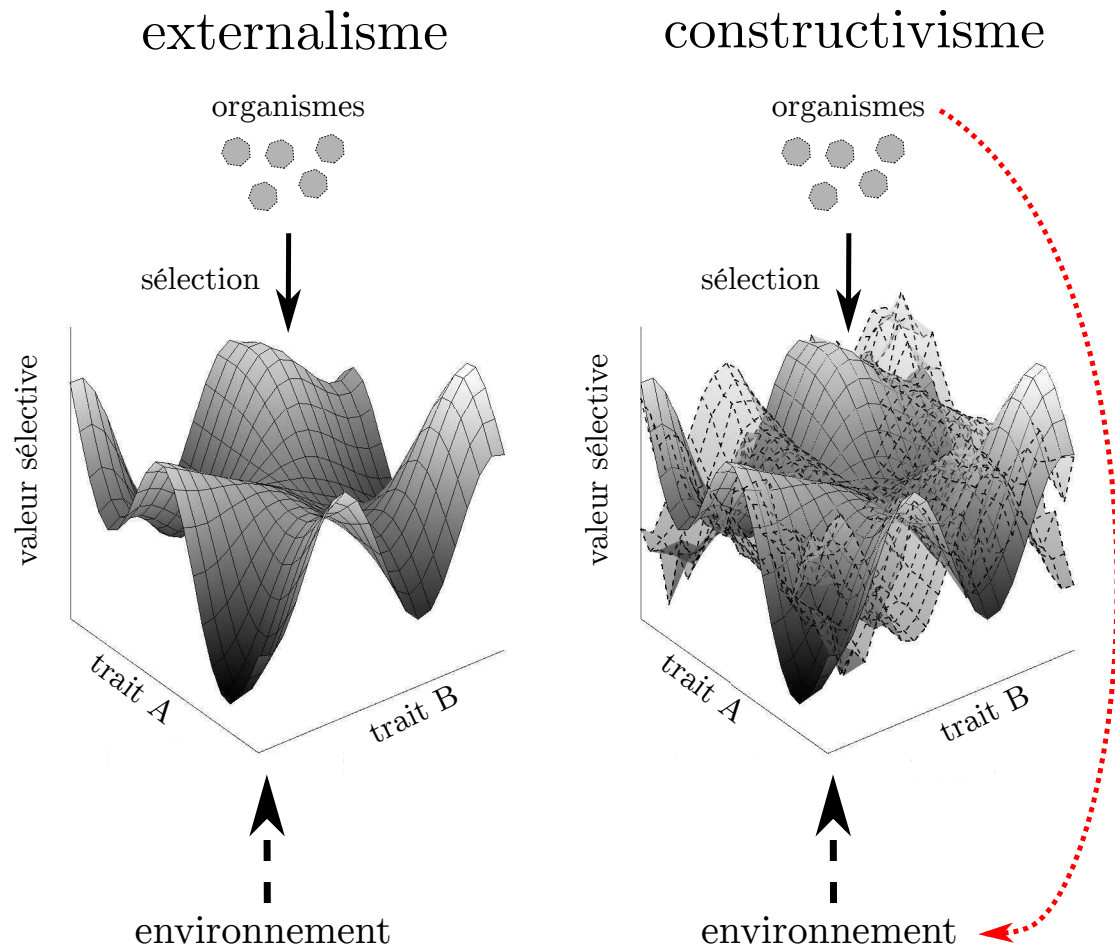


Figure I.8 – Externalisme : l’environnement est constitué de l’ensemble des processus abiotiques et génère un paysage adaptatif dans lequel les organismes vont être sélectionnés selon la valeur sélective donnée par leurs traits (ici seulement deux traits A et B pour l’exemple). Constructivisme : l’environnement est en interaction avec les organismes eux-mêmes, ainsi le paysage adaptatif est continuellement modifié par la présence des organismes et il existe un bouclage, une causalité réciproque, entre les organismes qui sont à la fois sélectionnés par l’environnement et générateurs de celui-ci. Les pointillés sur le panel de droite représentent les modifications du paysage adaptatif créées par l’interaction des organismes avec l’environnement.

et al., 2016; Odling-Smee et al., 2003). Effectivement, ce concept s’oppose à l’idée d’un environnement constitué de niches pré-établies et fixes, responsables de la sélection des organismes cherchant la meilleure exploitation de celles-ci. Au contraire, les interactions des organismes avec leur environnement induisent des modifications de celui-ci. Plus précisément le concept de niches a deux composantes : i) les organismes modifient leur environnement, ii) ces modifications induisent un changement des forces sélectives sur les organismes. Un exemple classique est le cas des vers de terre (Darwin, 1892). À travers leurs actions de fouissage ils introduisent de la matière organique dans le sol, la mélangent avec de la matière inorganique, et globalement modifient la structure physico-chimique du sol (Hayes, 1983; Kretzschmar, 1983; Stout, 1983). Ces modifications favorisent la croissance des plantes, en améliorant le recyclage des nutriments, ce qui bénéficie en

retour aux vers qui consomment la litière. Ces modifications de l'environnement s'étalent sur plusieurs générations de vers de terre, et certains de leurs phénotypes ont co-évolué avec ces modifications ([Turner, 2009](#)).

Cependant, la causalité réciproque entre écologie et évolution ne considère pas forcément que ces deux processus partagent des échelles de temps proches. En reprenant l'exemple de construction de niche des vers de terre, la construction prend certainement plusieurs générations de vers de terre. De fait, la dynamique évolutive des vers de terre est à une échelle de temps différente de leur dynamique écologique (démographique). Une méthode de modélisation développée pour intégrer les deux types de dynamique, la méthode de dynamique adaptative, intègre une distinction temporelle entre l'écologie et l'évolution ([Geritz et al., 1998](#)). En première approche, ces modèles considèrent que les organismes interagissent par des équations démographiques et que ces interactions sont modulées par leurs traits soumis à évolution. L'introduction d'une nouvelle valeur de trait se fait en calculant, à l'équilibre démographique, quelle valeur de trait a une valeur sélective d'invasion positive ([Dieckmann and Law, 1996](#)). Ceci se traduit pour un mutant possédant ce trait par un taux d'accroissement positif lorsqu'il est introduit à faible densité dans la population à l'équilibre. Après l'introduction d'une nouvelle valeur de trait, on laisse le modèle atteindre le nouvel équilibre démographique avant de calculer la possibilité d'introduction d'un nouveau mutant. Bien que les deux dynamiques écologique et évolutive soient dans ce cas considérées, elles ne sont pas entremêlées. Une limite possible de cette approche est de "manquer" certaines possibilités d'assemblage de traits qui résulteraient de l'introduction simultanée de plusieurs mutants. Par exemple, [Kotil and Vetsigian \(2018\)](#) montrent qu'il est possible avec des mutations "simultanées" (c'est-à-dire plus proches dans le temps que celui nécessaire au système pour converger vers un équilibre démographique) d'atteindre des communautés évolutionnairement stables - c'est-à-dire où aucun mutant ne peut plus s'implanter - inatteignables par un processus d'évolution mutation par mutation. De plus, la possibilité de multiples mutations simultanées, ou autrement dit un taux évolutif élevé, a été relevé dans plusieurs travaux ([Hairston Jr et al., 2005](#); [Hendry and Kinnison, 1999](#); [Thompson, 1998](#)).

Les évolutions récentes qui ont affecté les modèles éco-évolutifs montrent une tendance à s'affranchir d'une réelle méthode de dynamique adaptative. Les nouveaux traits apparaissent par mutations sans considérer leur valeur sélective d'invasion, et ceux-ci sont directement sélectionnés par la dynamique écologique ([Allhoff et al., 2015](#); [Brännström et al., 2011](#); [Loeuille and Loreau, 2005](#)). Bien qu'il soit possible que des mutations simultanées se produisent, les taux de mutation sont en général suffisamment faibles pour que ce phénomène demeure hautement improbable.

Le chapitre III de cette thèse inclut la causalité réciproque écologie-évolution dans sa composante "construction de niche" en s'intéressant à l'émergence du mutualisme. Le modèle utilisé est celui d'une interaction entre un hôte et un symbionte. Tandis que leur interaction détermine leur reproduction, les densités en hôte déterminent la compétition qui elle-même joue un rôle dans les forces sélectives formant ainsi le bouclage éco-évolutif de construction de niche.

Dans le chapitre IV, le modèle ressource-consommateur développé considère la causalité réciproque écologie-évolution à travers l'émergence de communautés dont la diversi-

fication évolutive des traits des organismes dépend de leurs interactions écologiques. De plus, l'évolution des traits des organismes a des conséquences sur des propriétés écologiques de la communauté (biomasse, productivité, diversité, stabilité).

I.4 Persistence de systèmes complexes dans une vision dialectique

Le deuxième point de convergence entre les trois chapitres est la notion de persistance d'un système. Ainsi, dans le chapitre II nous questionnons la persistance du système pyrale-buis, dans le chapitre III nous testons la persistance du système avec mutualisme après son émergence en perturbant l'équilibre éco-évolutif, enfin dans le chapitre IV nous testons la persistance des communautés face à des perturbations croissantes pour mesurer leur stabilité.

Cependant, en se plaçant dans une vision dialectique, le terme de "persistance d'un système" peut sembler flou. Effectivement, les notions de "persistance" et de "système" sont toutes deux complexes lorsque incluses dans une vision dialectique dans laquelle un système ne peut pas se définir uniquement par ses parties, ni uniquement par son tout, et dans laquelle le changement est considéré comme étant un élément fondamental de tout système (pour rappel, quatrième principe de la vision dialectique, [Levins and Lewontin \(1985\)](#)).

Pour définir le "système" qui persiste nous conservons la logique suivie jusqu'à présent : l'important n'est pas les parties du système, ni même le tout, mais l'ensemble des interactions entre les parties et le tout formant une causalité réciproque. Ainsi, ce sont les interactions qui seront persistantes, ou autrement dit les processus réalisés par le système. Le système pourrait voir ses parties changer au cours du temps, ainsi que son tout, mais le système persiste tant que les processus réalisés par l'ensemble des interactions au sein de ce système restent maintenus. Nous définissons ainsi une notion de persistance qui contient en elle-même une notion de changement.

Cette question de la persistance dans le changement est au fondement de la question de l'individualité en biologie ([Buss, 1987](#); [Pradeu, 2016](#)), et il est possible de remonter jusqu'à Plutarque (Ie siècle apr. J.-C.) et sa légende du bateau de Thésée. En effet, une fois que toutes les vieilles planches du bateau furent remplacées au fil du temps par des nouvelles de telle sorte que plus aucune planche originelle ne constituait encore le bateau, pouvait-on toujours considérer qu'il s'agissait du même bateau ? Une question à peu près similaire peut se poser pour un organisme dont les cellules sont "remplacées" au fil du temps, ou bien un écosystème dont les organismes sont "remplacés" jusqu'à ce qu'à un temps donné l'écosystème ne comporte plus aucun des organismes qu'il contenait à un temps antérieur. L'idée de persistance des processus propose un axe de réponse à cette difficile question : "It's the song, not the singer" ([Doolittle and Booth, 2017](#); [Doolittle and Inkpen, 2018](#)) et permet une nouvelle définition de la valeur sélective à travers la persistance ([Bouchard, 2008, 2011, 2014](#)). Nous reviendrons sur cette notion de valeur sélective par la persistance dans la partie discussion, étant donné son caractère fondamental dans l'idée d'évolution par sélection naturelle des écosystèmes.

Ainsi, dans chacun des chapitres la notion de persistance peut se percevoir sous sa forme dialectique. Dans le chapitre II, on considère que le système buis-pyrale persiste à partir

du moment où les deux espèces continuent à être en interaction, malgré les changements continus qui peuvent affecter les densités de chacune, ainsi que la structure du paysage. Dans le chapitre III, l'équilibre éco-évolutif après émergence du mutualisme est dynamique ; les densités en parasites et en mutualistes sont en constante variation et la structure du paysage également avec l'effondrement et la formation de groupes. Cependant, nous explorons la persistance des interactions entre les niveaux d'organisation et de la causalité réciproque qui assurent le maintien d'une certaine proportion de mutualistes. Enfin, dans le chapitre IV nous testons la stabilité de communautés dont les densités en ressources et en consommateurs sont en constant changement, de sorte que même les propriétés à l'échelle de la communauté (telle que la biomasse totale) changent également au cours du temps. Ainsi, nous ne mesurons pas d'éventuels changements quantitatifs pour estimer la stabilité des communautés, mais au contraire directement la persistance de la communauté, qui est un processus dépendant de l'ensemble des interactions entre ressources et consommateurs incluant une causalité réciproque écologie-évolution.

I.5 Conclusion

Nous avons tissé à travers cette introduction les liens conceptuels entre les différents chapitres (Figure I.9). La problématique initiale de l'évolution des écosystèmes par sélection naturelle est plus particulièrement explorée par le chapitre III, tandis que le chapitre IV offre l'intéressante perspective de spatialiser le modèle d'écosystème dans un cadre plus complexe. Le chapitre II, issu d'un projet initié antérieurement à la thèse, demeure plus éloigné de cette problématique. Cependant, nous montrons que l'approche multi-échelles que nous mettons en perspective avec la vision dialectique permet de connecter les trois parties.

Un autre point commun entre les trois chapitres est leur approche par modélisation qui est un outil adapté à ces questions conceptuelles ([Huneman and Dutreuil, 2014](#)), notamment quand il s'agit de causalité réciproque. Effectivement, dans un cadre empirique on considère en général un traitement que l'on va effectuer sur l'objet d'étude pour mesurer sa réaction par rapport au même objet sans traitement. Mais dès lors que la causalité réciproque est considérée comme importante, l'effet retour de l'objet d'étude sur le traitement devrait être mesuré, ce qui nous éloigne de la méthodologie du cadre empirique. La modélisation permet également d'ajouter ou retirer des interactions aisément, et ainsi de tester la dépendance des propriétés d'un système soit à de simples interactions entre parties, soit à une causalité réciproque. En revanche, on perçoit rapidement que la vision dialectique constitue un cadre épistémologique et non une préconisation méthodologique. Effectivement, quand on étudie une métacommunauté par modélisation par exemple, le problème de la définition des communautés distinctes apparaît rapidement, malgré un positionnement en accord avec la vision dialectique. Finalement, que trois approches a priori distinctes puissent être reliées par des réflexions issues de la pensée dialectique démontre à quel point ces réflexions sont largement et implicitement répandues en écologie et évolution.

À travers cette introduction conceptuelle nous souhaitons rendre hommage à Richard Lewontin, décédé ce 4 Juillet 2021.

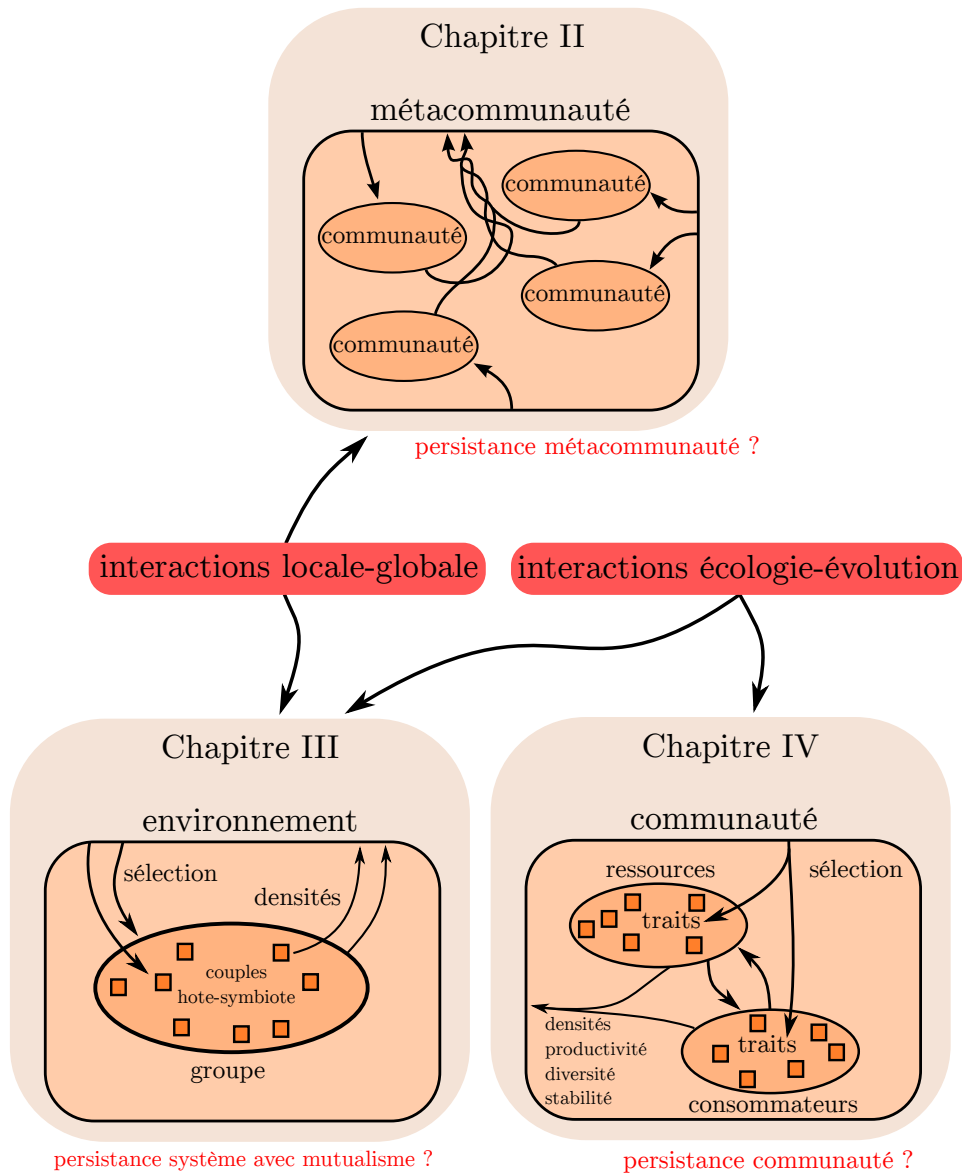


Figure I.9 – Structure globale de la thèse. Chaque chapitre s'intéresse à un système complexe ayant plusieurs niveaux d'organisation en interactions et causalités réciproques. Les bouclages peuvent se produire entre échelles spatiales locale et globale, ainsi qu'entre des dynamiques écologique et évolutive. La question des conséquences de ces causalité réciproques sur la persistance émerge pour chacun des modèles.

CHAPITRE II

CAUSALITÉ RÉCIPROQUE ENTRE ÉCHELLES SPATIALES LOCALE ET GLOBALE

II.1 Introduction et synthèse des résultats

Dans ce premier chapitre nous explorons la causalité réciproque entre échelles spatiales comprise dans le concept de métacommunauté. Le modèle d'application est celui de l'invasion du buis *Buxus sempervirens* par la pyrale du buis *Cydalima perspectalis*, telle qu'elle a pu être observée en Europe depuis 2006/2007.

Ce projet est né de l'observation de terrain suivante : lorsque la pyrale arrive dans un peuplement de buis, via la dispersion des adultes par le vol, il suffit de 2-3 années pour que la très forte densité de chenilles produise une défoliation totale du peuplement de buis. L'extinction de la pyrale dans ce peuplement peut alors se produire, en raison de l'épuisement total de la ressource. De plus, la co-extinction du buis peut aussi se produire, notamment lorsque les chenilles affamées consomment l'écorce superficielle du buis, ce qui annule quasiment toute chance de survie de l'arbre. La pyrale étant encore à l'heure actuelle dans sa phase d'expansion en Europe, la question se pose de la coexistence possible entre la pyrale et le buis malgré leur instabilité locale. Trois hypothèses peuvent être envisagées : i) la coexistence pyrale-buis, ii) l'extinction de la pyrale à cause de sa sur-exploitation de la plante hôte, iii) l'extinction de la pyrale et du buis si celui-ci finit par succomber à la sur-exploitation.

La littérature ne fait état que d'une seule étude d'un système plante-herbivore où la plante subit des extinctions locales à cause de la sur-exploitation (et a fortiori l'herbivore également). Il s'agit du système formé de l'Apiaceae *Aciphylla dieffenbachii* et du charançon monophage *Hadramphus spinipennis*, deux espèces endémiques de Nouvelle-Zélande. De fortes densités locales de l'insecte herbivore entraînent une extinction de la plante (Schöps, 2002), et la modélisation des interactions plante-herbivore montre que la persistance du système est assuré par la structure spatiale (Johst and Schöps, 2003). Cette persistance peut s'expliquer par la faible capacité de dispersion de l'insecte - non-volant, et suffisamment lourd (les adultes font une vingtaine de centimètres) pour ne pas être dispersé par le vent - ce qui permet, lorsque qu'une structure spatiale est présente, de limiter la sur-exploitation des plantes à une échelle locale. Ainsi, bien que des extinctions locales de l'insecte puissent se produire, potentiellement associées à celle

des plantes, à l'échelle du paysage il reste toujours des plantes disponibles ainsi que des insectes capables d'atteindre par dispersion ces plantes. Cependant, la structure spatiale peut disparaître, soit lorsque les plantes colonisent l'ensemble du paysage, soit à cause de la forte capacité de dispersion de l'insecte. Dans ce cas, la sur-exploitation de la plante risque d'être généralisée et temporellement synchronisée en tout point de l'espace, causant à minima l'extinction de l'insecte voire celle des deux espèces. Nous insistons ici sur la dépendance de la structure spatiale aux deux processus : la distribution des plantes dans l'espace et la dispersion de l'insecte. Effectivement, même si les plantes sont distribuées en dèmes dans l'espace - donc selon une structure spatiale - une forte dispersion de l'insecte (c'est-à-dire une dispersion intense et à grande distance) peut gommer cette structure et rend le système équivalent à un système local à un seul dème. Le caractère "flou" du concept de métacommunauté est ainsi illustré. En effet, dans notre cas la métacommunauté est composée des différents dèmes de plantes et des communautés "insecte-plante" associées. Cependant, l'indépendance des communautés dépend de la dispersion de l'insecte. Lorsque celui-ci a une faible capacité de dispersion comme *Hadramphus spinipennis* alors il est effectivement possible de considérer l'ensemble comme une métacommunauté formée de communautés distinctes. Mais lorsque la dispersion est intense et à grande distance les interactions entre toutes les communautés deviennent tellement prononcées que finalement l'ensemble se comporte plus comme une seule grande communauté que comme une métacommunauté avec une structure spatiale (Figure II.1).

La différence fondamentale entre le système buis-pyrale et le précédent est la capacité de dispersion de la pyrale. En effet, que ce soit par le vol des adultes ou par des vecteurs anthropiques (commerce du buis), la pyrale a une forte capacité de dispersion dont la distance moyenne est estimée à 13 kilomètres par an ([Van der Straten and Muus, 2010](#)). C'est d'ailleurs par le commerce du buis que la pyrale est initialement arrivée en Europe depuis l'Asie par l'Allemagne et les Pays-Bas ([Bras et al., 2019](#); [Kenis et al., 2013](#); [Van der Straten and Muus, 2010](#)). Ainsi, la structure spatiale des buis et la désynchronisation temporelle des périodes de sur-exploitation posent la question de la persistance du système.

Pour explorer cette question nous avons développé un modèle de dynamique des populations de type métacommunauté. Nous considérons un espace en deux dimensions dont chaque cellule peut correspondre à une communauté locale, c'est-à-dire un peuplement local de buis. La distribution des cellules contenant du buis se fait soit par la reproduction d'un espace réaliste à partir de données de présence du buis dans l'arc alpin français, soit de manière artificielle afin de tester le rôle de la structure de l'espace dans la persistance du système (proportion de cellules avec du buis et taille de l'espace total). Les communautés communiquent entre elles par les dispersions respectives de la pyrale et du buis, cette dernière étant plus faible et locale.

En accord avec la vision multi-échelles qui sous-tend cette thèse, notre modèle dépasse le paradigme de dynamique de dèmes des modèles classiques de métacommunautés ([Hanski and Gilpin, 1991](#)). En effet, plutôt que de considérer des processus d'extinction-colonisation au niveau des dèmes, nous modélisons les dynamiques démographiques au sein de chaque dème et ce sont ces dynamiques qui dictent les processus d'extinction et de dispersion. De plus, les observations empiriques de la dynamique locale (extinction

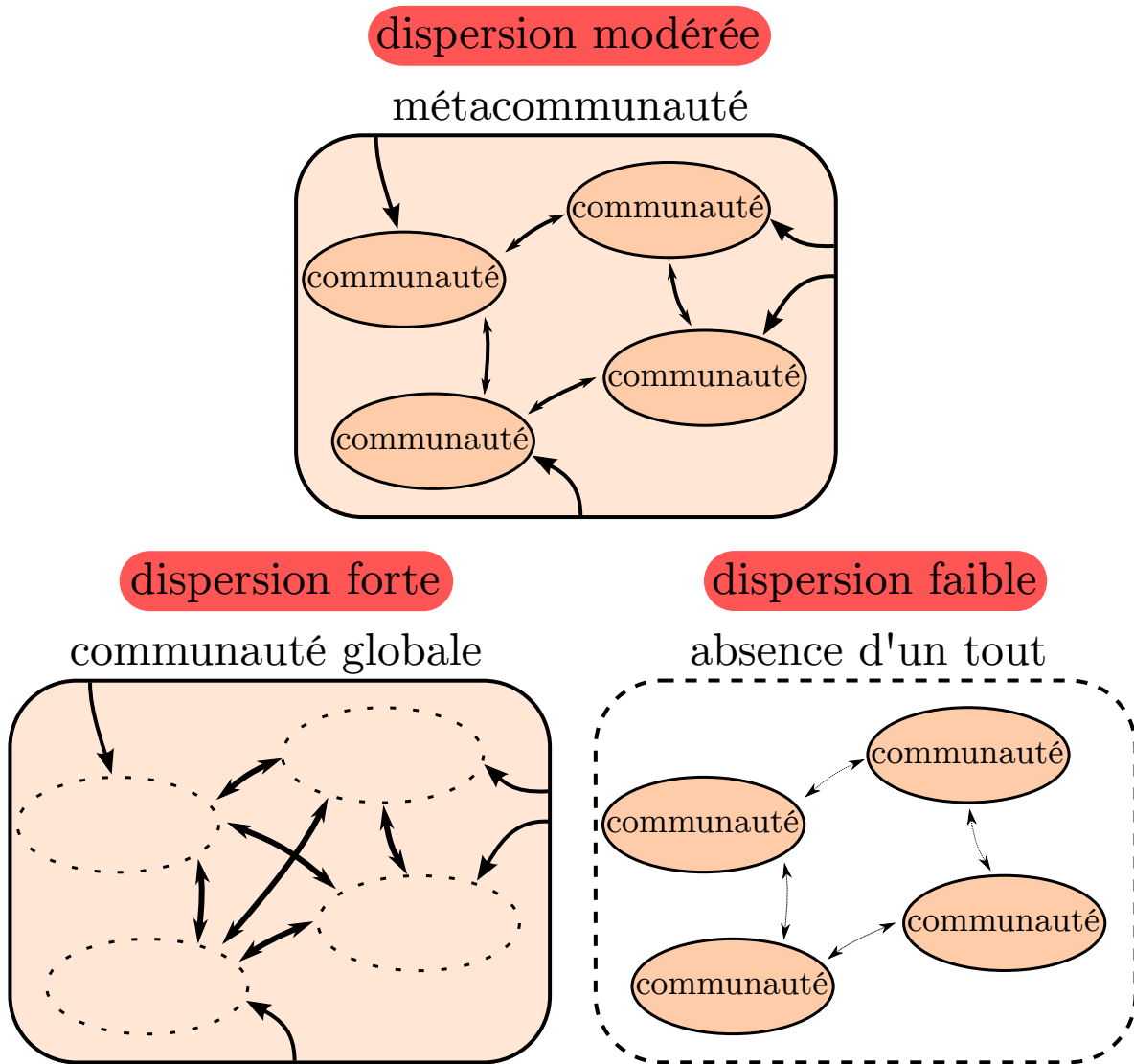


Figure II.1 – Relation entre métacommunauté et dispersion. Le concept de métacommunauté implique l'existence de communautés distinctes connectées entre elles par des processus de dispersion. Cependant, la distinction des communautés peut devenir floue lorsque la dispersion augmente entre celles-ci, à tel point que l'ensemble des communautés peut se comporter comme une communauté globale lorsque la dispersion est suffisante. À l'inverse, une dispersion trop faible ne suffit pas à générer un tout à partir des interactions. Ainsi, seules les dynamiques locales de chaque communauté sont présentes.

de la pyrale par sur-exploitation) permettent de calibrer le modèle démographique pour reproduire cette dynamique locale avant de spatialiser le modèle. Celui-ci a également été calibré par des mesures sur le terrain (par exemple la mortalité du buis après une défoliation totale), ainsi qu'une manipulation en mésocosme où nous avons testé l'effet de différentes intensités d'herbivorie sur le buis, paramétrant ainsi la fonction de consommation des feuilles par les chenilles ainsi que la fonction de survie de celles-ci. Ce calibrage du modèle permet de prétendre à des résultats intéressants également du

point de vue appliqué. En ce sens, la manipulation en mésocosme sert également pour un projet en cours en dehors du cadre de la thèse (porté par Christiane Gallet) sur la métabolomique du buis et les activités enzymatiques du sol en fonction de l'intensité d'herbivorie. La dispersion des pyrales dans l'espace s'effectue selon une distance et une direction aléatoire. Tandis que la direction est générée selon une loi uniforme, la distance de dispersion est générée par une distribution de puissance exponentielle (Klein et al., 2006) qui, selon son paramétrage, peut permettre la production d'événements de dispersion à longue distance. Cette fonction nous permet de produire des distances de vol crédibles en la paramétrant à partir de données de distance de vol en laboratoire fournies par l'INRAE (Audrey Bras, communication personnelle). Enfin, le rôle de la distance de dispersion dans la persistance du système sera évalué en modifiant les paramètres de la distribution.

Le résultat principal est que la coexistence des deux espèces est possible à l'échelle de la métacommunauté dans l'espace réel pour des paramètres écologiquement crédibles malgré l'instabilité locale du système pyrale-buis. De plus, la coexistence est maintenue pour une gamme assez large de paramètres. Cependant, les valeurs limites de la dispersion lorsqu'elle devient soit excessivement locale, soit excessivement globale peuvent empêcher cette coexistence. Si la dispersion demeure localisée, l'interaction entre les communautés n'est pas assez forte pour constituer un tout persistant (la métacommunauté). Ainsi, le système a une dynamique similaire à une communauté locale et la pyrale risque de s'éteindre par sur-exploitation du buis (Figure II.1). À l'inverse, lorsque la dispersion devient intense et globale, la structure spatiale de la métacommunauté se désagrège et sa dynamique devient similaire à celle d'une communauté locale, c'est-à-dire extinction de la pyrale par sur-exploitation du buis. Nous montrons aussi que cette perte de coexistence est étroitement liée à la capacité de repousse du buis. Si la repousse de l'arbre est suffisamment rapide la coexistence est assurée même en cas de forte dispersion car il se trouve toujours au moins un dôme de buis exploitable dans l'espace. Ce résultat peut guider les travaux empiriques en incitant à mieux mesurer et quantifier la réponse du buis face à la défoliation.

Nous élargissons ensuite ces résultats en nous affranchissant de l'espace réel et en évaluant le rôle des propriétés du paysage dans la persistance. En générant des espaces aux propriétés différentes nous montrons que la persistance de la pyrale nécessite un espace suffisamment étendu et à l'inverse une proportion en buis limitée. La capacité de persistance réside dans la structure spatiale qui empêche la sur-exploitation globale. Si l'espace est trop limité ou si la proportion en buis est trop importante la structure est perdue et la dynamique est similaire à une communauté locale. De plus, nous montrons qu'à partir d'un espace initialement saturé en buis (persistance possible si l'espace est suffisamment grand), les processus d'extinction et recolonisation du buis régis par l'interaction avec la pyrale mènent à l'émergence d'une structure spatiale favorisant la persistance du système. À la lumière de ce cadre conceptuel, nous pouvons considérer que dans ce cas les interactions entre les parties génèrent un tout, et la dynamique de cet ensemble mène à une restructuration des parties à travers une causalité réciproque - incluant l'extinction de certaines d'entre elles - qui elle-même mène à la persistance du tout.

II.2 Article : Spatial structure of natural boxwood and the invasive box tree moth can promote coexistence

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II.2.1 Abstract

In the absence of top-down and bottom-up controls, herbivores eventually drive themselves to extinction by exhausting their host plants. Poorly mobile herbivores may experiment only local disappearance, because they can recolonize intact plant patches elsewhere, leaving time to previously over-exploited patches to regrow. However, most herbivores such as winged insects are highly mobile, which may prevent the formation of spatial heterogeneity.

We test if long-distance dispersal can preclude coexistence using the invasion of box tree moth (*Cydalima perspectalis*) in Europe as a model system. We build a lattice model and estimate the parameters with a combination of field measurements, experimental data and literature sources. Space corresponds either to a realistic boxwood landscape in the Alps, or to theoretical landscapes of various sizes.

We find that both species persist under a large range of realistic parameter values, despite a severe reduction in boxwood biomass, with an alternation of outbreaks and near-to-extinction moth densities. Large landscapes are necessary for coexistence, allowing the formation of spatial structure. Slow plant regrowth combined with long-distance dispersal could drive moths to extinction, because of resource depletion at the global scale even without a complete synchronization of the local dynamics. The spatial dynamics leads to formation of small plant patches evenly distributed in the landscape, because of a combination of local plant dispersal and global indirect competition between plants through their positive effect on moth population size. Coexistence is favored by such heterogeneous landscapes, because empty patches increase moth mortality during dispersal: the system thus creates its own stability conditions.

Keywords: source-sink dynamics, green world, spatial asynchrony, metacommunity, invasive species

Author contributions : CG, SI and JG originally formulated the idea, CG, SI, JG and LL developed methodology, LL conducted fieldwork, SI, JG and LL developed the mathematical model, LL performed the numerical analyses, all authors participated in writing the manuscript.

II.2.2 Introduction

In general, most herbivores do not exhaust their resources because they are top-down controlled by their predators (Hairston et al., 1960) as well as bottom-up limited by the defense compounds and the poor nutritional quality of plants (Polis, 1999). However, in some cases such top-down

and bottom-up mechanisms are insufficient to regulate herbivore populations, turning the green world to brown. In such cases, it has been suggested that the spatial dynamics of plant-herbivore metacommunities may favor their coexistence (Wilkinson and Sherratt, 2016). This hypothesis builds upon long-standing theoretical work which has shown that spatial structure promotes the persistence of otherwise unstable prey-predator systems (Amarasekare, 2008; Comins and Hassell, 1996; Hassell et al., 1991), thanks to local extinctions followed by recolonization, in line with metapopulation and metacommunity dynamics (Hanski and Gilpin, 1997; Holyoak et al., 2005). These theoretical predictions have received robust empirical support from experiments based on an animal prey-predator system (Taylor, 1991), as protists (Fox et al., 2017; Holyoak and Lawler, 1996) and field studies with arthropods (Nachman, 1988; Winder et al., 2001).

However, there is little evidence showing that the spatial dynamics resulting from interactions between plants and herbivores leads to a green world - or at least to a bi-coloured world with green and brown patches. Many herbivorous insect populations persist thanks to metapopulation dynamics (Tschardt and Brandl, 2004), but this persistence generally relies on other mechanisms than the depletion of plant resources. For instance, local extinctions can depend on patch size (Eber and Brandl, 1996), on plant resource fluctuations (but for other reasons than the herbivore itself, Halley and Dempster (1996)), or on a combination of ecological succession and catastrophic events (Stelter et al., 1997). In the well-studied ragwort / cinnabar moth system, the moth can locally disappear following defoliation, but plant patches persist (Myers, 1976; Myers and Campbell, 1976). Although cinnabar moths contribute to local plant extinction, local plant persistence ultimately depends on habitat suitability, which leads to a source-sink dynamics rather than to a classical metapopulation scenario (Van der Meijden, 1979; Van der Meijden and Van der Veen-van, 1997). Moreover, the high dispersal ability of cinnabar moths prevents asynchronous local dynamics for the moth, which rules out a metapopulation model of coexistence (Harrison et al., 1995; Van der Meijden and Van der Veen-van, 1997). As far as we know, the only documented plant-herbivore system where the plant goes locally extinct due to over-exploitation comprises the Apiaceae *Aciphylla dieffenbachii* and the monophagous weevil *Hadramphus spinipennis*, two species endemic to the Chatham Islands (New Zealand). Increased local weevil densities are associated with local plant extinction (Schöps, 2002), and numerical simulations have shown that spatial structure allows the persistence of the system, provided that the dispersal distance of the herbivore is intermediate (Johst and Schöps, 2003). However, the ecological conditions which promote the persistence of this particular system may not hold for other plant-herbivore interactions. In particular, the weevil *H. spinipennis* is wingless and of a large size, which considerably reduces its dispersal ability either by itself, by wind or by birds. In contrast, many insects can disperse over long distances (Gillespie et al., 2012; Wilson and Thomas, 2002). Long-distance dispersal can promote metapopulation persistence, except when strong density dependence triggers local extinctions (Johst et al., 2002). In that case, long-distance dispersal events synchronize local extinctions which eventually lead to the extinction of the whole metapopulation (Johst et al., 2002; Palmqvist and Lundberg, 1998). In plant-herbivore metacommunities, strong density dependence occurs when herbivores over-exploit their host down to local extinction.

In order to test if plant-herbivore metacommunities can persist despite high abilities of herbivores to disperse, we study the system formed by the common European boxwood *Buxus sempervirens* L. and the invasive box tree moth *Cydalis perspectalis* (Walker, 1859) (Lepidoptera: Crambidae) in Europe. This invasive species first arrived and established in Germany in 2006/2007 (Van der Straten and Muus, 2010) human assisted via the boxwood trade from Asia (Bras et al., 2019; Kenis et al., 2013; Van der Straten and Muus, 2010). Then, the moth rapidly spread over Europe, invading almost the entire European boxwood range by

2021 as expected (Nacambo et al., 2014). This rapid invasion suggests the occurrence of human-mediated and natural long-distance dispersal events. Moreover, this species causes severe defoliation mainly because its fecundity is high and the individuals lay masses of eggs directly on the leaves. Thus, defoliation caused by moth larvae can lead to the death of the boxwood, especially when the bark is also consumed (Kenis et al., 2013). After this possibly total defoliation, boxwood can either grow back or wither completely and die if the defoliation becomes too recurrent or when bark is consumed (Kenis et al., 2013). This harmful impact of the moth may have major economic consequences (Mitchell et al., 2018). The local extinction of boxwood has already been observed in the Nature Reserve of Grenzach-Whylen in Germany (Kenis et al., 2013). In the meantime, the moth goes extinct locally after total defoliation of boxwood stands, even if it grows back several years after the moth outbreak. Within its home range, the moth, which also consumes boxwood, is regulated by its natural enemies (Wan et al., 2014) and no local extinction of either plant and insect species is observed, but potential European natural enemies do not significantly alter the invasive moth population dynamics (Kenis et al., 2013; Leuthardt and Baur, 2013). Moreover, although box trees contain highly toxic alkaloids (Ahmed et al., 1988; Devkota et al., 2008; Loru et al., 2000), the moth larvae can sequester them in their body (Leuthardt et al., 2013). Thus, in absence of top-down and bottom-up control of this invasive species, the question remains: will the European boxwood stands remain green ? In contrast to our system, the question does not arise with the ragwort / cinnabar and Apiaceae / weevil systems mentioned earlier since both insects are native and may therefore be top-down controlled by local natural enemies. However, in North America, Australia and New Zealand, the ragwort and the cinnabar are both non-native, thus they are both free of top-down and bottom-up controls which is also different from our system (CABI, 2021).

Metacommunity dynamics with local moth extinctions followed by recolonization may be an alternative mechanism to top-down and bottom-up control favouring coexistence in Europe. In the particular context of biological invasions, spatial effects have not been widely addressed (Melbourne et al., 2007), although they may favour coexistence. The metacommunity mechanism requires spatial heterogeneity among local communities, which is likely because of the fairly fragmented distribution of boxwood in Europe, and because of the temporal shift between different patch invasions. As long as the invasion does not start simultaneously in all stands, the moth may disperse from its current totally defoliated stand to a green intact stand. The defoliated stands may then recover and be recolonized lately. Thus, despite local extinctions and recolonizations, local fluctuations may be averaged on a large spatial scale, leading to a global stationary regime called 'statistical stability' (Amarasekare, 2008; De Roos et al., 1991; Holyoak et al., 2005). However, unlike the wingless weevil *H. spinipennis*, the highly mobile *C. perspectalis* can fly or be transported by exogenous factors (wind, human activities) (Bras et al., 2019). Its high mobility may prevent spatial heterogeneity and therefore precludes coexistence by spatial effects (Johst and Schöps, 2003; Johst et al., 2002). Thus at large spatial scale, three ecological scenarios are likely to occur. First, the moth might very quickly overexploit its host, causing its own extinction but not the one of its host, which in turn slowly grows back. Second, the moth might persist long enough to exhaust its host, leading to the disappearance of both species. Third, coexistence might result from the balance between local moth extinctions and recolonizations, without complete resource depletion. Our study focuses on the conditions that favor such coexistence, based on the following hypotheses :

1. Long-term coexistence of boxwood and moth is possible at the landscape scale through spatial stabilizing effects (1a). Those effects rely on asynchronous local dynamics (1b).

2. Despite cycles of local extinctions and recolonizations, the coexistence regime is stationary at the regional scale, which corresponds to statistical stability.
3. Dispersal is double-edged : very limited dispersal might prevent the colonization of green patches (3a), whereas long-distance dispersal may synchronize local dynamics (3b).
4. The coexistence regime depends on the landscape properties, in particular the landscape size and the proportion of boxwood patches in the landscape. First, larger landscapes favor coexistence (4a). Secondly, the effect of the proportion of boxwood patches is uncertain, since it provides more resources to the moth, but also favors outbreaks and resource depletion (4b).

In order to address these four hypotheses, we develop a population model dynamics for the boxwood and moth system. First, a local model reproduces the local invasion dynamics, which invariably leads to moth extinction in the field. Then, a spatially explicit model simulates the dynamics of the moth in a landscape. Our model is calibrated from the literature, *in situ* measures, and through mesocosm experimentation.

II.2.3 Study system & theoretical model description

Species involved : boxwood and box tree moth

The box tree moth, *Cydalima perspectalis*, is an herbivorous lepidoptera belonging to the Crambidae family (Mally and Nuss, 2010). In Europe, five to seven larval instars are necessary to the larvae to become pupae for about ten days before emerging as moths (Kawazu et al., 2010). During the winter, the larvae are at the beginning of their development in stages two, three or even four (Poitou et al., 2020) and form cocoons to enter in hybernaculi (Nacambo et al., 2014). The moths live up to two weeks during which they reproduce and lay eggs on boxwood leaves. The moth has a high fecundity rate, with between 300 and 400 eggs laid per female in its native range, and until 800 eggs in Europe in masses of 5 to 30 eggs (Kawazu et al., 2010; Tabone et al., 2015; Wan et al., 2014). In Asia, two to five generations are possible per year, with a break during the winter when the caterpillars are dormant (Maruyama and Shinkaji, 1987, 1991). In its invasion range in Europe, the moth completes from 2 (in the north) to 4 (in the south) generations per year (Göttig, 2017; Nacambo et al., 2014). The mean intrinsic dispersal distance of moths has been estimated around ten kilometers per year (Van der Straten and Muus, 2010).

The moth exhibits no preference for any particular boxwood species (Leuthardt and Baur, 2013), so the common European boxwood *Buxus sempervirens* is widely consumed, as well as Caucasus boxwood *Buxus colchica*, and even the rarer European species *Buxus balearica* (Kenis et al., 2013). These natural boxwood stands, which have already undergone a major decline over the last millennia (Di Domenico et al., 2012), are now subject to this additional threat. In Asia, *C. perspectalis* also consumes other species, including holly (*Ilex purpurea*), charcoal (*Euonymus japonicus*, and *E. alatus*). Fortunately these species do not seem to be consumed in Europe (Göttig, 2017). Despite natural regulation by native predators and parasites, this moth remains a threat to ornamental boxwood in Asia, where its potential targets are protected by insecticides (Wan et al., 2014). Instead, in Europe *Bacillus thuringiensis* is commonly used as a sustainable control method. However, its efficiency is offset by its low persistence and more importantly its wide target range. Thus, current efforts are being made to develop more long-term specific treatments. Biological control solutions are also being explored, such as the use of nematodes (Göttig and Herz, 2018) and parasites from the genus *Trichogramma* (Göttig and Herz, 2016). Efforts are also being made to seek out predators and parasites from

the box tree moth's area of origin that might act in areas of invasion (Göttig, 2017). The use of pheromone traps is widespread, both for monitoring and control (Göttig and Herz, 2017; Santi et al., 2015), but their effectiveness appears to be insufficient at a large scale. Even if effective control for ornamental boxwood could be introduced, natural boxwood and associated ecosystems will likely suffer dramatically from the *C.perspectalis* invasion.

Boxwood has a fairly heterogeneous distribution in Europe that consists mainly of small and fragmented stands, but some large areas of continuous boxwood occur in the French Pyrenees, the Pre-Alps and the Jura (Di Domenico et al., 2012). It is a long-lived, slow-growing shrub that thrives on calcareous substrate. It can tolerate a wide gradient of light incidence, and can therefore be found in a range of plant communities, from canopy areas in heaths to under cover in forests (Di Domenico et al., 2012). It can play an important role in structuring ecosystems, by trapping sediment and storing water. It also influences the establishment and survival of tree species in woodland succession (Mitchell et al., 2018). A total of 286 species are associated with the shrub, including 43 fungi that are exclusively observed on boxwood (Mitchell et al., 2018). However, boxwood is scarcely predated by native species.

Local demographic model

We start with a local model that describes the interaction between BTM and its host BT at a small homogeneous spatial scale. The model projects the population size m of Box Tree Moths (BTM) and the population density of Box Trees (BT), which are separated in two variables : leaf density l and wood density w , from moth generation n to $n + 1$. This time representation is used to avoid the problem of multiple generations per year and its spatial variation. However, we are able to project the population of BTM and BT from year to year if we know the number of generations per year in each specific location. We write

$$\begin{cases} l_{n+1} &= S_l(\mu_n) F_l(l_n) l_n + r_0 w_n \\ w_{n+1} &= S_w(\mu_n, \rho_n) F_w(w_n, \rho_n) w_n \\ m_{n+1} &= S_m(\mu_n) F_m m_n \end{cases} \quad (\text{II.1})$$

to indicate that during the projection interval, BT and BTM grow and reproduce (F), and survive (S). The BT reproduction functions were constructed using a Ricker model, which includes the intrinsic population growth rates r_f , r_w and the carrying capacities of the environment L_{max} , W_{max} , while the BTM reproduction function is linear and only includes the fecundity of adults f and their survival s . The survival of the species is determined by the consumption of leaves and bark by the BTM as well as the intraspecific competition for the resource faced by BTM. The survival and reproduction functions F and S depend on both the current population l, w, m , and the environmental descriptors μ and ρ .

Environmental descriptors. The environmental quality is described using the following two quantities:

$$\mu_n = \frac{f m_n \alpha}{l_n} \quad \text{and} \quad \rho_n = \frac{l_n}{w_n}$$

The descriptor μ corresponds to the ratio between the number of leaves needed by all the larvae to fulfil their cycle complete development and the number of available leaves (α is the amount of leaves needed per larva). The number of larvae depends on the number of moths (m_n) through its product by the moth fecundity (f). And each larva needs α leaves to complete its cycle. The ratio μ thus quantifies the pressure for the resource, which plays a direct role in

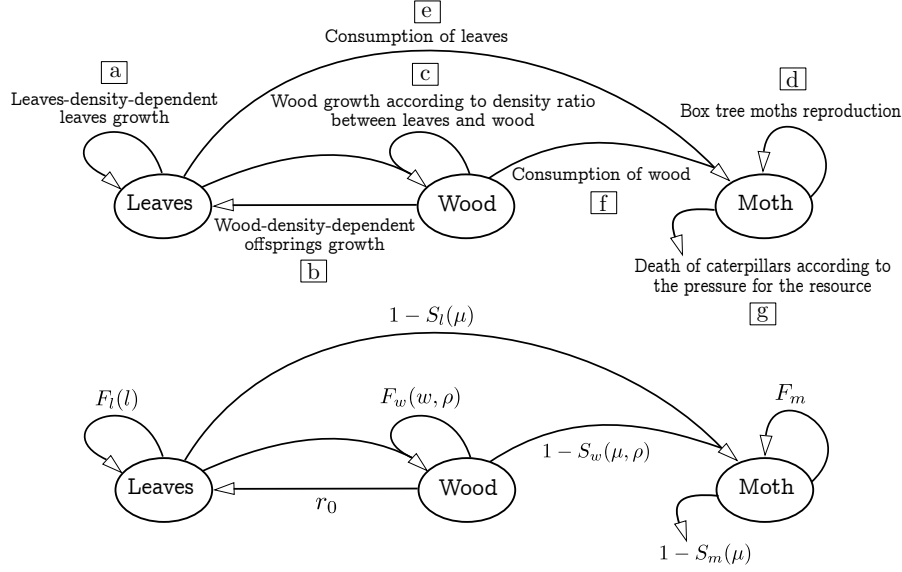


Figure II.2 – Model of dynamics between the boxwood, separated into wood and leaves, and the box tree moth. The arrows show the interaction between the three variables.

the intensity of consumption of leaves and wood, and therefore the survival of the larvae. The descriptor ρ is the quantity of leaves per unit of wood. This represents the level of boxwood defoliation, which has an impact on the growth of the wood.

Reproduction. The increase in foliage biomass is the result of two processes: the growth of leaves F_l , which depends on the current foliage (Figure II.2a), and the production r_0 of new shoots by the wood after defoliation (Figure II.2b). Without herbivory, the growth of leaves is limited only by senescence and its carrying capacity L_{max} . The leaves growth F_l is represented by a Ricker model of the following form

$$F_l(l) = \exp\left(r_f\left(1 - \frac{l}{L_{max}}\right)\right)$$

where r_f is the intrinsic growth rate of the leaves.

The wood growth function F_w (Figure II.2c) is constructed using a Ricker model. Positive growth is constrained by carrying capacity. Negative growth occurs after an important defoliation because branches or even a proportion of trunk can die after defoliation. For each projection interval, the intrinsic growth rate of the wood is defined as the balance between the production of new wood, which critically depends on the density of leaves per unit of wood ρ , and the mortality induced by severe defoliation. When the density of leaves is large ($\rho \gg 1$), the BT is healthy and its production of wood reaches a maximum. Conversely, when the density of leaves per unit of wood collapses due to severe defoliation, the production of wood is low while the mortality increases until a maximum which forces the growth rate to be negative (Supporting Information (SI) for details).

The reproduction rate of BTM (Figure II.2d) does not suffer from density dependence and results from the product of adult fecundity f and adult survival s

$$F_m = f s$$

Survival. The leaves may die by senescence at rate v , or be consumed by BTM at a rate which increases with the pressure of BTM on BT (μ) (Figure II.2e). In the absence of BTM, 0% of leaves are consumed, while if BTM have saturated the environment, 100% of the leaves are consumed (see SI for details).

The wood can suffer from both defoliation (Figure II.2c), which decreases its intrinsic growth rate, and bark consumption by the BTM (Figure II.2f). The wood mortality due to consumption increases with both the BTM pressure, μ and the BT health ρ . More precisely, the wood mortality saturates to d_{max} when the foliage is abundant. However, when the foliage is small, the bark consumption occurs while the superficial wood is available. Thus recently defoliated boxwood with small bark coverage (ρ close to 0) cannot be consumed by the larvae (see SI for details). We use a step function which allows to take into account that the consumption of superficial wood depends on the presence of available softwood, and thus a certain amount of foliage.

Survival of BTM during the larval stage depends mainly on the amount of available resource per larva μ . If the larva has enough available resource to complete its six stages, it will evolve into a moth, while a lack of resource during its growth will cause its death. The survival rate also takes into account intraspecific competition for resource caused by interference between the larvae (see SI for details).

Spatially explicit model

Using the local model which describes the interactions between BTM and BT at small homogeneous spatial scale, relevant for short time dynamics, we build a cellular automaton in order to investigate the BTM invasion over a regional heterogeneous landscape and long time scale. Indeed, while the local model evaluates the moth invasion on the scale of a few generations, the results with explicit space are obtained with a projection time of 1000 generations, i.e. 500 years in the case of two generations per year.

Landscape: French Alps and theoretical grid space. Our spatially explicit model describes the dynamics of the BT and BTM on a 2 dimensional landscape composed of two types of cells: habitat cells where BT can grow and urban cells where BT cannot establish. In each cell with BT, BTM can mate and lay eggs according to the local demographic model, while in cells without BT, BTM cannot become established. After the reproduction phase, BTM moths disperse over the landscape to find new areas to breed and lay eggs. BT can also disperse over the landscape to recolonise extinct areas. Simulations are initialized with a single moth invading a patch chosen at random, and carried out on a maximum of 1000 iterations if no specifications are given. We consider two types of landscape: a schematic map of the French-Alps and a theoretical landscape.

The French-Alps map was obtained from field observations provided by the National Alpine Botanical Conservatory. It is composed of 570 by 351 cells of 29 hectares each (about 58 000km², SI Figure II.9). It should be noted that these data focus on natural boxwood and neglect the presence of ornamental boxwood in urban areas. We focus on the French Alps because detailed botanical data are available, but in theory our model could be extended to the whole area of invasion. This landscape allows us to investigate the potential impact of the BTM in this region.

We also consider a more theoretical squared landscape to investigate the effect of the spatial structure on the invasion of the BTM. In particular, we use various initial size and proportion of boxwood patches. For each landscape, we also calculate an aggregation index by counting the number of pairs (adjacent boxwood patches) in the landscape and dividing it by the maximum number of possible pairs: $2n - |2\sqrt{n}|$, where n is the proportion of boxwood cells (Harary and Harborth, 1976). For each landscape size and boxwood proportion, we randomly generate 1000 landscapes with possibly different aggregation indices. The final aggregation index equals the difference between the index of the landscape of interest and the average index of the randomly generated landscapes.

Dispersal phase of BTM. A BTM dispersal event includes two stages: (1) emigrating from birth areas, and (2) searching for new areas (exploration) and settling to breed. Field observations suggest that the exploration phase is stochastic, composed of frequent short-distance dispersal by adult flight, and rare long-distance dispersal by anthropogenic action (boxwood trade) or long flight. *In situ* experimentation using a flight carousel has provided a mean dispersal distance per individual of 13km (Bras et al., personal communication), which is in accordance with the 10km dispersal distance observed by Van der Straten and Muus (2010). Bras et al. have also observed rare long-distance flights in their experiments, which may correspond to long-distance dispersal events that we model using a fat-tailed dispersal kernel. To this end, we use an exponential power distribution from Klein et al. (2006) which makes it possible to compare different shape of distribution tails while maintaining a fixed average dispersal distance. For ecologically realistic calibration the tail shape parameter is 0.5 (i.e fat-tailed dispersal kernel) and the average dispersal distance is 25 cells (i.e ≈ 13 km). In addition, to save computation time, we assume that BTM disperses as a swarm of 1000 individuals. This group dispersal may occur because BTM can be attracted by volatile boxwood compounds or avoid geographical barriers, or are influenced by weather conditions. Thus, during the searching and settling phase, each group of BTM settles in an area located at a random distance drawn in the exponential power distribution and chosen with a random turning angle run in a uniform distribution over $(0, 2\pi)$. The emigration rate for each location depends on the pressure for resource μ at the birth location. As long as pressure remains low, the moths have the possibility to find leaves to oviposit in their birth patch and thus dispersal is weak. When the resource pressure increases, there is not enough boxwood available for laying eggs and adults will disperse massively to another patch in search for resource. Such resource-dependent dispersal has also been modelled by the study of Johst and Schöps (2003) (see SI for details).

Dispersal of BT. Dispersal events for BT include (1) creation of seeds and (2) dispersal of seeds to surrounding areas by wind and birds. We assume that BT dispersal is very low and occurs only if the boxwood is in fairly good condition, meaning that it has sufficient foliage (see SI for details).

As such, the initial density of wood in a newly dispersed seedling depends on the parent patch density. Foliage is produced in the next generation after recolonization through the production of leaves by the wood. We assume that seeds from a location are transported randomly only in the 8 surrounding cells that has previously contained BT. We only make it possible for an extinct area to be recolonized by surrounding BT, and we make it impossible for BT to colonize new areas.

II.2.4 Parameter estimation and sensitivity analysis

To quantify the parameters of our model to our system study (Box Tree and Box Tree Moth), we use three different methods: 1) literature review, 2) experimental measurement (field data and mesocosm experiment) and 3) statistical analysis.

Literature review

From the recent literature on the Box Tree Moth ([Kawazu et al., 2010](#); [Tabone et al., 2015](#); [Wan et al., 2014](#)), we can evaluate the fecundity parameters f with a mean value of 120 and a range from 0 (i.e effects of oophagus predators and parasites) to 300 (see SI for more details). In addition, the maximum survival rate of the caterpillar is on average 49%. Then combining experimental results from T. Defferier and E. Tabone from the National Research Institute for Agriculture, Food and Environment (INRAE) and [Slansky Jr and Scriber \(1982\)](#), we estimate the parameter α around 0.3 (see SI for more details). From the experimental study of [Bras \(2015\)](#), we are able to quantify the average dispersal distance of the BTM α_d and the tail shape parameter c .

Experimental results

To assess some parameters describing the interactions between the two species we perform *in situ* measurements and a mesocosm experiment. First, we collect data in two boxwood areas located on the eastern slope of the Epine massif in Savoie (45°38'23.7"N 5°50'43.6"E and 45°41'33.2"N 5°50'56.2"E) at an altitude of 500 and 630 meters, respectively. In these patches, the invasion peak resulting in massive defoliation of the boxwood, occurred in July and August 2016, while we sampled in March 2017. From these measurements on already defoliated area, we estimate from 101 boxwoods its mortality due to leaves consumption by BTM $d_{max} = 0.74$ and from 49 boxwoods its shoot production parameter $r_0 = 5.10^{-5}$ (see SI for more details on the parameter estimates). Moreover, from dendrometry method and statistical analysis, we estimate the maximum growth rate of the wood to $r_{w,max} = 0.3$. Secondly, we perform a mesocosm experiment to model the consumption of leaves by caterpillars and the caterpillar survival with respect to the descriptor parameter μ . We created a gradient for the resource pressure μ by placing varying numbers of caterpillars on the box trees. The gradient have seven μ values (see SI for more details on the experiments and the statistical analysis).

Statistical analysis from the local model

In order to quantify the other parameters of the model, we use our local demographic model. Field observations show that when the box tree moth colonizes a patch, its population explodes within a few generations, eventually reaching a peak of density resulting in total defoliation of the boxwood stand. Hence, no more resources are available and the box tree moth disappears from this patch. This dynamics lasts for 3 to 4 years after the beginning of the invasion until the extinction of the moth. When two generations are carried out per year, it corresponds to 6 to 8 generations. Using statistical analysis, we look for parameters that reproduce this qualitative behaviour, and achieve plausible quantitative outputs (see parameters referred as "estimate" in Tables II.1-II.2 and details in SI).

Sensitivity analysis

First we discuss the outcome of the local demographic model. Although the moth population collapses for realistic parameter values as expected from the observations (Figure II.7 in SI), the model may reach a coexistence equilibrium for some parameter values. In particular, we look at two key parameters, the moth fecundity and moth survival that may vary during the course of the outbreak in Europe. Indeed, the accommodation of native predators and parasites could reduce the survival rate of caterpillars, and moth fecundity could be reduced by oophagous insects. From our local demographic model, we show that coexistence is only possible in a very narrow range of parameters values, which are far from the actual measured values (see Figure II.8 in SI). To go further in the understanding of the coexistence behavior, we look at two connected patches which may favour coexistence in plant-insect interactions ([Kang and Armbruster, 2011](#)). However, our numerical simulations show only a slight expansion of the coexistence area, which is far from sufficient to lead to coexistence with realistic parameters (see Figure II.8 in SI). Thus we really need a spatial model to understand the invasion of the BTM.

To further investigate the effect of BT and BTM interactions and the robustness of the spatially explicit model, we conduct a global sensitivity analysis of three outcomes of our model: the boxwood biomass, the percentage of dead boxwood cells and the probability of moth persistence. For each outcomes, we use the Partial Rank Correlation Coefficients (PRCC) ([Saltelli et al., 2004](#)) to quantify the strength of sensitivity for each of the 21 parameters and the direction of their impact on the model outcomes. If the PRCC is positive, the parameter increases the outcome, while it decreases for negative PRCC. We sample parameters in a wide range centered on the reference values of Tables II.1-II.2, that remains ecologically coherent (e.g. boxwood growth is slow). We use 1786 values sampled around the reference values of Tables II.1-II.2 for each parameter and 10 replicates per parameter values to compute the PRCC (see Figure II.15 for global sensitivity results).

II.2.5 Modelling results and discussion

Spatial structure promotes coexistence while resource depletion drives to extinction (Hyp 1)

Using a spatially explicit model, including local population dynamics and short to long range dispersal events, we show that coexistence of the moth/boxwood system occurs across a wide range of parameters. At a regional scale, dispersal allows box tree moth persistence in a cycle outbreak dynamics ([Berryman, 1987](#)), through recurrent recolonization of patches that have been previously defoliated and which have had time to recover. The spatial structure therefore allows coexistence, in line with hypothesis 1a. The coexistence mechanism is similar to the rock-paper-scissors game with the corresponding states: patches of defoliated box tree, patches of box tree with foliage and patches of box tree invaded by the moth. These three states compete with each other following a circular hierarchy, as defoliated box trees 'lose' against box trees with foliage, which are in turn invaded by box tree moths, which finally leads to defoliated box trees. Similar rock-paper-scissors games have been described in other ecological contexts such as polymorphic bacterial strains ([Kerr et al., 2002](#)) and plant-mutualist-exploiter systems ([Szilágyi et al., 2009](#)).

The sensitivity analysis (SI Figure II.15) reveals that fecundity and survival of the box tree moth significantly reduce its persistence over the landscape. Thus, we explore moth persistence over a larger range of fecundity and survival parameters than those estimated. Predation on the moth and on the caterpillars is currently low ([Kenis et al., 2013](#)), in part because the box

tree moth accumulates boxwood alkaloids in its body (Leuthardt and Baur, 2013). However, native predators may become efficient to feed on the moth following phenotypic plasticity or adaptation (Carlsson et al., 2009). Native egg parasites like trichograms often used in biological control may also become able to feed on the moth, thereby reducing its fecundity. We find that the moth could rapidly go extinct only for very low fecundity and survival rates (lower-left corners of Figure II.3a and f). It is therefore unlikely that the accommodation of native natural enemies will trigger moth extinction. Elevation can also have an important influence on larvae survival and fecundity (via egg survival), as well as on the nutritional quality of the boxwood that controls larvae growth. However, we show that elevation does not change qualitatively the outcomes of the model even if it reduces the above mentioned parameters by 50% (SI Figure II.15). Lastly, the sensitivity analysis shows that moth persistence is significantly impacted by the boxwood productivity and survival (SI Figure II.15). Thus environmental changes induced by human exploitation, climate changes or boxwood parasites, should have a critical impact on the BTM persistence through its effect on boxwood at local and global scale.

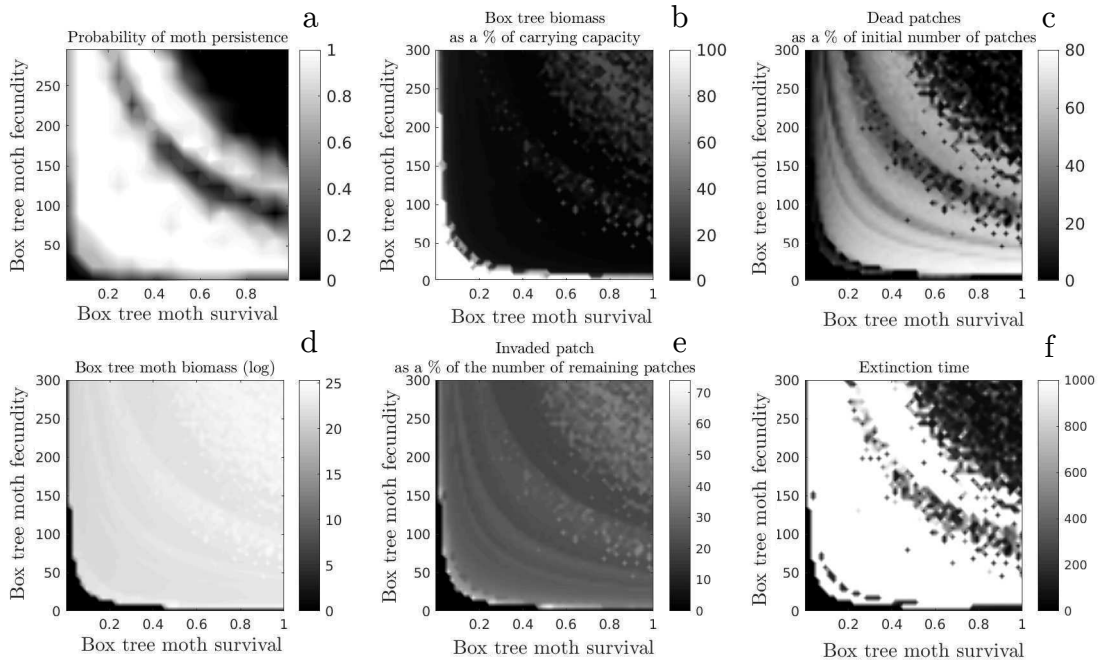


Figure II.3 – Final state maps in the real landscape in function of fertility f and maximum survival $S_{m,max}$. (a) landscape-scale probability of moth persistence, (b) landscape-scale wood biomass expressed as a percentage of the landscape-scale carrying capacity, (c) number of boxwood patches disappearing as a percentage of the initial number of boxwood patches, (d) landscape-scale moth biomass, (e) number of patches invaded as a percentage of the number of boxwood patches present, (f) time of moth persistence. The ecologically realistic parameter values are $f = 120$ and $S_{m,max} = 0.5$. For each couple of parameters 50 simulations are carried out and results are averaged.

One step further, hypothesis 1b postulates that long-term coexistence is due to asynchronous dynamics, and that moth extinction is due to the synchronisation of the local dynamics. If we artificially ensure that the invasion begins with a moth in each cell, we observe that all boxwood stands are defoliated simultaneously and that the moth disappears globally in a

dynamics of type pulse outbreak (Berryman, 1987): perfect synchronization indeed leads to moth extinction. But if all stands are initially invaded except a single one, this is enough for the occurrence of desynchronisation, and the whole system becomes viable. The moth can therefore disappear due to perfect synchronization, with 100% of the patches invaded simultaneously. However, any other mechanism that globally reduces drastically the resources may also cause moth extinction. Indeed, with high moth fecundity and survival rates (upper-right corners of Figure II.3a and f) the moth depletes the resource until its own extinction. This negative effect of fecundity and survival of the BTM was expected from the sensitivity analysis (see f and S_{max} in SI Figure II.15). In contrast to the results obtained with *H. spinipennis*–*A. dieffenbachii* system, our results indicate that global resource depletion is responsible for moth extinction, rather than synchronisation of local dynamics (Johst and Schöps, 2003). This is in line with the individual-based model of Uchmański (2019), who found that forest insect pests may go extinct when adult fecundity or larvae survival increase. Within the coexistence regime, the average density of moths and the average intensity of the invasion are insensitive to moth fecundity and survival; the moth either persists at the coexistence density or goes extinct (Figure II.3).

Interestingly, the moth population can persist even when it periodically invades 99% of the patches (SI Figure II.11 top), provided that leaves grow back fast enough to prevent global resource depletion. In this case the moth invades a significant proportion of the patches even during troughs (about 12%); the cyclic dynamics are therefore getting closer to a permanent outbreak (Berryman, 1987). The same process occurred in the model of Uchmański (2019), where leaf growth rate was expressed by a parameter defining the number of years needed for their regeneration. In his model, when the leaf growth rate increased the dynamics of the cyclic outbreak was accelerated, with shorter periods between peaks and troughs. The system then transited to a permanent outbreak for very rapid leaf growth rates. On the contrary, a slow leaf growth rate led to the extinction of the insects (SI Figure II.11). In our model, we also show the positive effect of the wood survival and the leaf productivity on the moth persistence (see Figure II.15)

Spatial structure generates periodical invasions (Hyp 2)

We further postulate that, despite local cycles of extinction and recolonization, the coexistence regime is stationary at the landscape scale (hypothesis 2), a phenomenon called statistical stability (Amarasekare, 2008; De Roos et al., 1991; Holyoak et al., 2005). Instead, we find that the coexistence regime is periodic at the landscape scale (Figure II.4a). A similar pattern has been observed in the *H. spinipennis*–*A. dieffenbachii* system (Johst and Schöps, 2003) and in Uchmański (2019). The global period ranges between 20 generations (high leaf growth rate, SI Figure II.11 top) and 40 generations (low leaf growth rate, SI Figure II.11 bottom). In contrast, the invasion of a local patch lasts 5 generations when 1000 moths are introduced at once, and 7 generations when a single moth colonizes the patch (SI Figure II.7). This discrepancy between the local and global timescales suggests that periodicity at the global scale results from the combination of the local time scale and the pace of dispersal. During peaks, between 60 and 99% of the boxwood patches are simultaneously invaded by the moth, and 1-5% during periods of minimal abundance, depending on parameter values. Periodic travelling waves explain this pattern, which have been described in prey-predator systems (Lambin et al., 1998; Sherratt, 2001). However, such prey-predator systems are locally periodic as well, and long-term coexistence does not require spatial structure. In contrast, in our study system, the periodic waves emerge from the spatial structure, instead of being a mere

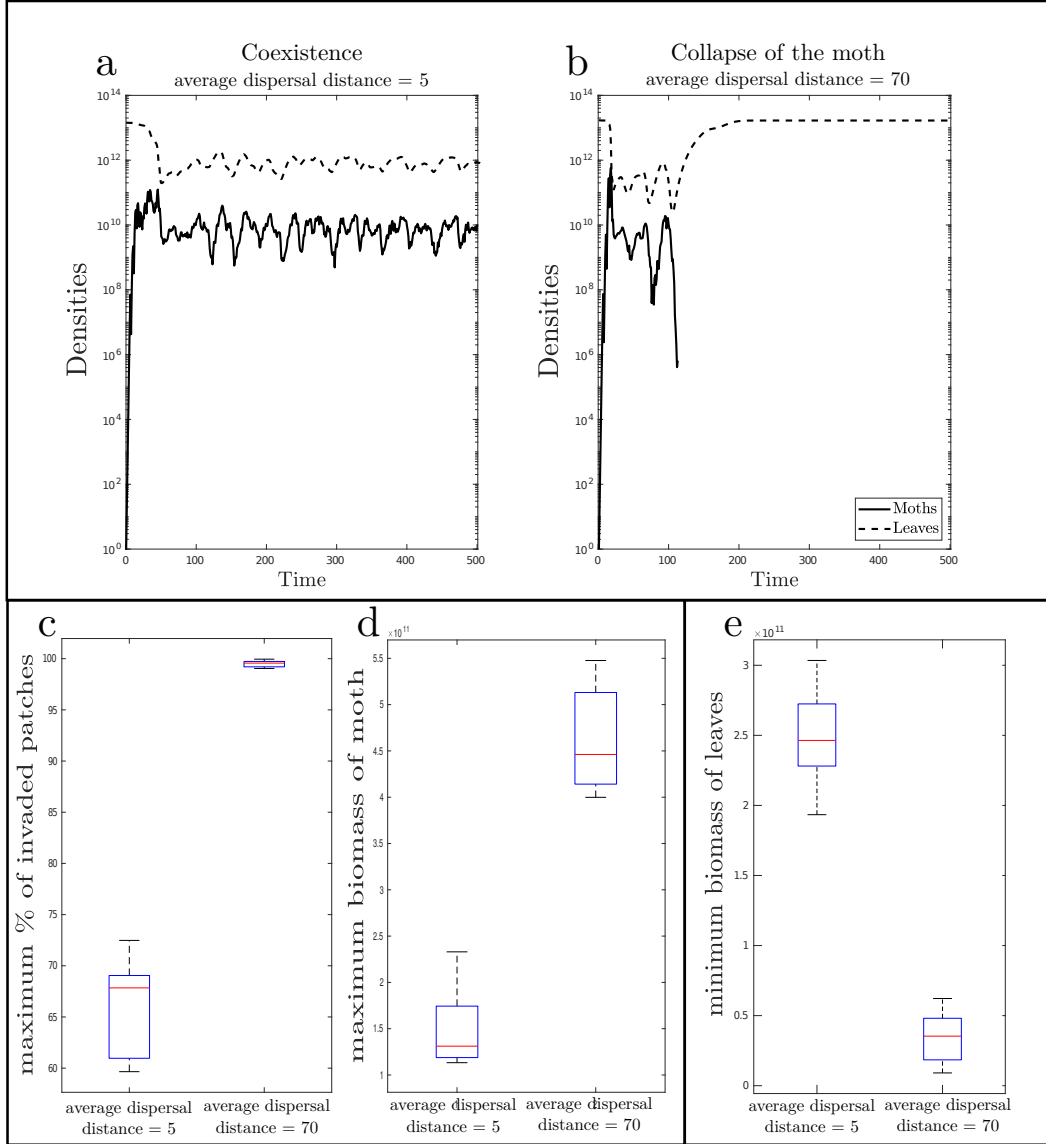


Figure II.4 – Example of global population dynamics in the case of coexistence (a) and moth collapse (b). (c) maximum % of invaded patches. (d) maximum moth biomass. (e) minimum leaf biomass. Parameters values as in Tables II.1-II.2, except for $r_0=2 \times 10^{-3}$ and for the average dispersal distance α_d which either equals 5 cells (moth persistence) or 70 cells (moth collapse). Boxplots are produced from 50 simulations.

consequence of local periodicity.

If the mean dispersal distance is very low (1 cell on average, keeping rare long-distance events), the amplitude of the oscillations is also very low (Figure II.5b) and the system tends to be statistically stable.

Intermediate intensity of long-distance dispersal prevents BTM from extinction

Hypothesis 3 posits that asynchronous local dynamics require intermediate dispersal distance (Myers, 1976; Myers and Campbell, 1976), because very limited dispersal might prevent suitable boxwood patches from colonization (3a), whereas very long-distance dispersal may synchronize local dynamics (3b). The sensitivity analysis reveals that the moth persistence significantly decreases with an increase of migration parameters, i.e. $M_{w,max}$ and α_d , migration rate including mortality during dispersal and mean dispersal distance (SI Figure II.15). However, with the measured parameter values we find that the long-term probability of moth persistence is insensitive to dispersal distance. This is shown in Figure II.5a, where the measured value for the production of new leaves from wood after total defoliation r_0 equals $5 * 10^{-3}$ (-2.3 on a log scale). In that case, the moths persist whatever the mean dispersal distance is (1, 25 or 70 cells), because boxwood produces new shoots after total defoliation fast enough to enable moth persistence even when the global leaf biomass is low. Meanwhile, previously infected areas produce enough leaves to support another moth outbreak. Conversely, when r_0 equals $2 * 10^{-3}$ (-2.7 on a log scale, which may happen under climatic stress for instance), it turns out that the moth does not persist when the mean dispersal distance equals 70 cells (Figure II.4b). The moth initially invades 99% of the patches (Figure II.4c) and reaches very high densities (Figure II.4d). This reduces the global leaf biomass (Figure II.4e) and the moth eventually collapses due to resource depletion. In the case of coexistence (Figure II.4a) the maximal % of invaded patches is around 60-70%, the maximal moth density is 3 times lower and the minimal leaf biomass is 5 times higher than in the extinction case.

We also find that when the mean dispersal distance is very short (1 cell on average) the probability of moth persistence is not affected by the offshoot production rate. Because of short-distance dispersal, the moth does not generate periods of global invasion and intact patches are always present at the border of its slow moving invasion front. In that case, relatively high offshoot production rates are unnecessary as the moth populations do not rely on the new growth of recently defoliated patches. In contrast, when the average dispersal distance is larger (e.g. 25 and 70 cells), the probability of persistence increases with the offshoot production rate (Figure II.5a). In such cases, the moth needs to recolonize recently defoliated patches because during peaks a large proportion of patches are defoliated at the same time. Therefore, relatively high offshoot production rates are necessary to avoid global over-exploitation.

The influence of the mean dispersal distance on moth persistence is therefore studied with a relatively low offshoot production rate, $r_0 = 2 * 10^{-3}$. As expected by hypothesis 3b, frequent long-distance dispersal events lead to the extinction of the moth due to global resource depletion (Figure II.5b, continuous line). This effect of long-distance dispersal was not present in Uchmański (2019), this can be explained to the use of a thin-tailed Gaussian kernel characterized by very rare long-distance dispersal events, thus insect pests could not reach the distant trees which had time to regenerate after their last defoliation.

Furthermore, hypothesis 3a posits that the moth goes extinct in the case of limited dispersal, because it would not be able to escape over-exploited patches. However, the fat-tailed dispersal kernel prevents such phenomenon: even when the mean dispersal distance is very low (1 cell), the moth can persist thanks to frequent long-distance dispersal events. Things change when we constrain dispersal to a uniform distribution, which ranges between 1 cell and a given maximum of cells. In that case, when the maximum number of cells is low enough (up to 4 cells), the moth invasion can get stuck in a landscape dead end and it disappears because of local resource depletion, and not global resource depletion (Figure II.5b, dotted line). Prey-predator systems subject to limit cycles were also stabilized by limited dispersal in

the individual-based model of [Cuddington and Yodzis \(2000\)](#), where limited dispersal reduced the average predation rate and thereby avoided local instability. However, if dispersal is too limited the consumer can go extinct because of a drastic reduction in the rate of predation, as is the case in our model when long distance dispersal events are extremely rare due to uniform dispersal kernel (Figure II.5b, dotted line).

The results obtained using the fat-tailed dispersal seems the most plausible, indeed rare long-distance dispersal events mediated either by wind or by human dispersal likely occur in the case of the box tree moth. With a fat-tailed dispersal kernel, multiple invasion fronts are created far away from invaded patches because long-distance dispersal events are frequent ([Shaw, 1995](#)). This created a fragmented landscape of defoliated and intact boxwood, in which the moth does not end up in a dead end. Such a fragmented invasion front can be observed in Europe. The moth was first observed in Germany in 2006/2007; in the same year it spread to Switzerland and the Netherlands and reach France ([Feldtrauer et al., 2009](#)) and the United Kingdom ([Salisbury et al., 2012](#)) in 2008, Austria in 2009, Italy ([Bella, 2013](#)) in 2010, and Portugal, Iran and Armenia in 2016 ([Bras et al., 2019](#)). Long-distance dispersal might be due to the boxwood trade between European countries, and probably to a much lesser extent by the natural dispersal of moths. We therefore expect that in practise only frequent long-distance dispersal can lead to the extinction of the moth, due to global resource depletion.

However, this prediction might be mitigated by a dispersal cost resulting from higher mortality encountered during a long-distance flight, a fertility decline with flight distance or even delayed mating effect that reduces the fitness of moth dispersing at long-distance. Indeed, those mechanisms tends to reduce the high invasion potential of the long-distance dispersal events by limiting the effective dispersal distance. And our model already shows that moth persistence is higher with intermediate-distance dispersal. Moreover, these ecological processes are unlikely to reduce dispersal to the extreme case of a uniform distribution at short distances, and therefore do not significantly affect the persistence of the box tree moth. Indeed, we show that a reduction of the swarm size with dispersal distance gives qualitatively unchanged results on the moth persistence (SI Figure II.10)

Fragmented landscape with low amount of resource prevents extinction (Hyp 4)

Next, we predict that the coexistence regime depends on the landscape characteristics, in particular its size (4a) and the proportion of suitable boxwood patches (4b). To do so, we use wrapped landscapes (with no edge effect) of different sizes and different proportions of randomly distributed suitable patches (Figure II.6a). Below 200*200 cells, which corresponds to about 12 000 km², coexistence does not occur within the realistic range of parameter values, because previously defoliated patches are quickly recolonized by the moth and lack time to grow back. This induces a global resource collapse and drives the moth to extinction. Above the 200*200 threshold, the larger the landscape is, the more likely the coexistence occurs, in line with hypothesis 4a. In the previous sections, we restrict our model to the French Alps, but we expect that long term coexistence is even more likely on the European scale because larger landscapes favor coexistence. The influence of landscape size is also apparent in the real landscape, with a uniform and short-range dispersal kernel: when the invasion begins in a relatively isolated area of the landscape, coexistence is impaired by small size.

A priori, the effect of the initial proportion of boxwood patches on coexistence is unclear (4b) because on the one hand a higher proportion of suitable patches provides more resources to the moths, while on the other hand it may trigger moth outbreaks which ultimately leads

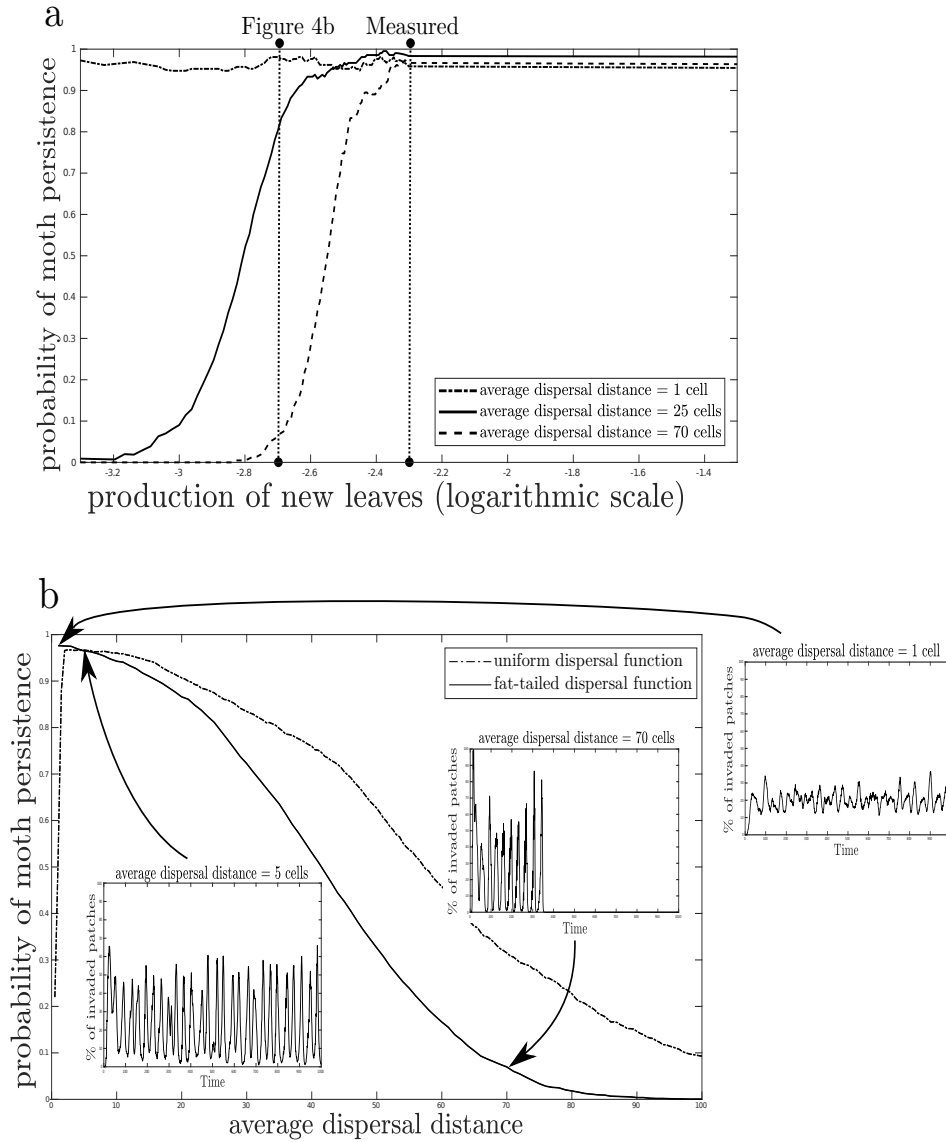


Figure II.5 – (a) Effect of the rate of new leaves production by the wood (r_0) on the probability of moth persistence. For each tested value, the probability of persistence is obtained by 50 simulations conducted on the realistic landscape with random initial patch of invasion. Three average dispersal distances are tested, a realistic distance of 25 cells, a very short distance of one cell, and a very large distance of 70 cells. (b) Effect of the average dispersal distance on the probability of moth persistence. For each tested value, the probability of persistence is obtained by 50 simulations conduct on the realistic landscape with random initial patch of invasion. Each time two dispersal functions are tested: a fat-tailed function, and an uniform function. The minimum dispersal distance is one cell. The inserts show the percentage of patch invaded over time for three selected average dispersal distances of 1, 5 and 70 cells with the fat tail dispersal function. For each parameter values 50 simulations are carried out and results are averaged.

to resource depletion. We find that the latter mechanism is on the driver's seat: reducing the proportion of boxwood patches increases the probability of moth persistence (Figure II.6a).

More precisely, the landscapes larger than 400×400 cells filled with less than 20% of boxwood patches almost always allow coexistence. In such cases, most dispersal events fail to find suitable patches, lowering the moth population density, which in turn leaves more time for leaves to grow back. On the contrary, a high proportion of suitable patches results in high moth densities which leads to global over-exploitation, despite a potentially higher leaf biomass. Thus, we postulate that any environmental changes due to climate changes or human activities, that reduces boxwood biomass would not necessarily drive the BTM towards extinction.

The coexistence regime has interesting consequences on the final proportion of boxwood patches, which corresponds to the initial proportion minus the proportion of complete withering patches due to over-exploitation. Under coexistence, the final proportion increases linearly with the initial proportion with a weak slope of about 0.1, whereas the slope is close to 1 in the case of moth extinction (Figure II.6b). This indicates that the local extinction of boxwood patches is not responsible for global moth extinction. Instead, the final proportion of boxwood patches is a long-term consequence of coexistence and results from their gradual death (Figure II.6c). During each moth outbreak, a small proportion of the boxwood patches disappears due to over exploitation. Then, right after the outbreak a few boxwood patches are recolonized from neighbouring patches (only previously occupied patches can be recolonized), which induces a clustered distribution of the boxwood patches. As a result of clustering, the aggregation index is always positive, which indicates that the landscapes created by long-term coexistence are more aggregated than random landscapes. Boxwood patches relatively isolated in the initial landscape experience larger extinction rates and create holes in the landscape. In contrast, areas where boxwood patches are initially more abundant persist more often, which creates clusters. Moreover, the aggregation increases with the average moth dispersal distance (Figure II.6d). Boxwood patches favor moth outbreaks: increasing the boxwood patches proportion over the landscape produces severe outbreaks. This induces apparent competition between boxwood patches because of their shared pest. With low dispersal distance, apparent competition between patches is mainly local, which limits the formation of clusters. Instead, with high dispersal distance apparent competition is global and the aggregated pattern results from the interplay between local facilitation (recolonization of boxwood patches is purely local) and global competition, as in many spatially self-structured systems (Kéfi et al., 2007, 2008). This is confirmed by simulations where boxwood recolonization is global, in that case the aggregation process vanishes (details not shown).

We further explore how the aggregation process creates boxwood clusters of different sizes, for various dispersal distance. To do so, we start with landscapes which are initially filled with boxwood patches, and run simulations after invasion by the moth. At the end of the simulations, we fit a power-law model to the final distribution of the cluster sizes (SI Figure II.12 top). Clusters smaller than 5 boxwood patches are excluded from the fit. We find that small dispersal distance leads to a cluster size distribution closer to a power-law than large dispersal distance. When the dispersal distance is large (10 to 50 cells), the cluster size distribution follows a truncated power law (SI Figure II.12 top), which indicates that large clusters are under-represented. Large dispersal distance leads to an increase of herbivory, which produces two distinct effects. On the one hand, it favors aggregation due to global apparent competition, as discussed earlier (Figure II.6d). On the other hand, it increases the death rate of boxwood patches and thus reduces the final proportion of patches in the landscape (Figure II.6e). This is why under large dispersal distance (10 to 50 cells) the final landscapes have a homogeneous aspect of equally spaced small clusters (SI Figure II.12 bottom).

These regular patterns are similar to Turing instabilities (Murray, 2001; Turing, 1990) and result from "scale-dependent feedbacks" which combine short-distance positive feedbacks and long-distance negative feedbacks (Rietkerk and Van de Koppel, 2008). In the present case,

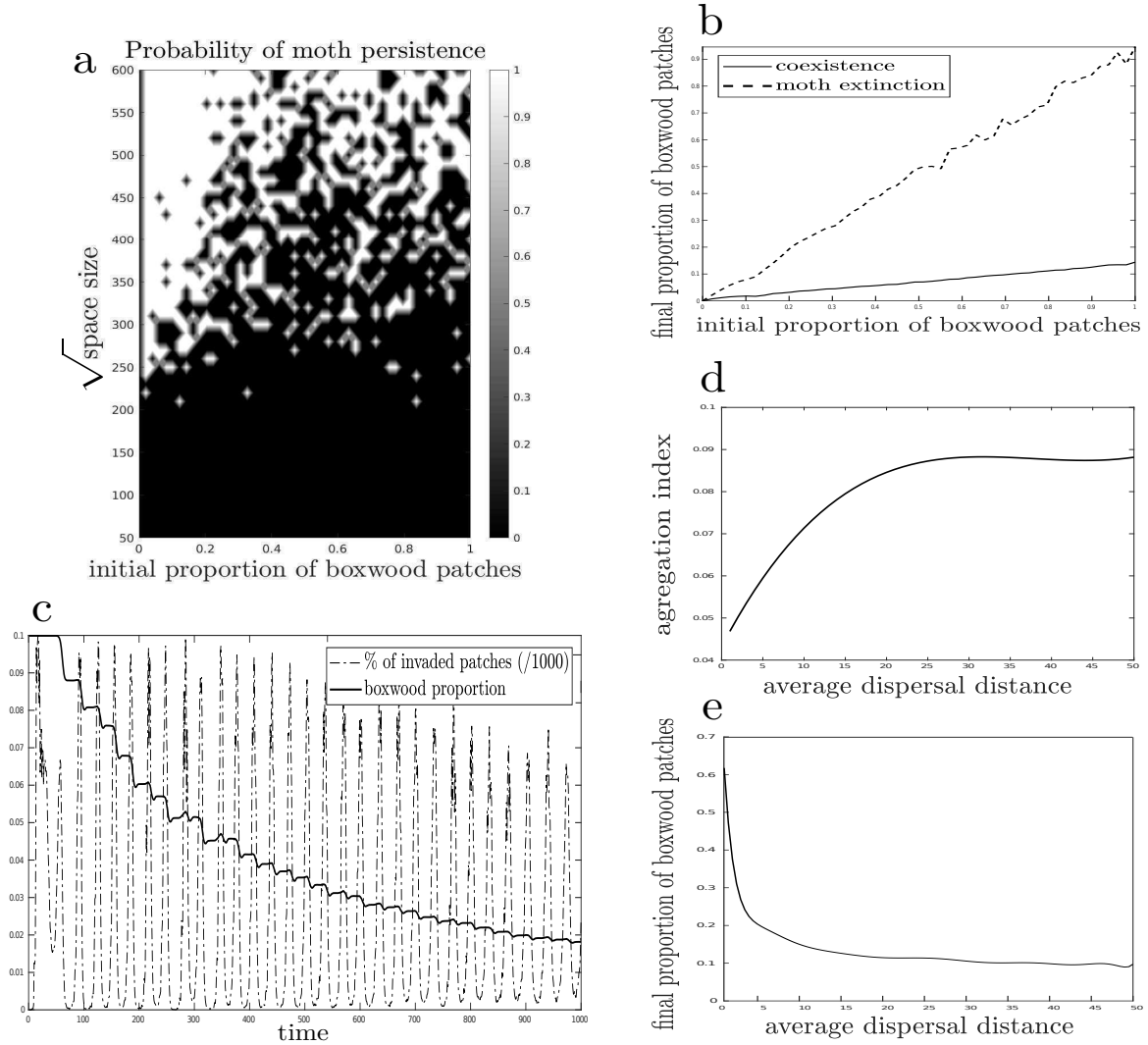


Figure II.6 – Simulation in theoretical landscapes. (a) The probability of moth persistence depends on space size and on the initial proportion of boxwood patches. (b) In the case of coexistence, the final proportion of boxwood patches is much lower than the initial proportion because moth outbreaks cause patch extinctions. (c) The boxwood proportion in the landscape declines during each moth outbreak. (d) The aggregation index increases along with the average dispersal distance. (e) In coexistence, increasing the dispersal distance reduces the final proportion of boxwood patches in the landscape. All other parameter values are set to the realistic values. For panels a, b, d and e, results are averaged from 50 simulations.

short-distance positive feedback correspond to local facilitation of boxwood due to recruitment while apparent competition between boxwood stands because of their shared pest mirror long-distance negative feedbacks. Several studies have investigated how spatial patterns can emerge from such scale-dependent feedbacks in a variety of ecological scenarios, such as plant-water interactions (Kéfi et al., 2010; Klausmeier, 1999; Meron et al., 2004; Rietkerk et al., 2002; Von Hardenberg et al., 2001), plant-plant interactions (Lejeune et al., 1999), or predator-prey interactions (Levin and Segel, 1976; Solé and Bascompte, 2012). It has been shown that such spatial patterns emerge in predator-prey systems when the predator has a larger dispersal

capacity than the prey (De Roos et al., 1998; Gurney et al., 1998). We demonstrate here that this can also be the case in the context of a plant-herbivore system, using a model calibrated empirically.

Implications for management

First, the most important finding for management purposes is that the moth heavily impacts boxwood stands. With the estimated parameter values, we find that in the study area only 10% of the initial boxwood biomass remains after invasion (Figure II.3b) and that 50% of the original boxwood patches completely disappear (Figure II.3c), which represents 2414 square kilometres in the French Alps. However, these quantitative predictions should be taken with caution. In particular the sensitivity analysis (SI Figure II.12) shows that the characteristics of boxwood are determining factors in the model, so a better understanding of the biology of boxwood and its response to defoliation seems essential to gain further insights into the impact of the box tree moth invasion. Under low moth fecundity and high caterpillar survival, the moths could persist longer in heavily defoliated patches. The severe decrease in box tree biomass can impact the many species associated with boxwood, as well as the ecosystem services provided by the shrub (i.e sediment trapping and water storage) (Mitchell et al., 2018). In stands where boxwood is severely weakened or extinguished, recolonization by neighbouring patches may be prevented by pioneer plants, potentially other invasive species such as *Buddleja davidii* or *Ailanthus altissima*, in a kind of 'invasion meltdown' process (Simberloff and Holle, 1999).

Next, the periodic invasion dynamics can lead to confusion regarding the persistence of the box tree moth. A period of low overall abundance should not be confused with a decrease in invasion, and moth control methods should take periodic invasion dynamics into account. Remote sensing methods may be appropriate in order to detect the few boxwood stands that provide refuge under low moth abundance (Kerr and Ostrovsky, 2003). We suggest that detecting stands of undefoliated boxwood that allow moth persistence during a period of low abundance could provide an interesting management strategy, since control efforts could be increased on these particular patches.

Finally, management actions might consider preventing anthropogenic long-distance dispersal. However, we find that only very limited dispersal could lead to moth extinction, which occurs with a uniform distribution of dispersal events of no more than 4 cells (Figure II.5b, dotted line). As soon as dispersal is higher, the moth could escape dead ends in the landscape and therefore persists. Even if anthropogenic long-distance dispersal is prevented, a few natural long-distance dispersal events might ensure moth persistence. It is therefore unlikely that management actions limiting dispersal can be able to eradicate the moth. However, such actions can reduce the impact on boxwood stands, since we find that long-distance dispersal increases the extinction rate of boxwood patches (Figure II.6e).

Three scenarios may occur after the invasion of box tree moth in Europe: extinction of both species, extinction of the moth only, or coexistence. Our theoretical approach combined with field and experimental data suggests that coexistence is the most likely outcome, with cycles of moth outbreaks and crashes. Coexistence comes along with a severe reduction of boxwood biomass at the landscape scale: boxwood stands may therefore become closer to brown than green. Moth extinction can also occur, which indicates that the invasion dynamics of exotic pests can be mitigated even in the absence of predators and effective plant defenses.

We further show that plant-herbivore coexistence through spatial effects does not require poorly mobile wingless species, as in our model a wide range of dispersal values result in coexistence. Coexistence occurs in large landscapes, long-distance dispersal thus requires a

spatial scaling-up for the persistence of the system. Particularly intense long-distance dispersal nevertheless leads to herbivore extinction, provided that plant grows back slowly. In that case, the herbivore depletes its resources at the global scale, which leads to its own extinction even without a complete synchronization of the local dynamics. Finally, coexistence is easier in patchy landscapes because unsuitable patches increase moth mortality during dispersal and thereby reduce the global insect population size. Interestingly, when plants disperse locally the spatial dynamics of the system lead to the formation of such a patchy landscape, with relatively small plant patches evenly distributed in the landscape. The system thus creates its own stability conditions.

II.2.6 Acknowledgements

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Conflict of interest: all authors declare that they have no conflict of interest.

II.2.7 Supporting Information

Local demographic model

Reproduction and survival functions In this section we detail the reproduction function and survival function involves in the local demographic model described in the main text.

Wood reproduction function. The wood growth function F_w is constructed using a Ricker model whose intrinsic growth rate $r_w(\rho_n)$ is defined as the balance between the production of new wood b_w , which critically depends on the density of leaves per unit of wood ρ_n , and the mortality induced by severe defoliation d_w .

$$F_w(w, \rho) = \begin{cases} \exp(r_w(\rho)(1 - \frac{w}{W_{max}})) & \text{if } r_w(\rho) > 0 \\ \exp(r_w(\rho)) & \text{if } r_w(\rho) \leq 0 \end{cases} \quad \text{with } r_w(\rho) = b_w(\rho) - d_w(\rho)$$

The production function b_w and the mortality function d_w takes the following form :

$$b_w(\rho) = \frac{\rho^{\beta_r}}{\rho^{\beta_r} + \theta_r^{\beta_r}} r_{w,max} \quad d_w(\rho) = (1 - d^{\frac{1}{\rho}}) r_{w,min} \quad (\text{II.2})$$

where β_r , θ_r and d are shape parameters.

Leaves survival. The survival function of the leaves is defined by

$$S_l(\mu) = v(\sigma_l)^\mu \quad (\text{II.3})$$

where σ_l is a shape parameter.

Wood survival. The wood mortality due to consumption increases with both the BTM pressure, μ and the BT health ρ . The wood mortality saturates to d_{max} when the foliage is abundant (large ratio $\rho \geq 1/3$). However, when the foliage is small (low ratio $\rho \leq 1/3$), the bark consumption occurs while the superficial wood is available. Thus recently defoliated boxwood with small bark coverage (ρ close to 0) cannot be consumed by the larvae.

$$S_w(\mu, \rho) = 1 - \frac{\mu^{\beta_s}}{\mu^{\beta_s} + \theta_s^{\beta_s}} D_{max}(\rho) \quad (\text{II.4})$$

where β_s and θ_s are shape parameters and D_{max} is the maximal mortality rate which grows linearly with ρ until a threshold $1/3$, at which point it saturates to its critical value d_{max} .

$$D_{max}(\rho) = \begin{cases} 3d_{max} \rho & \text{if } \rho < 1/3 \\ d_{max} & \text{if } \rho \geq 1/3 \end{cases} \quad (\text{II.5})$$

This step function takes into account that the consumption of superficial wood depends on the presence of available softwood, and thus a certain amount of foliage. The threshold value $1/3$ for BTM pressure ρ corresponds to the approximate ratio when there is as much foliage as wood, the density of the wood being three times greater.

Box Tree Moth survival. Survival of BTM during the larval stage depends mainly on the amount of available resource per larva μ . If the larva has enough available resource to complete its six stages, it will evolve into a moth, while a lack of resource during its growth will cause its death. The survival rate also takes into account intraspecific competition for resource caused by interference between the larvae. The survival function is defined using a shape parameter σ_m as

$$S_m(\mu) = \begin{cases} S_{m,max} \left(1 - (\sigma_m)^{\frac{1}{\mu}}\right) & \text{if } \mu < 2 \\ 0 & \text{if } \mu > 2 \end{cases} \quad (\text{II.6})$$

The threshold $\mu = 2$ fits a given situation that occurs when there is a shortage of resource for the larvae, even if some larvae die during their development.

Local model dynamics and parameter estimation

Field observations show that when the box tree moth colonizes a patch, its population explodes within a few generations, eventually reaching a peak of density which results in total defoliation of the boxwood stand. At this point no more resources are available and the box tree moth disappears from this patch. This local dynamics observed in the field lasts between 3 and 4 years between the beginning of the invasion and the extinction of the moth. When two generations are carried out per year, the local dynamics represents 6 to 8 generations. We use these local dynamics to validate the calibration of model parameters that could not be measured or found in literature. Thus, we estimate the parameters in order to reproduce this qualitative behaviour, and to achieve plausible quantitative outputs (these parameters are referred as "estimate" in Tables II.1-II.2).

The figure II.7 simulates the invasion dynamics as expected. The boxwood (leaf and wood) starts at its carrying capacity, which is calculated from a simulation without moths, and a single box tree moth is added to the patch. As the model does not consider sexual reproduction, this unique moth will be able to produce eggs, otherwise we can also consider that this initial moth is a gravid female. Within six generations, the moth population reaches its peak abundance. During the 7th generation, the ratio μ between the number of leaves needed by the larvae and the available leaves becomes too large and the survival of the moth drops to 0. At this point, the effect on boxwood density is maximal. Leaves are entirely consumed by the early larval stages, which cannot reach their final stages and die from starvation. Still, leaf density does not reach 0 because new leaves grow from wood (at rate r_0w). In a more ecologically accurate representation, the density of the leaves would drop to 0 and then new leaves would only be produced in the next generation, but this would not change the model's outputs. Moreover, this phenomenon is implicitly present since all of the moths in the 7th generations die from starvation and cannot consume the new leaves produced, so it is comparable to a production of new leaves during the next generation. In natural conditions, however, intact boxwood patches will be more likely invaded by a larger number of moths. In the spatial version of the model, dispersal events occur with groups of 1000 individuals due to volatile compounds or other exogenous attractors, and in that case the peak is reached as early as the 4th generation, and the moth population crashes at the 5th generation.

Although the moth population collapses for realistic parameter values, with different parameters the model allows a positive equilibrium for the three state variables, i.e. the coexistence of moth and boxwood (wood and leaves). We therefore built map of the final model state in function of moth fecundity and moth survival, two key parameters which may vary during the course of the outbreak in Europe. The accommodation of native predators and parasites could indeed reduce the survival rate of caterpillars, and moth fecundity could

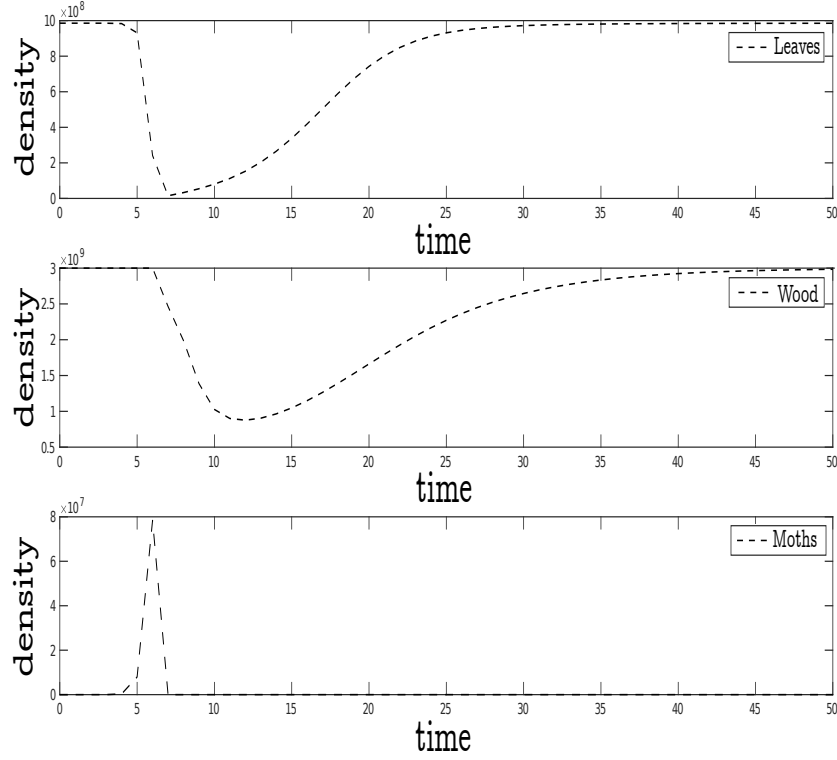


Figure II.7 – Visualization of invasion dynamics in the local model. Simulation with ecologically realistic parameters given in Tables II.1-II.2

be reduced by oophagous insects. The final state map (see Figure II.9) clearly shows that coexistence is only possible in a very narrow range of parameters values, which are far from the actual measured values.

Two connected patches instead of one can sometimes be enough to favour coexistence in plant-insect interactions ([Kang and Armbruster, 2011](#)), but simulations conducted on a two-patch model show only a slight expansion of the coexistence area, which is far from sufficient to lead to coexistence with realistic parameters (see Figure II.8 in Supporting Information). More precisely, in the two-patch case, patches are initially saturated with boxwood, and the patch 1 contains just one moth. This spatialization of the model into two patches leads to new peculiar and rare end states at the frontier between coexistence and extinction which are not represented. We observe five states: i) overall disappearance of the moth and persistence of the boxwood (black) ii) global coexistence of the two species (white) iii) extinction of the moth and the boxwood in patch 1 and coexistence in patch 2, iv) extinction of only the moth in patch 1 and coexistence in patch 2, v) coexistence of the two species in patch 1 and the absence of moth in patch 2. It is important to note that cases iii) and iv) are not actually final states; the increase in simulation time shows that in fact the moth population in patch 2 decreases slowly until its extinction. For iii), after the extinction of the moth, the boxwood recovers in patch 2 until it reaches a state where it could disperse and recolonize patch 1. Moreover, before the moth extinction, during its decline the dispersal to patch 1 is still active, though low. Thus, in this situation patch 2 is a source of moths, and patch 1 is a well since migrating moths find no resource and die immediately. On the other hand, for iv), moth densities are too low in patch 2 and there is no dispersal towards patch 1. Cases iii) and iv) are not asymptotic states, but they are still taken into account because on an ecologically

reasonable time scale they are actually present. Nevertheless, except for the states i), global extinction of the moth, and ii), global coexistence of the two species, the other states are highly anecdotal because they correspond to only a few very precise parameter values and are almost invisible in the parameter space. What is remarkable in the space of parameters, however, is the slight expansion of the space corresponding to the coexistence of boxwood and moth.

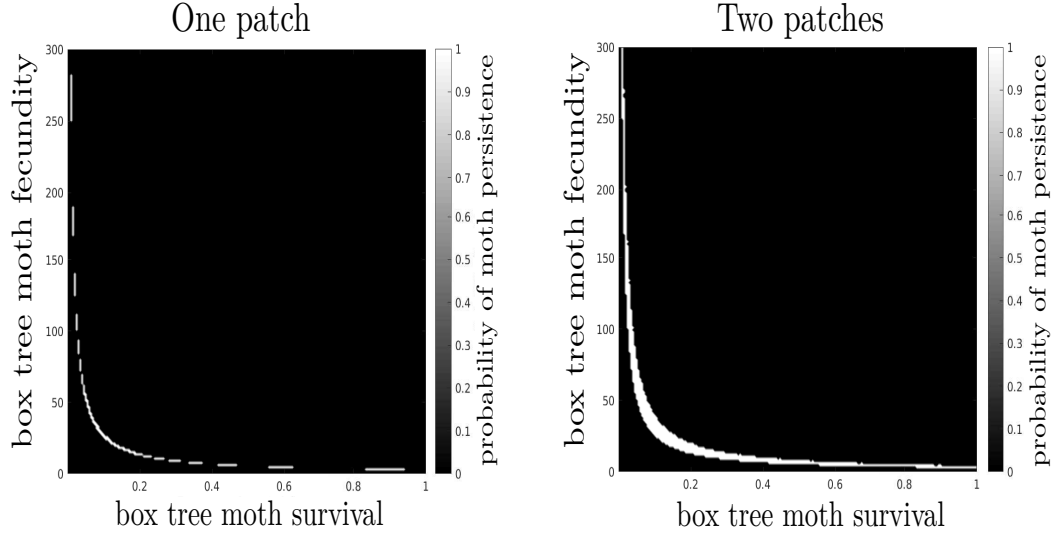


Figure II.8 – Final state map for the mean field model (left) and the double-patches model (right) as a function of fertility f and maximum survival $S_{m,max}$. The parameter values considered ecologically real are $f = 120$ and $S_{m,max} = 0.5$.

Spatially explicit model

In this section, we first describe in details the dispersal process for the BT and BTM. Then we describes the landscapes: French Alps and theoretical space.

Dispersal phase of BTM. The migration rate M_m of BTM depends on μ and it takes the following form :

$$M_m(\mu) = (1 - \delta^\mu)M_{m,max} \quad (\text{II.7})$$

where the maximal dispersal rate $M_{m,max}$ takes into account mortality during the dispersal. Thus the number of dispersal events at each location is given by $\frac{M_m(\mu)m}{1000}$.

Dispersal of BT. The dispersal rate of BT depends on the foliage ratio per BT (ρ) and it takes the following form :

$$M_w(\rho) = \begin{cases} (\omega_w)^{1/\rho} M_{w,max} & \text{if } \rho > 1/3 \\ 0 & \text{otherwise} \end{cases} \quad (\text{II.8})$$

Real landscape the French Alps From field observations provided by the National Alpine Botanical Conservatory, we obtained a map of the French Alps composed of 570 by 351 cells of 29 hectares each (about 58 000km², see Figure II.9). It should be noted that these data focus on natural boxwood and neglect the presence of ornamental boxwood in urban areas. We focus on the French Alps because detailed botanical data are available, but in theory our model could be extended to the whole area of invasion. Green cells correspond to areas with BT, grey cells correspond to areas without BT, while blue cells represent urban areas. We use the basemap from OpenStreetMap ([QGIS Development Team, 2021](#)).

Simulations are initialized with a single moth invading a patch chosen at random, and carried out on a maximum of 1000 iterations if no specifications are given.

Effect of elevation and dispersal distance We aim to investigate the effect of elevation and dispersal distance on the box tree characteristics after an invasion.

Elevation is assumed to reduce egg survival (thus fecundity), larvae survival and the nutritional quality of boxwood, up to a maximum reduction of 50%. One thousand simulations are performed on real space, each time a uniform random matrix is drawn to determine the elevation of each cell (with ten replicates). We measure as proxies the persistent boxwood biomass as a percentage of the carrying capacity and the percentage of bead boxwood patches.

In addition, the size of the dispersal swarms reduces linearly with the dispersal distance to a minimum of one individual.

Effect of the leaf intrinsic growth rate In this section we are interested in the effect of the leaf intrinsic growth rate r_f on the mean percentage of invaded patches during the invasion period that lasts for 1000 generations in our simulations. We observe that the mean percentage increases with respect to the leaf intrinsic growth rate. Moreover, the percentage drop to zero when the moth do not persist which occurs when $r_f < 0.22$ in our simulation cases.

In addition, from the two inserts showing the invasion dynamics over time for two value of r_f , we see that the moth can persist even if it periodically invades 99% of the patches. The moth persists in this case because the leaves grow back fast enough to prevent global resource depletion.

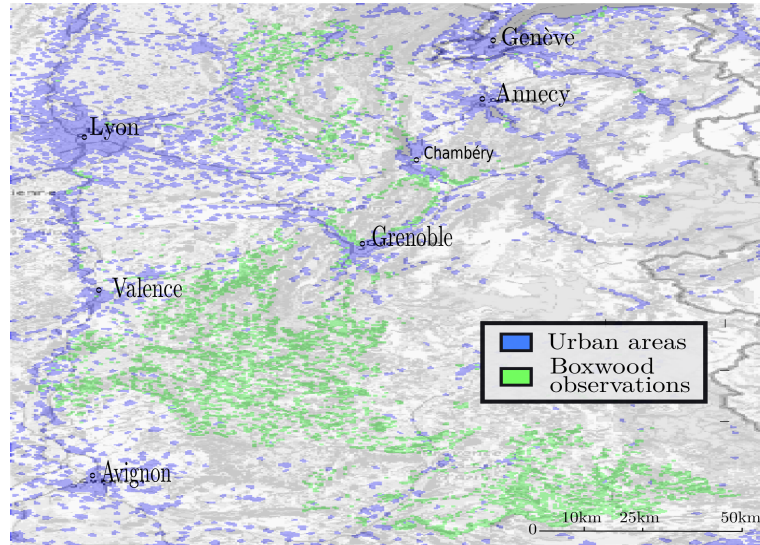


Figure II.9 – Simulation space of the cellular automaton representing the distribution of boxwood in the French alpine arc, based on data from the National Alpine Botanical Conservatory. 570 by 351 cells of 29 hectares each, about 58 000km². The background map is from OpenStreetMap (QGIS Development Team, 2021). Green cells correspond to areas with BT, grey cells correspond to areas without BT, while blue cells represent urban areas.

Theoretical landscape and spatial structure To investigate the effect of the spatial structure we run our model on a square landscape with various initial size and proportion of boxwood patches. For each landscape, we also calculate an aggregation index by counting the number of pairs (adjacent boxwood patches) in the landscape and dividing it by the maximum number of possible pairs: $2n - \lfloor 2\sqrt{n} \rfloor$, where n is the proportion of boxwood cells (Harary and Harborth, 1976). For each landscape size and boxwood proportion, we randomly generate 1000 landscapes with possibly different aggregation indices. The final aggregation index equals the difference between the index of the landscape of interest and the average index of the randomly generated landscapes.

Cluster detection is done using the function Matlab® FINDCLU from the File Exchange of MathWorks. To fit the power-law to the cluster-size distribution, we define size-classes of five cells and evaluate the number of clusters in each class.

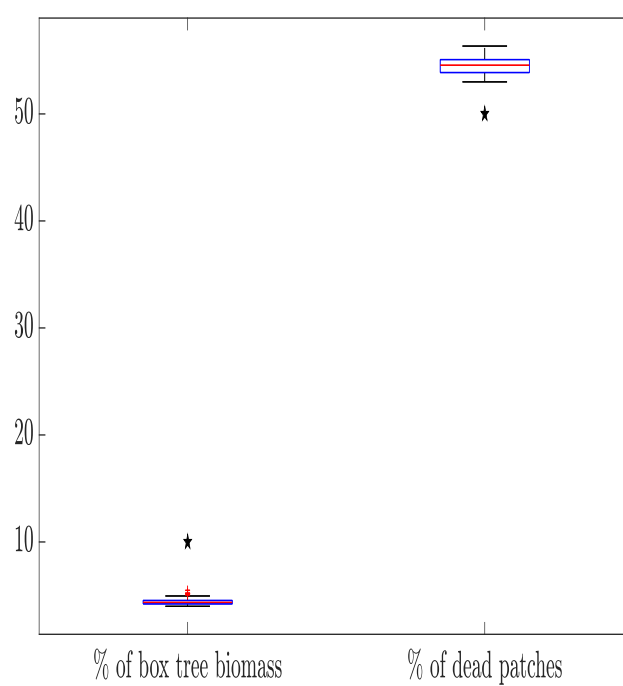


Figure II.10 – Comparison of simulations including additional ecological processes (boxplots), i.e. possible effects of elevation and dispersal distance, with reference simulations (stars).

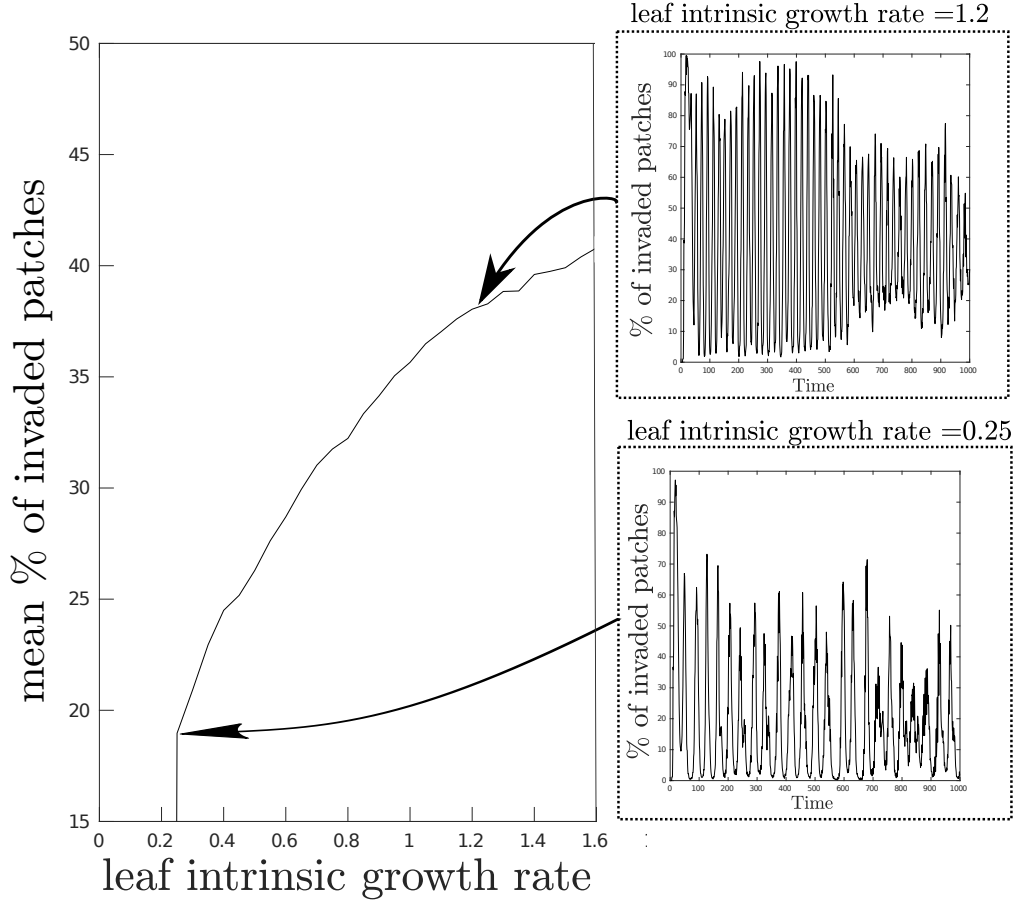


Figure II.11 – Effect of the leaf intrinsic growth rate on the mean percentage of invaded patches. The percentage drop to zero when the moth do not persist in these conditions (when $r_f < 0.22$). The two inserts show the invasion dynamics for two growth rate values. For each value of leaf intrinsic growth rate 50 simulations are carried out and results are averaged.

Experimental data

Mesocosm experiment. We performed a mesocosm experiment from April 4 to late May 2018, located on the University of Savoie Mont Blanc campus, in an isolated grassy area (45°38'30.0"N 5°52'02.7"E). Climatic conditions were close to those of nearby natural boxwood stands. We created a pressure range for the resource by placing varying numbers of caterpillars on the box trees. The range included seven μ values, with four replicas for each and four controls. Each of the 32 boxwood were isolated in cages of 1m³ covered by mesh (insect proof netting PE 22:30, 920x920; DIATEX, Saint Genis Laval, France) to prevent movement of the larvae between the boxwood. All of the boxwood shrubs came from the same supplier and had received no chemical treatment. They measured 30 cm high and were cultivated in 1 liter pots.

To establish the pressure range, we estimate the parameter α corresponding to the amount of leaves needed by a moth for its larval cycle, for each value of μ . [Slansky Jr and Scriber \(1982\)](#) provide a mean value of ingested food conversion efficiency (ECI) of 20% for herbivorous Lepidoptera. Knowing that $ECI = B/I$ with B being gained mass and I being ingested food, we obtain I through measurements of dry caterpillar masses performed by T. Defferier and E.

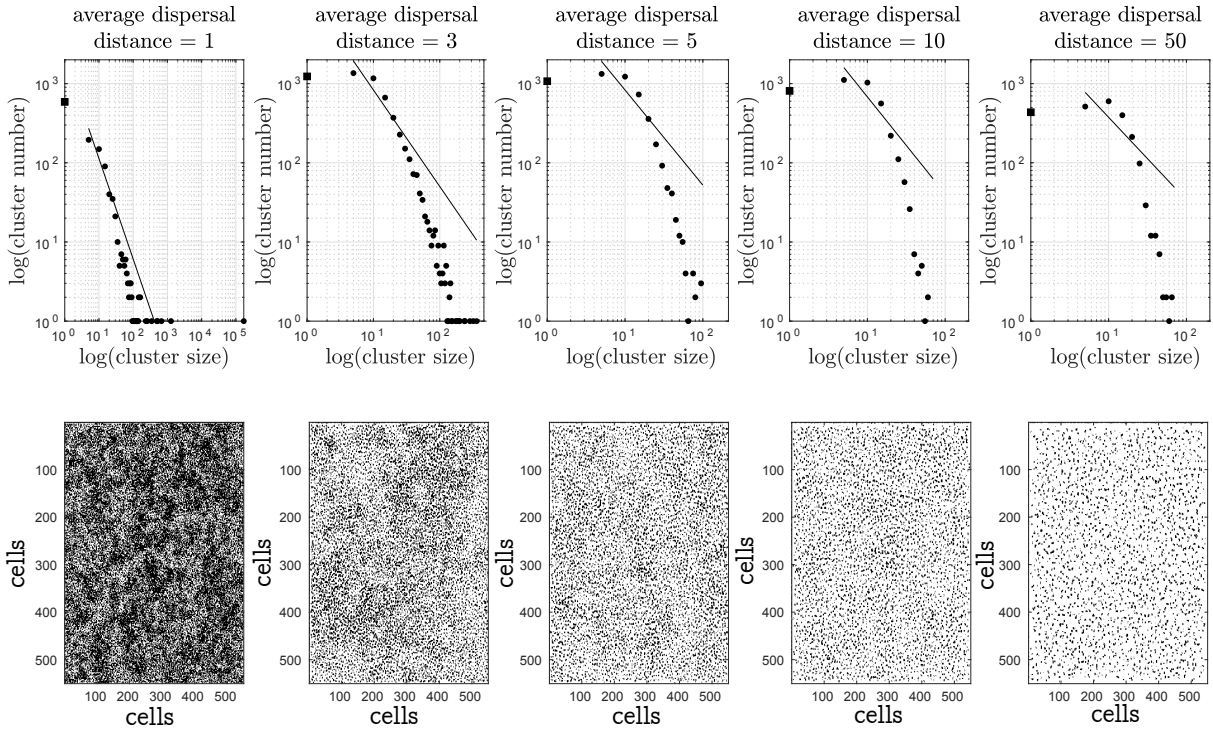


Figure II.12 – Effect of moth dispersal distance (increasing from left to right) on the size distribution of boxwood clusters at the end of the simulations (5000 time steps), in large theoretical landscapes of 550*550 cells. Top: regression lines correspond to the fit to a power-law distribution. The first size class (black square) has been excluded from the regression. Bottom : snapshot of the landscape at the end of the simulation, black cells indicate live boxwood patches. All other parameter values are set to the realistic values.

Tabone from the National Research Institute for Agriculture, Food and Environment (INRAE). Then, using the average dry mass of the leaves, we convert I into the number of leaves ($I = 25$ leaves). Finally, the number of leaves was counted for each boxwood. Therefore, the value of simulated μ could be determined when a certain number of caterpillars were deposited on a particular box tree. The range used was: $\mu = [2; 1; 0.75; 0.5; 0.25; 0.13; 0.07]$ (see Figure II.13).

					Rn : 0 Leaves : 1760 Larvae : 0	Rn : 0.07 Leaves : 1497 Larvae : 4	Rn : 0.13 Leaves : 2013 Larvae : 11	Rn : 0.25 Leaves : 1515 Larvae : 15	
Rn : 0.5 Leaves : 1886 Larvae : 38	Rn : 0.25 Leaves : 2129 Larvae : 21	Rn : 0.13 Leaves : 1553 Larvae : 8	Rn : 0.07 Leaves : 1683 Larvae : 5	Rn : 0 Leaves : 2021 Larvae : 0	Rn : 2 Leaves : 1987 Larvae : 160	Rn : 1 Leaves : 1660 Larvae : 67	Rn : 0.75 Leaves : 1370 Larvae : 41	Rn : 0.5 Leaves : 1841 Larvae : 37	
Rn : 0.75 Leaves : 1749 Larvae : 53	Rn : 1 Leaves : 1911 Larvae : 77	Rn : 2 Leaves : 2163 Larvae : 174	Rn : 0 Leaves : 2428 Larvae : 0	Rn : 0.07 Leaves : 2091 Larvae : 6	Rn : 0.13 Leaves : 2161 Larvae : 11	Rn : 0.25 Leaves : 2018 Larvae : 20	Rn : 0.5 Leaves : 2368 Larvae : 48	Rn : 0.75 Leaves : 1899 Larvae : 57	
Rn : 2 Leaves : 1711 Larvae : 137	Rn : 1 Leaves : 1694 Larvae : 68	Rn : 0.75 Leaves : 2121 Larvae : 64	Rn : 0.5 Leaves : 1644 Larvae : 33	Rn : 0.25 Leaves : 1960 Larvae : 20	Rn : 0.13 Leaves : 2021 Larvae : 11	Rn : 0.07 Leaves : 2536 Larvae : 7	Rn : 0 Leaves : 1609 Larvae : 0	Rn : 2 Leaves : 2220 Larvae : 178	Rn : 1 Leaves : 1645 Larvae : 66

Figure II.13 – Schema of the mesocosm manipulation. R_n represents the competition for the resource. The spatial layout is due to the topography of the installation site

II.2 Article : *Spatial structure of natural boxwood and the invasive box tree moth can promote coexistence*

	Settings	Measured	Values	Unit	Meaning	Source
Leaves	v	No	0.98	$\frac{1}{t}$	Leaf survival rate at senescence	estimate
	r_f	No	0.4	$\frac{1}{t}$	Leaf growth rate	estimate
	L_{max}	No	$\frac{1}{3}W_{max}$	$g.ha^{-1}$	Leaf carrying capacity	estimate
	r_0	Quantitative	$5 * 10^{-3}$	$\frac{1}{t}$	Offshoot production rate	field
	σ_l	Qualitative	0.01	-	Consumption function setting	experiment
Wood	W_{max}	No	$3 * 10^9$	$g.ha^{-1}$	Wood carrying capacity	estimate
	d_{max}	Quantitative	0.74	-	Saturation value of the maximum mortality function $D_{max}(\rho)$	field
	β_s	No	10	-	Setting of the wood mortality function by consumption (curvature)	estimate
	θ_s	No	1.2	-	Setting of the wood mortality function by consumption (inflection point)	estimate
	β_r	No	5	-	Setting of the wood growth function (curvature)	estimate
	θ_r	No	$5 * 10^{-5}$	-	Setting of the wood growth function (inflection point)	estimate
	$r_{w,max}$	Qualitative	0.3	-	Saturation value of the wood growth function	field
	$r_{w,min}$	No	1	-	Saturation value of the growth deficit function γ_0	estimate
	d	No	0.95	-	Setting of the growth deficit function γ_0	estimate
	ω_1	No	0.1	-	Setting of the wood dispersal function	estimate
	ω_{max}	No	$1 * 10^{-5}$	-	Maximum proportion of wood that can contribute to dispersal	estimate

Table II.1 – Model parameters. The values correspond to those most representative of actual ecological conditions. The parameters are either measured quantitatively, i.e. a direct value of the parameter concerned is measured, or qualitatively, i.e. the measurement of a process allows the calibration of the associated parameter. We estimate the unmeasured parameters from the model simulations, and aim to be consistent with the ecological situation. The source listed as "experiment" corresponds to the measurements of moth weights made by the INRAE for α , and the mesocosm experiment for σ_m , σ_l and $S_{m,max}$. "Flight carousel experiment" corresponds to the measurements made by Bras et al. from the INRAE.

Field samples; Two wild boxwood locations are used to make *in situ* measurements. These boxwood areas are located on the eastern slope of the Epine massif in Savoie (45°38'23.7"N 5°50'43.6"E and 45°41'33.2"N 5°50'56.2"E) at an elevation of 500 and 630 meters, respectively. This massif has large stands of wild boxwood under trees in limestone soil. The peak invasion and defoliation of the boxwood occurred in July and August 2016, and mortality measurements

	Settings	Measured	Values	Unit	Meaning	Source
Box tree moth	f	Quantitative	120	individual	Box tree moth fecundity	literature (Kawazu et al., 2010) (Wan et al., 2014)
	α	Quantitative	0.3	g	Amount of leaf needed by a box tree moth for its larval cycle	literature (Slansky Jr and Scriber, 1982) and experiment
	σ_m	Qualitative	0.85	-	Setting of caterpillar survival function	experiment
	$S_{m,max}$	Quantitative	0.49	$\frac{1}{t}$	Maximum caterpillar survival rate	literature (Kawazu et al., 2010) and experiment
	s	No	0.4	$\frac{1}{t}$	Survival rate of adults (moths)	estimate
	$M_{m,max}$	No	0.01	$\frac{1}{t}$	Survival rate of adults during dispersal	estimate
	δ	No	0.01	-	Parameter of the dispersal function	estimate
	c	Qualitative	0.5	-	Tail shape parameter of the Exponential power distribution	flight carousel experiment
	α_d	Quantitative	25	cells	Average dispersal distance of the Exponential power distribution	flight carousel experiment

Table II.2 – Model parameters. The values correspond to those most representative of actual ecological conditions. The parameters are either measured quantitatively, i.e. a direct value of the parameter concerned is measured, or qualitatively, i.e. the measurement of a process allows the calibration of the associated parameter. We estimate the unmeasured parameters from the model simulations, and aim to be consistent with the ecological situation. The source listed as "experiment" corresponds to the measurements of moth weights made by the INRAE for α , and the mesocosm experiment for σ_m , σ_l and $S_{m,max}$. "Flight carousel experiment" corresponds to the measurements made by Bras et al. from the INRAE.

were made in March 2017.

Estimating parameters from experimental work and literature review

We use our experimental data, our field samples and literature reviews to estimate some parameters of our model.

Fecundity parameter f . Females lay about 300-400 eggs at a time (Kawazu et al., 2010; Wan et al., 2014). However, the model does not separate males from females, and survival is calculated for caterpillars but not for eggs. The sex ratio seems significantly skewed in favor of males, with only $43\% \pm 10\%$ of the population being females, according to Götting (2017). The hatchability rate is about $79.7\% \pm 2\%$ according to Kawazu et al. (2010). The fertility parameter is therefore estimated with these bibliographic data using the value: $f = \text{number}$

of eggs * percentage of female * hatchability rate = 120, with a range from 0 (i.e effects of oophagus predators and parasites) to 300 (potentially higher fertility in Europe (Tabone et al., 2015)).

Box tree moth survival function and wood consumption function. To determine the survival function according to the pressure for resource μ , the maximum caterpillar survival $S_{m,max}$ is estimated using the bibliographic data. Through lab experimentation, Kawazu et al. (2010) have obtained the following parameters: a larvae survival rate of 78%, a pupation rate of 70%, and an emergence rate of 89%. Thereby, we estimate $S_{m,max} = 49\%$ which seems appropriate because in this laboratory experiment the caterpillars have not undergone any starvation stress. However, for this function, the second parameter σ_m also has to be set; this parameter is difficult to measure because it has no ecological interpretation. Nonetheless, it is possible to obtain different survival values for different μ in order to make a qualitative adjustment of the survival curve.

Our mesocosm experiments makes it possible to calibrate the leaf consumption function (σ_l). At the end of the experiment, when the surviving larvae had reached the adult stage, we counted the living leaves on the boxwood in order to obtain the percentage of leaves that were consumed. The insect-free controls allowed us to distinguish between mortality caused by caterpillars and mortality due to the environment. The qualitative calibration of the consumption curve is thus established using the consumption percentages as a function of μ . These results are highly dependent on heat unit accumulation during the experimental period. However, the sensitivity analysis (Figure S.9) shows that among the three parameters measured with this experiment, two have a rather low correlation coefficient despite a significant p-value (σ_l and σ_m), which means that their impact on the model outputs remains moderate. For the maximum survival of the larvae ($S_{m,max}$), the sensitivity analysis shows that its influence on the model is a bit stronger, we investigate the influence of this parameter in more detail further on.

Wood mortality function. Boxwood mortality by senescence is very low and some boxwood may be over 600 years old. However, box trees attacked by 2 or 3 successive generations may have high probabilities of death (Kenis et al., 2013). It is necessary to calibrate mortality due to consumption of superficial wood by the late larva stage caterpillars, D_{max} , and notably the parameter d_{max} .

Mortality is assessed in terms of biomass rather than in terms of individuals. We use our field sample to compute the mortality using the following procedure: the percentage of living biomass is measured on completely defoliated boxwood according to the level of branching (trunk or branch). For the trunk, the percentage of the total height of the boxwood with shoots (h) is measured, and for branches the percentage of branches with shoots (r), is measured. The mortality d_{max} is estimated by: $d_{max} = 1 - \frac{h+r}{2}$. The measurements made on 101 boxwoods give $d_{max} = 0.74$.

Shoot production parameter. The production of shoots from wood, r_0 , is measured by estimating the biomass of shoots produced by wood whose 1) live biomass is estimated and 2) defoliation date is known. First, the average mass of a shoot is measured from 250 shoots. Then, for each measured boxwood ($N = 49$), the living wood biomass is estimated by considering the trunk as a cone whose volume could be calculated using its circumference and height, with the same calculations made for the branches. This volume, multiply by the density of the wood ($0.95g.cm^{-3}$), gave the biomass of living wood. We count number of shoots and are able to obtain the biomass of the shoots. Thus, $r_0 = \frac{\text{shoots biomass}}{\text{wood biomass}} * \frac{1}{\text{time}}$ with

time being the number of generations since defoliation. For the 49 boxwoods measured, the amount of new growth varies from 1 to 154 with an average of 45, giving $r_0 = 5 * 10^{-5}$.

Wood growth function. Calibration of the growth function from empirical measurements is performed only for the maximum growth value $r_{w,max}$. For this, a method of dendrometry is used. We have cut some trunk sections with different circumferences (1.5, 2.4, 3.8, 4, 4.9, 5.6, 7.8 centimeters), and we have counted their rings number (respectively 11, 15, 20, 25, 32, 36, 50). We assume that boxwood is a cone whose increase in height is proportional to its increase in width, and its growth is proportional to its density. Thus we can infer the maximal growth rate per year $r_{w,max} = 0.134$ using a linear regression. Thus, the growth per generation in the case of two generations of moth per year is 0.067. We obtain a low estimate because we consider that the growth of individuals is already occurring, but not the formation of new individuals while $r_{w,max}$ takes it into account. From the simulation of the model in the absence of herbivory, and this experimental value, $r_{w,max} = 0.3$ is used to model a consistent boxwood growth rate.

Moth survival and leaves consumption functions. Two functions are calibrated according to the experiment: a function for the consumption of leaves by caterpillars (see Figure II.14a) and a function for caterpillar survival (see Figure II.14b). These two functions are dependent on competition for the resource through μ . For the leaf consumption function, we quantify the mortality due to senescence from the difference between the average number of initial and final leaves in absence of moth pressure ($\mu = 0$), and then deduct that from the initial number of leaves for each boxwood. This allows one to express in the results only the proportion of dead leaves due to the action of the caterpillars, but it implies the hypothesis that all boxwood suffer about the same mortality due to senescence. Therefore, the control box trees had 100% of non-consumed leaves.

Leaf consumption reaches a threshold for $\mu = 1$, i.e. when resources present and resources needed are similar, above which the entire resource is consumed. Similarly, it is the threshold at which survival reaches its lowest value and nearly stagnates. The results presented here show survival until the pupal stage, but at the end of the experiment no moths emerge in the box trees when $\mu = 2$, which is why the survival function is set to 0 for $\mu = 2$.

These results are remarkable because they are similar to those expected with a defoliation saturation threshold at $\mu = 1$ and a drastic drop in moth survival. They support our model and minimise the uncertainties that we may have on other parameters.

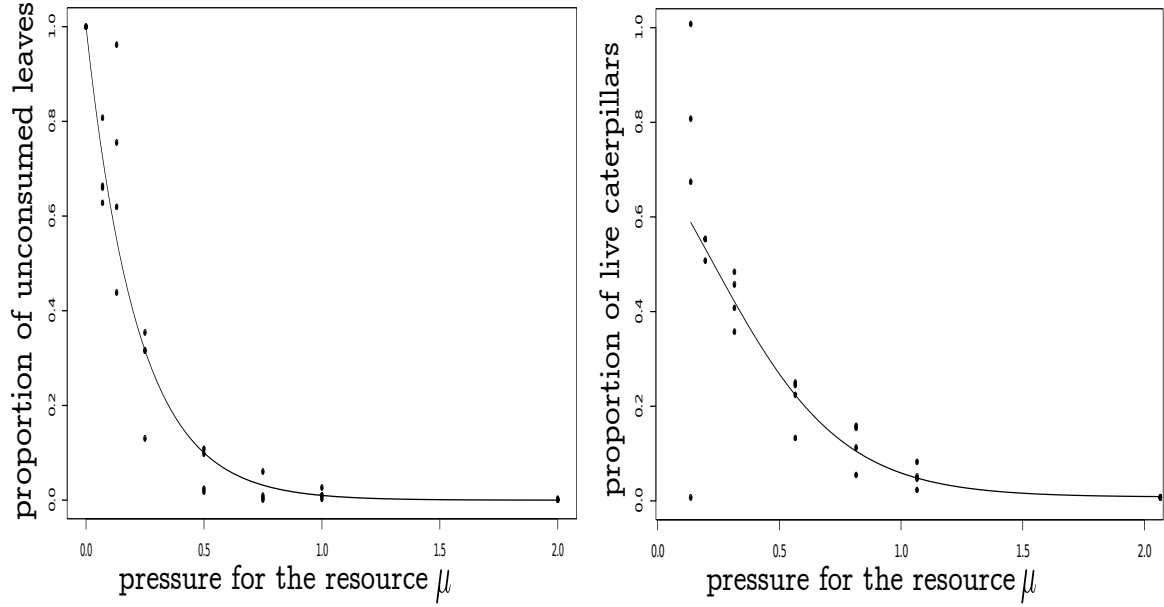


Figure II.14 – Main results of mesocosm manipulation with measurement of defoliation intensity and box tree moth survival according to competition for the resource μ . (a) leaf consumption function $\frac{S_l(\mu)}{v}$. (b) box tree moth survival function $S_m(\mu)$.

Sensitivity analysis

To further investigate the effect of BT and BTM interactions and the robustness of the model, we conduct a global sensitivity of three outcomes of our model: the boxwood biomass, the percentage of dead boxwood patches and the probability of moth persistence. For each outcomes, we use the Partial Rank Correlation Coefficients (PRCC) to quantify the strength of sensitivity for each of the 21 parameters. Moreover, the PRCC provides the direction of the impact of each parameters on the model outcomes. If the PRCC is positive, the parameter increases the outcome, while it decreases for negative PRCC. We sample parameters in a wide range that remains ecologically coherent (e.g. boxwood growth is slow). More precisely, we use 1786 values sampled around the reference values of Tables II.1-II.2 for each parameter and 10 replicates per parameter values to compute the PRCC. Thus, in general, the sampling considers a range of values from minus 10% to plus 10% around the reference value. For the experimentally measured parameters, the low and high limites of the sampling correspond to the 95% interval. We assume that a parameter is significant for an outcome as soon as its significant p-value associated to the outcome is lower than 0.2 in absolute value.

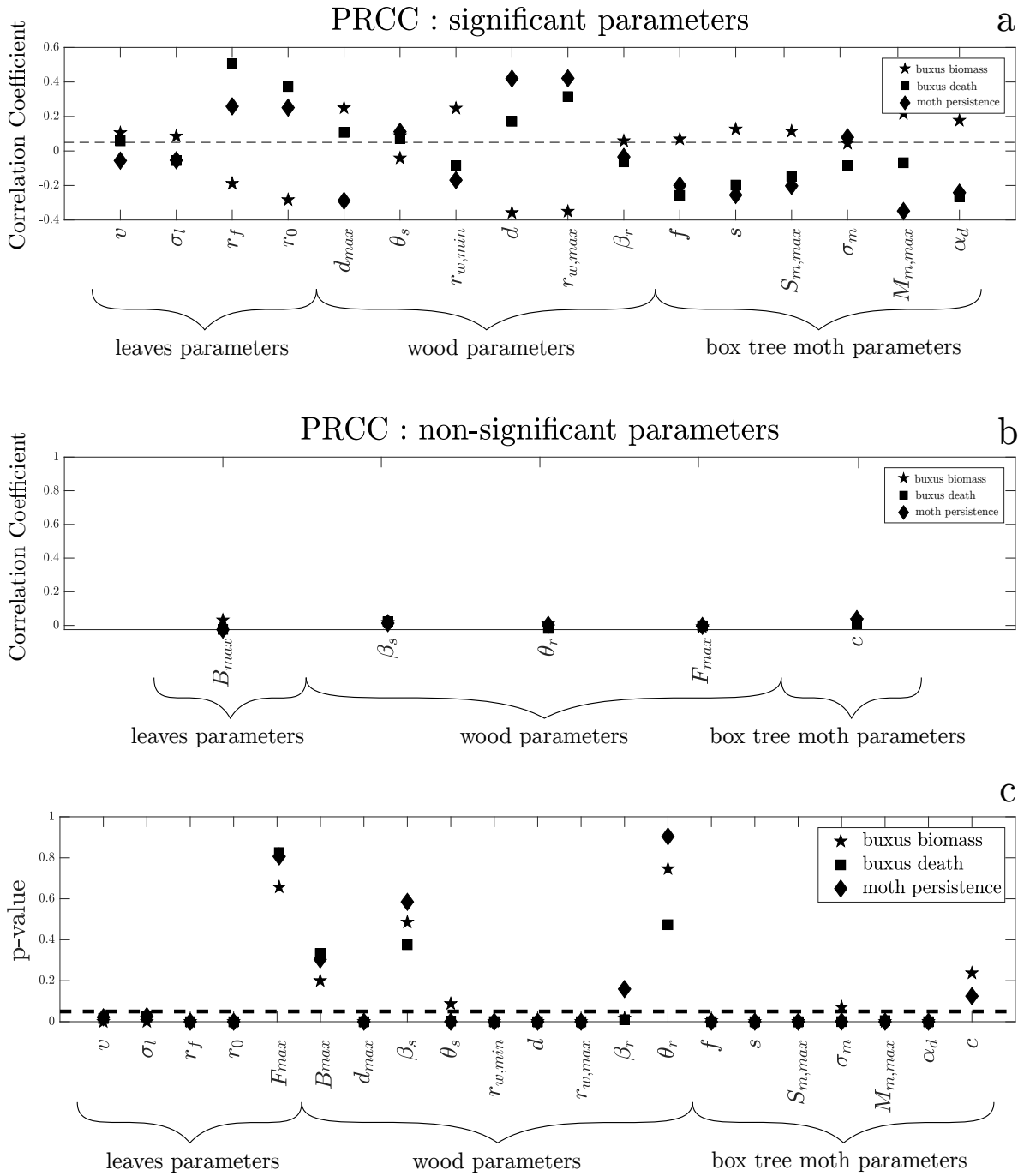


Figure II.15 – Results of the sensitivity analysis. a) Partial Rank Correlation Coefficients of the significant parameters on the three proxies. b) Partial Rank Correlation Coefficients of the significant parameters on the three proxies. c) P-value for all parameters, the dotted line shows the 5% threshold.

CHAPITRE III

CAUSALITÉ RÉCIPROQUE ENTRE NIVEAUX DE SÉLECTION

III.1 Introduction et synthèse des résultats

Dans ce chapitre nous explorons la causalité réciproque entre niveaux de sélection, elle-même en lien avec la causalité réciproque entre échelles spatiales.

Comme discuté dans le chapitre introductif, la causalité réciproque entre niveaux de sélection est à la base de la théorie de sélection multi-niveaux, et l'évolution de la coopération constitue un exemple classique de son application. Effectivement, en absence de mécanismes influençant le choix du partenaire à l'échelle de l'individu, par exemple l'altruisme réciproque ([Axelrod, 1981](#)), l'évolution de la coopération entre individus nécessite plusieurs niveaux d'interactions. Typiquement, le niveau de l'individu ne favorise pas la coopération mais privilégie l'égoïsme ou le parasitisme. En revanche, aux niveaux supérieurs la coopération peut être favorisée. En effet, au niveau de l'individu, un phénotype non-coopératif ne paie pas le coût associé à la coopération et pourtant il peut profiter de l'interaction des autres individus coopératifs (en l'absence de mécanisme de choix du partenaire). Ainsi, en se focalisant sur le niveau de sélection de l'individu - ou avec une vision gène-centrée sur le niveau du gène, ou du complexe de gènes responsable du phénotype coopératif ou non coopératif, - le phénotype non-coopératif est sélectionné. En revanche, la structure spatiale permet la considération de groupes distincts au niveau desquels le phénotype coopératif est sélectionné. Les frontières des groupes peuvent être définies par une structure spatiale extrinsèque due à l'environnement (par exemple la distribution des ressources ([Pepper and Smuts, 2002](#))), ou bien par les interactions entre les individus en fonction de leurs traits comme le propose le "structured demes model" caractérisé par des "trait-group" ([Wilson, 1977](#)). Par exemple, si le trait est défini par l'action de produire un cri d'alarme à la vue d'un prédateur, le trait-group est déterminée par la distance à laquelle ce cri est entendu par les autres individus. Dès lors, les groupes comportant une proportion supérieure du phénotype coopératif vont être plus productifs et/ou persistants. Ainsi, "Selfishness beats altruism within groups. Altruistic groups beat selfish groups. Everything else is commentary" ([Wilson, 2015](#)).

Nous partageons cette réflexion, la théorie multi-niveaux répond à la question de l'évolution de la coopération de la manière la plus fondamentale possible. Nous pensons que la persistance du débat sur la sélection de groupe est en grande partie un faux débat qui s'accroche en fait à critiquer la sélection de groupe naïve antérieure aux années 1960-1970 ([Eldakar and Wilson, 2011](#)), que nous critiquons nous-même en introduction en empruntant le terme "d'holisme idéaliste" à Lewontin. À la lumière de l'ensemble des travaux explorant et affinant la théorie

de sélection multi-niveaux et menant à sa forme actuelle (Okasha, 2006; Wilson and Wilson, 2007), les critiques de (Dawkins, 1976) sur la sélection de groupe nous semblent proches du sophisme de l'homme de paille¹. Enfin, le débat est aussi alimenté par une vision compétitive entre la théorie multi-niveaux et la théorie de fitness inclusive alors que toutes deux sont formellement équivalentes (Queller, 1992). Cependant, malgré cette équivalence formelle, la théorie multi-niveaux permet une meilleure compréhension des relations causales en jeu et s'inscrit mieux dans la vision dialectique, c'est pourquoi nous favorisons cette approche. Comme énoncé plus haut, il est possible de penser que "Everything else is commentary", mais ces commentaires semblent importants. Effectivement, une fois accepté le fait que "Altruistic groups beat selfish groups", de nombreuses questions persistent, notamment sur l'origine de la formation de ces groupes, donc sur l'origine de la structure spatiale, ainsi que sur la persistance de celle-ci.

Dans le chapitre II consacré à la causalité réciproque entre échelles spatiales, nous avons montré que la notion de structure spatiale est en étroite relation avec la dispersion des organismes. De la même manière qu'une métacommunauté peut être considérée comme une communauté globale si les organismes dispersent fortement, des groupes distincts peuvent se réunir pour former un unique ensemble s'ils interagissent fortement entre eux. Ainsi, une population structurée en groupes dans laquelle la coopération est variable, verrait celle-ci régresser si la structure spatiale est détruite par une dispersion trop intense des organismes. Des questions préliminaires s'imposent : comment des groupes émergent dans la population ? Quel est le rôle des interactions directes entre individus sur la structuration spatiale de la population ? Plus fondamentalement encore, la question sous-jacente est de savoir comment des interactions entre des niveaux d'organisation inférieurs peuvent donner naissance à des niveaux d'organisation supérieurs (Szathmáry and Smith, 1995), susceptibles de devenir des niveaux de sélection (Figure III.1).

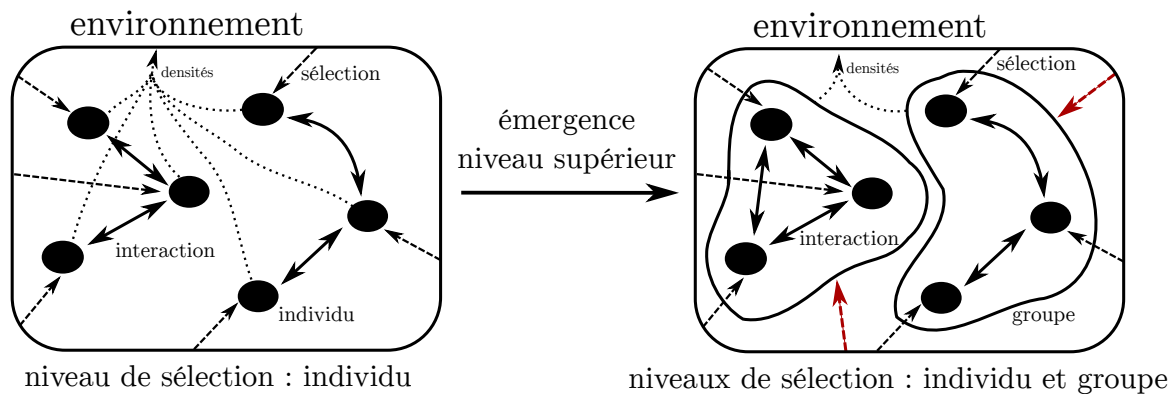


Figure III.1 – Schéma de l'émergence d'un niveau de sélection supérieur à partir des interactions au niveau inférieur. Dans cet exemple nous considérons des individus en interaction au sein d'un environnement et avec cet environnement. La sélection agit sur chacun des individus. Cependant, si les individus n'interagissent que localement avec certains de leurs proches voisins cela génère des groupes et donc un nouveau niveau d'organisation supérieur. La sélection n'agit plus seulement au niveau de l'individu, mais également au niveau du groupe (flèches rouges).

¹Le sophisme de l'homme de paille consiste à critiquer une version caricaturée d'une thèse et de considérer que cette critique est valable pour la véritable thèse.

Nous adressons ces questions de l'émergence et la persistance de la structure spatiale, et de la causalité réciproque entre niveaux de sélection qui en découle, en explorant comment le mutualisme peut émerger du parasitisme. Des considérations semblables ont inspiré des travaux relatifs à la coévolution de la coopération intraspécifique avec la dispersion ([Hochberg et al., 2008](#); [Koella, 2000](#); [Le Galliard et al., 2005](#); [Mack, 2012](#); [Mullon et al., 2018](#); [Purcell et al., 2012](#)). Ces travaux répondent à la question de l'évolution de la coopération alors même que les individus non-coopératifs ont la possibilité d'être sélectionnés vers une dispersion globale pouvant déstabiliser la structure spatiale. Le résultat principal partagé par les différents modèles est l'émergence d'une corrélation négative entre l'intensité de dispersion et la coopération. En général, en maintenant une dispersion locale, les individus coopératifs peuvent coexister avec les individus non-coopératifs caractérisés par une dispersion plus globale. Cependant, parmi ces travaux seul ([Mack, 2012](#)) s'intéresse à une situation de mutualisme (interaction interspécifique entre deux espèces), alors que les autres traitent d'altruisme (interaction intraspécifique). Le cas du mutualisme induit une difficulté supplémentaire car impliquant une corrélation spatiale positive entre deux espèces pour évoluer. Des conditions permettant l'évolution de l'altruisme ne permettent pas systématiquement l'évolution du mutualisme. Cependant, nous relevons deux limites à ces travaux : 1) l'interaction la plus "faible" correspond à un neutralisme, or chaque espèce peut être moins "incitée" à développer une interaction positive quand l'espèce partenaire a un effet parasite, 2) l'unique travail à notre connaissance de coévolution s'intéressant au mutualisme ([Mack, 2012](#)), considère une condition initiale polymorphe (deux phénotypes, coopératif et non-coopératif) mais ne considère pas de mutation, s'affranchissant ainsi du risque d'invasion des groupes mutualistes depuis l'intérieur.

Nous cherchons à répondre à ces limites avec un modèle considérant une population hôtes-symbiotes dans un espace en deux dimensions dans lequel les symbiotes sont initialement parasites des hôtes. Cette conjonction d'un système hôte-symbiote et d'une transition du parasitisme vers le mutualisme nous permet de nous inscrire dans le cadre des transitions majeures ([Szathmáry and Smith, 1995](#)), en l'occurrence le cas d'une transition égalitaire ([Estrela et al., 2016](#); [Queller, 1997](#)), qui implique la formation d'un nouveau tout à partir de parties constituées d'espèces différentes (Figure III.2). L'interaction entre l'hôte et son

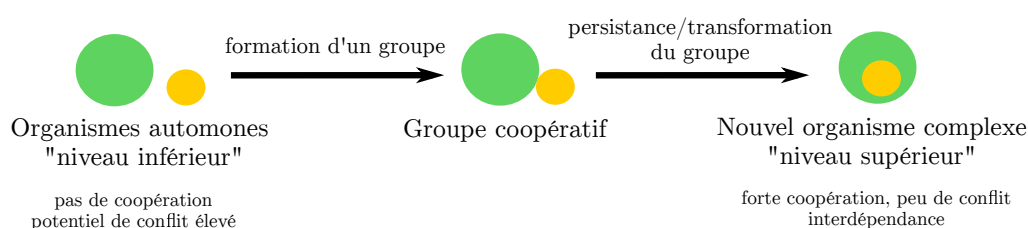


Figure III.2 – Schéma du concept de transition égalitaire, recopié de ([Estrela et al., 2016](#))

symbiote est régie par des traits d'interactions respectifs définissant l'effort mutualiste investi par chaque partenaire (par exemple un transfert de nutriments). Cette interaction va modifier la reproduction de chaque partenaire. Lorsque le symbiote investit suffisamment dans l'effort mutualiste, les échanges avec l'hôte sur-compensent le coût métabolique que sa présence provoque chez lui et l'interaction devient mutualiste. De plus chaque hôte et symbiote possède un second trait déterminant l'échelle (locale/globale) de la dispersion des propagules. Afin de questionner l'émergence d'une structure spatiale, la dispersion est exclusivement globale en condition initiale. L'hôte et le symbiote se différencient par leur dépendance respective initiale : si l'hôte est initialement indépendant du symbiote, c'est-à-dire que les propagules d'hôtes peuvent s'implanter dans les cellules vides de l'espace, le symbiote en revanche a besoin

pour s'installer d'une cellule déjà colonisée par un hôte. Nous considérons que seul un hôte et un symbiote peuvent s'implanter par cellule, et non pas plusieurs individus. L'évolution des traits d'interaction et de dispersion est assurée par une probabilité de mutation lors de la formation des propagules. Enfin, les hôtes subissent une compétition - pouvant être plus ou moins locale/globale - densité-dépendante pour d'autres ressources que l'espace.

Nos résultats montrent que l'émergence du mutualisme, via la transition depuis le parasitisme, est possible par coévolution avec la dispersion et mène à une corrélation négative entre mutualisme et dispersion globale. Ainsi, pour l'hôte comme pour le symbiote - bien que ce soit plus prononcé pour le symbiote - les individus mutualistes ont une dispersion plutôt locale tandis que les individus non-mutualistes/parasites une dispersion plutôt globale. Dans le cadre des transitions majeures, il est intéressant de noter que lorsqu'un hôte et un symbiote se dispersent localement, leurs descendants ont une probabilité significative d'être également en interaction. La transmission se rapproche alors d'une transmission verticale, bien que nous n'ayons pas eu besoin de supposer qu'il existait un mécanisme développemental qui la rende systématique, et celle-ci est connue pour favoriser la symbiose mutualiste (Akçay, 2015; Estrela et al., 2016; Ferdy and Godelle, 2005; Herre et al., 1999; Kerr and Nahum, 2011; Maynard, 1998; Queller and Strassmann, 2016; Wilkinson and Sherratt, 2001).

De façon assez surprenante, cette transition vers le mutualisme n'est possible que lorsque la compétition densité-dépendante entre hôtes est suffisamment forte et globale. Effectivement, la structure spatiale émerge grâce à l'évolution vers une dispersion locale et une plus grande productivité des groupes de couples hôtes-symbiotes mutualistes. Cependant, ces deux mécanismes ne suffisent pas au mutualisme pour émerger et persister. En fait, considérer un système uniquement constitué de parasites viables en conditions initiales implique que l'unique avantage des groupes mutualistes se mesure en terme de nombre de descendants. Cette caractéristique associée à la capacité d'invasion des groupes mutualistes par des individus parasites grâce à leur dispersion plutôt globale confère un avantage sélectif trop faible aux groupes mutualistes par rapport à l'avantage sélectif des parasites au niveau individuel. Cependant, dès lors qu'il existe une compétition densité-dépendante globale entre les hôtes l'avantage sélectif au niveau des clusters est renforcé. En effet, la présence d'individus mutualistes dans la population, résultant de la variabilité phénotypique due aux mutations, et bien que ces mutualistes soient contre-sélectionnés à long terme, augmente la densité en hôtes. Cette augmentation de densité implique une augmentation de la compétition et si celle-ci devient assez forte les couples hôte-symbiote dont le symbiote est parasite ne sont plus viables. Ces couples produisent toujours des descendants mais à long terme leur taux d'accroissement est négatif. Ainsi, avec cette forte compétition l'avantage sélectif des groupes mutualistes n'est plus seulement une meilleure production de descendants mais également une capacité de persistance temporelle que n'ont plus les couples avec parasite. Dès lors, le conflit de sélection entre le niveau des individus et le niveau des groupes s'équilibre pour mener à la coexistence de mutualistes et de parasites. Enfin, la compétition doit être suffisamment globale pour conférer un avantage suffisant au mutualisme. En effet, si la compétition est trop locale, les groupes mutualistes dans lesquels les densités sont importantes vont subir leur propre compétition, tandis que les régions de l'espace riches en parasites - et aux densités plus faibles - ne subiront pas la compétition.

La transition du parasitisme vers le mutualisme implique donc trois niveaux d'organisation. En effet, les deux niveaux de sélection (individu et groupe) constituent les deux premiers niveaux d'organisation, mais la compétition globale fait entrer en jeu le niveau d'organisation de l'ensemble du paysage. Tandis que le niveau d'organisation de l'individu exerce une pression de sélection contre le mutualisme, les deux niveaux d'organisation du groupe et du paysage

exercent des pressions de sélection en faveur du mutualisme (Figure III.3).

Bien que l'intérêt de notre étude porte principalement sur la causalité réciproque entre

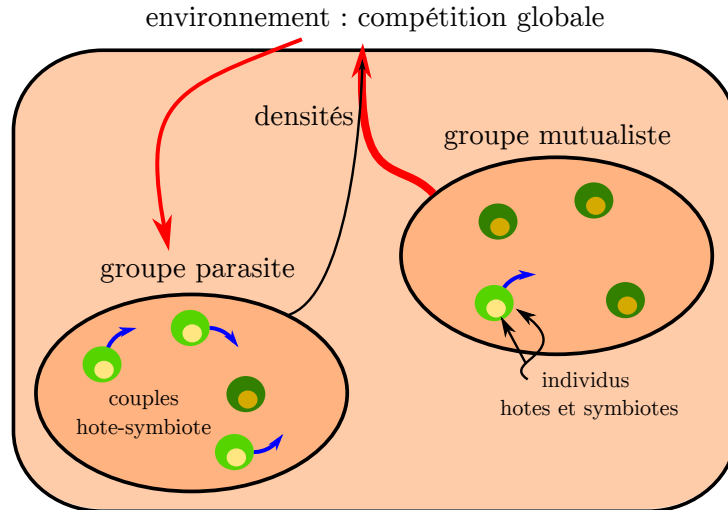


Figure III.3 – Schéma de synthèse des différents niveaux d'organisation et de sélection impliqués dans l'évolution du mutualisme dans notre modèle. On considère que les pressions de sélection émergent de trois niveaux d'organisations, les individus, les groupes, et le paysage (compétition globale), et s'exercent sur deux niveaux de sélection, les individus et les groupes. Les flèches rouges indiquent des pressions de sélection en faveur du mutualisme, les flèches bleues en faveur du parasitisme. Les individus couples parasitiques sont en couleurs vives, les couples mutualistes en couleurs foncées.

niveaux de sélection, les résultats impliquent également une causalité réciproque entre écologie et évolution, à la fois dans sa composante construction de niche comme dans sa composante temporelle. En ce qui concerne la composante temporelle nous soulignons le fait que la hausse de compétition causée par la hausse de densité en hôte, elle-même causée par la présence de symbiotes mutualistes, ne peut se produire que parce que nous considérons des mutations relativement fréquentes et simultanées. Si nous avions considéré des mutations très rares, de sorte à distinguer la temporalité des dynamiques écologique et évolutive, la densité d'individus mutualistes (contre-sélectionnés) dans la population suffisante pour induire une hausse de compétition n'aurait jamais été atteinte. Plus encore, si nous avions considéré une approche par dynamique adaptative (Geritz et al., 1998), nous n'aurions jamais introduit de mutualistes dans la population car leur fitness d'invasion est négative à faible densité. En ce qui concerne la composante de construction de niche nous pouvons remarquer que la hausse de compétition induite par la présence de mutualistes dans la population peut s'interpréter comme une construction de niche du point de vue des mutualistes. En augmentant la reproduction de leur partenaire, les mutualistes changent l'environnement (représentée par la compétition globale), et ce changement implique une modification des pressions de sélection en faveur des mutualistes. Ainsi, les mutualistes construisent les conditions permettant leur évolution depuis le parasitisme. De plus, les mutualistes sont en mesure de re-construire ces conditions si celles-ci sont détruites, par exemple dans le cas de l'extinction d'une large partie de la population suite à une perturbation - réduisant la compétition indispensable au mutualisme.

III.2 Article : Mutualists construct the ecological conditions that trigger the transition from parasitism

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III.2.1 Abstract

The evolution of mutualism between hosts and initially parasitic symbionts represents a major transition in evolution. Although vertical transmission of symbionts during host reproduction and partner control both favour the stability of mutualism, these mechanisms require specifically evolved features that may be absent during the transition. Therefore, the first steps of the transition from parasitism to mutualism are not fully understood. Spatial structure might be the key to this transition. We explore this hypothesis using a spatially explicit agent-based model. We demonstrate that, starting from a parasitic system with global dispersal, the coevolution between mutualistic effort and local dispersal of hosts and symbionts leads to a stable coexistence between parasites and mutualists. The local dispersal evolution mimics vertical transmission and triggers the formation of mutualistic clusters, counteracting the individual selection level of parasites that maintain global dispersal. However, the transition also requires competition between hosts in order to occur. Indeed, the transition occurs when mutualistic symbionts increase the density of hosts, which strengthens competition between hosts and disfavours parasitic host/symbiont pairs: mutualists create ecological conditions that allow their own spread. Therefore, the transition to mutualism may come from an eco-evolutionary feedback loop involving spatially structured population dynamics.

Keywords: mutualism, major transition, spatial structure, dispersal evolution, eco-evolutionary feedbacks, niche construction

Author contributions: SI, JG and LL originally formulated the project; all authors developed the model; LL and MR performed the numerical analyses; LL, SI and JG wrote the manuscript.

III.2.2 Introduction

In their bestseller, [Szathmáry and Smith \(1995\)](#) explored several major transitions in biology, from the origin of chromosomes to the evolution of social groups. Most of these transitions resulted from the formation of a larger entity from smaller entities. In addition, smaller entities specialize within the larger ones and often become dependent on them (e.g., for reproduction), eventually making the transition irreversible.

Following the work of [Queller \(1997\)](#), [Szathmáry \(2015\)](#) adopted a dichotomy between fraternal transitions such as multicellularity arising from a division of labour among closely related

units and egalitarian transitions such as mutualistic symbiosis (Bronstein, 2015), where more distant units come together to complement their functions in a larger unit.

For a transition to occur and persist, evolutionary conflicts between the subentities must not overtake the whole's fate. In the case of fraternal transitions, this is prevented by the strong relatedness between subentities (Fisher et al., 2013; Hamilton, 1964a,b; Queller, 2000). However, in the case of egalitarian transitions, the subentities generally belong to different species. Thus, it can be advantageous for them to remain autonomous and exploit the other subentities. This selfish behaviour occurs at the expense of the whole, as for the tragedy of the commons (Garrett, 1968; Hardin, 1998). For instance, a parasitic symbiont may remain parasitic rather than collaborate in mutualistic symbiosis (Drew et al., 2021). The resulting evolutionary conflict might be circumvented by vertical transmission of the symbionts, which ensures that all subentities share a common fate (Wilson and Sober, 1994). As a result, vertical transmission of symbionts promotes the transition to mutualism (Akçay, 2015; Estrela et al., 2016; Ferdy and Godelle, 2005; Herre et al., 1999; Kerr and Nahum, 2011; Maynard, 1998; Queller and Strassmann, 2016; Wilkinson and Sherratt, 2001).

The importance of vertical transmission has been highlighted by experiments on microbial systems (King et al., 2016; Sachs et al., 2011; Shapiro and Turner, 2018; Shapiro et al., 2016) as well as *in natura* observations of a Wolbachia-insect system (Weeks et al., 2007).

However, in many mutualistic systems, the symbiont is transmitted horizontally (Wilkinson and Sherratt, 2001), such as legume-rhizobium (Denison and Kiers, 2004), squid-vibrio (McFall-Ngai, 2014), mycorrhizae (Allen, 1991) or plant ants (Bronstein et al., 2006; Rico-Gray and Oliveira, 2008). In such cases, several mechanisms such as partner selection, sanction or fidelity and costly exploitation, can counteract the selection for selfishness (Akçay, 2017; Estrela et al., 2016; Foster and Wenseleers, 2006; Genkai-Kato and Yamamura, 1999; Sachs et al., 2004; Wilkinson and Sherratt, 2001).

For instance, in legume-rhizobium, mycorrhizal and plant-ant associations, the plants can sanction the less beneficial (or even detrimental) symbionts by allocating them fewer resources (Akçay, 2015; Bever et al., 2009; Denison and Kiers, 2004; Edwards et al., 2006; Kiers et al., 2003; West et al., 2002).

However, it is unclear whether these mechanisms are present at the beginning of the transition. Since they require the evolution of complex and specific traits, they may occur in later stages, providing additional stability to the system. In the absence of such traits, what mechanism could promote the start of a transition to mutualism? Using a theoretical model, the present work aims to show that the coevolution between mutualistic effort and local dispersal of hosts and symbionts triggers the formation of mutualistic clusters which can resist the invasion of parasites. In addition to the spatial structure, we show that the competition between hosts truly promotes the start of the transition.

A similar issue exists with respect to the evolution of altruism, since partner choice/control mechanisms, such as voluntary reciprocal altruism (Axelrod, 1981), may be restricted to higher animals or may appear during later evolutionary stages. Spatial structure has been recognized as a general mechanism promoting the transition to altruism (Débarre et al., 2012; Lion and Van Baalen, 2007, 2008; Mitteldorf and Wilson, 2000). Spatial structure generally stems from local dispersal, which triggers the formation of clusters dominated by altruistic individuals, while individuals with similar phenotypes are positively assorted in space (Pepper, 2007; Wilson and Dugatkin, 1997). The balance between individual-level selection favouring cheaters and cluster-level selection favouring altruists ultimately determines the evolutionary outcome (Mitteldorf and Wilson, 2000; Van Baalen and Rand, 1998). Moreover, the coevolution of cooperation and dispersal can allow the emergence of altruism, with spatial clusters of altruistic

individuals promoting the persistence and spread of altruistic phenotypes (Hochberg et al., 2008; Koella, 2000; Le Galliard et al., 2005; Mullon et al., 2018; Purcell et al., 2012). Empirical evidence on the evolution of reduced virulence (Boots and Meador, 2007), the evolution of altruism (Harcombe, 2010), and the evolution of restraint predation (Kerr et al., 2006) also supports the crucial role of the spatial structure.

With respect to altruism, spatial structure can allow mutualists to overcome non-mutualists (Akçay, 2017; Yamamura et al., 2004), and this can involve the evolution of dispersal (Mack, 2012). However, this may not be sufficient to account for the transition from parasitism to mutualism, since parasitic symbionts should discourage hosts from initiating the transition, whereas non-mutualists have a weaker impact (Mack, 2012; Yamamura et al., 2004). Moreover, in previous attempts, mutualistic efforts were initially polymorphic but were not subject to mutations (Mack, 2012). In that case, mutualistic clusters cannot be invaded from inside through parasitic mutations, which favours mutualism. The present work therefore constitutes, to our knowledge, the first spatially explicit eco-evolutionary model where the mutualistic efforts and dispersal abilities of hosts and symbionts coevolve, beginning from a fully parasitic interaction. If some hosts and symbionts simultaneously become mutualists and start dispersing locally, this may lead to the formation of mutualistic host/symbiont clusters producing more offspring than parasitic host/symbiont pairs, thereby initiating the transition. Meanwhile, parasitic symbionts should continue dispersing globally to invade such clusters, which could homogenize the spatial structure and compromise the transition. Therefore, it is unclear whether mutualists will invade, whether mutualists will replace parasites, or whether both strategies will coexist, as is often the case in nature (e.g., (Borges, 2015; Després and Jaeger, 1999)).

The concept of major transitions also implies that the host and the symbiont become dependent upon each other (Szathmáry, 2015; Szathmáry and Smith, 1995), with each partner needing the other to perform essential functions. Dependence is often accompanied by gene loss and gene exchange, rendering the transition irreversible (Estrela et al., 2016). For instance, aphids and their intracellular bacterial symbiont *Buchnera aphidicola* are irreversibly mutually dependent since the symbiont provides essential amino acids to its host (Akman Gündüz and Douglas, 2009; Bennett and Moran, 2015). However, most mutualistic interactions do not exhibit such physiological or reproductive dependencies (e.g., plant-ants or legume-rhizobium mutualisms), and several reverse pathways are often possible from mutualism to parasitism (Sachs and Simms, 2006; Week and Nuismer, 2021; Werner et al., 2018). Since the present work focuses on eco-evolutionary dynamics, we will not consider any physiological or developmental dependency or irreversibility and will instead assume that hosts are always able to produce offspring when alone. Nevertheless, the number of offspring produced by the hosts can depend on the mutualistic efforts of both species as well as on the population densities, which are expected to change during the transition. Under these altered ecological conditions, isolated hosts may exhibit a negative population growth rate, although they are physiologically able to produce offspring. This is hereafter called "ecological dependence".

To sum up, we tackle the following issues:

- **Main question:** Can the transition from parasitism to mutualism occur when mutualistic effort coevolves with local dispersal in the absence of vertical transmission and partner control?
- **Q1:** How do mutualistic clusters arise during the first steps of the transition? Is their formation necessary for the transition?

- **Q2:** By maintaining global dispersal, can non-mutualistic hosts and parasitic symbionts coexist with mutualists?
- **Q3:** Do mutualistic hosts become ecologically dependent on their symbiont

To investigate these questions, we built an agent-based model using a two-dimensional space lattice that supports an autonomous host and a host-dependent symbiont. Hosts compete for space and other resources, while symbionts compete for available hosts. This situation occurs in many biological systems, such as plant-ant, plant-fungi, or plant-seed eating pollinator. To model the transition from parasitism, the symbiont is initially detrimental to the host, and the host provides it the minimal energy possible, without any spontaneous mutualistic effort, as would be the case after an antagonistic evolutionary arms race. Moreover, the host-parasite system is ecologically viable even in the absence of any mutualistic agent in the landscape. At first, both species disperse globally; this situation corresponds to the most disadvantageous conditions for the emergence of mutualism. Through continuous mutations, mutualistic and locally dispersing symbionts and hosts can appear, establish and eventually change the population dynamics, triggering feedback on their own evolutionary dynamics. In addition to these general hypotheses, no assumptions specific to a particular biological system were required.

III.2.3 Model description

Main rules Our model considers two types of agents, hosts and symbionts, living on the same two-dimensional space lattice. The interaction between the two species occurs when they share the same cell. Each cell can assume three states: i) empty, ii) occupied by a solitary host (only one host is allowed per cell), iii) occupied by a host-symbiont couple, (only one symbiont is allowed per host). Each individual brings two traits, the mutualistic interaction trait (α) and the dispersal trait (ϵ). Both influence fecundity.

At every time point, agents undergo each following steps (see appendix III.2.7 and Figure III.10 for more details and schematic representation of the life cycle):

- The host and symbiont die with fixed probability m .
- They produce offspring, possibly with different traits from them due to mutations. The fecundity of the parents depends on their traits and on their interactions with their possibly cell-sharing partner.
- The offspring are dispersed according to the parents' dispersal traits ϵ .
- The host offspring may establish only in empty cells, while the symbiont offspring can only establish in cells already occupied by a solitary host. If several individuals come to implant in the same cell, a uniform lottery determines which one will implant, while the others die.

Fecundity rate and mutualism/parasitism The fecundity rate f of an agent depends on its mutualistic interaction trait α as well as the trait of its cell-sharing partner. This continuous trait, ranging between 0 and 1, determines the intensity of the agent investment in the mutualistic relationship. We assume a positive interaction trait dependence between agents. A mutualistic agent tends to increase the fecundity of its cell-sharing partner. On the other hand, a mutualistic agent has an intrinsic cost, reducing its fecundity. Thus, the effective agent fecundity results from the gain induced by the mutualistic behaviour of its partner weighted by its own intrinsic cost of mutualism (for mathematical details see appendix

III.2.7).

In addition, the cost of mutualism is a developmental characteristic that applies regardless of the actual interaction. Thus, a solitary mutualistic host always pays the cost of mutualism. Therefore, we consider "strong mutualism", where no direct feedback occurs for mutualists and mutualism always has a cost.

The hosts are autonomous, i.e., their fecundity is nonzero when they are alone in their cell without a symbiont. In addition, while hosts are always beneficial to symbionts, because they are necessary for their establishment, symbionts can be parasitic to hosts. Indeed, we assume that the presence of a symbiont induces a cost for the host. Thus, if the symbiont invests insufficiently in the mutualistic interaction, it does not compensate for this cost, and the host has reduced fecundity than if it was alone; the symbiont is parasitic to the host. The symbiont becomes mutualistic when it sufficiently invests in the mutualistic interaction so that the host has a higher fecundity than if it was alone. In our model, a symbiont is parasitic if $\alpha < 0.475$ and mutualistic if $\alpha > 0.475$ (see Figure III.4).

We note interaction traits of the host and the symbiont α_h and α_s , respectively. The fecundity rate ranges between a positive low value that depends on the agent type and a maximum rate of 8 corresponding to the maximum number of direct neighbours in a 2D space (Figure III.4).

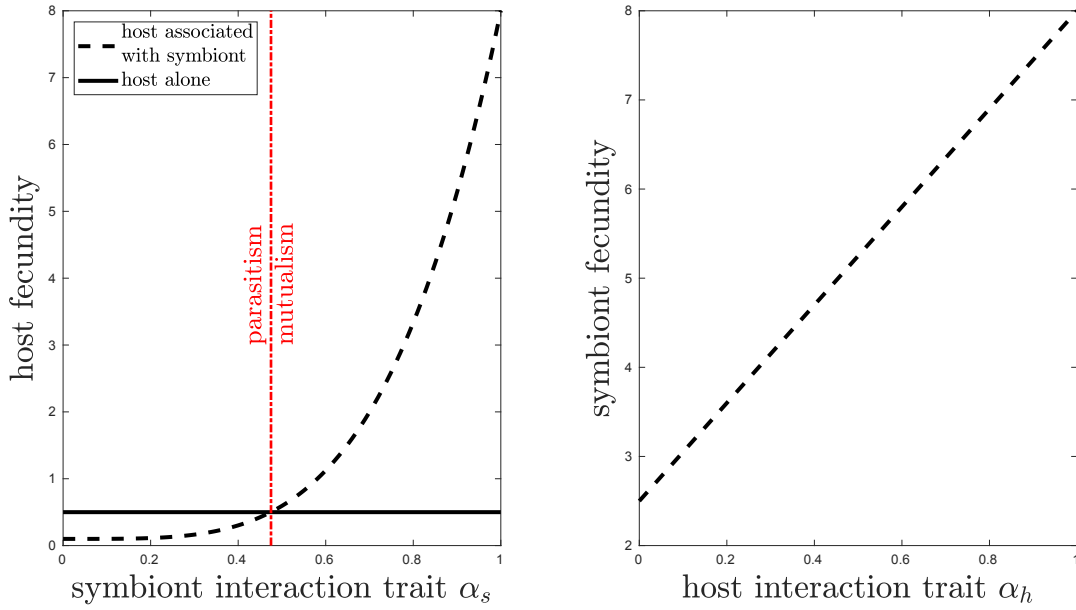


Figure III.4 – Fecundity rates of hosts and symbionts according to the interaction trait of their partners (dashed lines). Plain line: fecundity of a solitary host. The dashed-dotted red line corresponds to the threshold α_s^* between the parasitic symbiont (solitary host fecundity higher than the fecundity of a host associated with a symbiont of trait $\alpha_s < \alpha_s^*$) and mutualistic symbiont (solitary host fecundity lower than fecundity of a host associated with a symbiont of trait $\alpha_s < \alpha_s^*$).

Mutation Offspring inherit traits from their parents with variability due to mutations. The effects of mutations on each trait are independent, and can be either beneficial or detrimental. We describe these effects using an exponential distribution that allows for rare mutations with large effects. We set a maximum mutation distance d ; if a distance from the exponential distribution is greater than d , the mutation is cancelled. Similarly, a mutation is cancelled if it

implies that the trait exceeds the limits of its domain $[0, 1]$.

Dispersal The parents are sessile, whereas their descendants are dispersed. The individuals can invest in two modes of dispersal, a local dispersal considering the 8 neighbouring cells of the parent's cell and a global dispersal corresponding to a uniform dispersal across the entire space.

Their dispersal trait ϵ provides the proportion of offspring globally dispersed uniformly in the space. The remaining proportion $1 - \epsilon$ is locally dispersed uniformly in the cells around the parent. Similar dispersal was used in Kéfi et al. (2007, 2008).

Global dispersal implies an additional cost that reduces the number of offspring. Therefore, effective fecundity f_e is equal to the fecundity rate f reduced by a cost that is linearly proportional to the investment in global dispersal: $f_e = f(1 - d\epsilon)$, with d a coefficient to modulate cost intensity.

Competition The host is subject to intraspecific density-dependent competition, which influences the establishment success of the offspring. The establishment probability P_I decrease with the host density ρ_h as follows:

$$P_I = 1 - (\rho_h)^{\gamma_C} \quad (\text{III.1})$$

where ρ_h is the proportion of cells occupied by hosts and γ_C is the competition strength. The competition is strong when $\gamma_C < 1$ (sub-linear function), while it is weak when $\gamma_C \geq 1$ (super-linear function).

Parasitic system and transition To tackle the issue of transition to mutualism, we assume that the system is viable without mutualism. More precisely, we chose parameters such that the extinction probability of a population with parasitic global dispersers (minimal interaction traits, $\alpha_s = \alpha_h = 0$ and dispersal trait $\epsilon = 1$) was less than 1 in the absence of mutation. Moreover, this parasitic population without evolution stabilizes around a demographic equilibrium called the "parasitic system". From our perspective, this situation is the worst-case scenario because interactions are parasitic and dispersal cost is maximal. However, under evolution, mutations generate diversity, and mutualistic symbionts can appear. Starting from the parasitic system, mutations lead to the presence of approximately 2% of mutualistic symbionts in the population. They are not selected but simply result from the phenotypic variability induced by mutations. Then, the system can either remain in this state, or a transition to mutualism can occur. The transition is characterized by a significant increase of the percentage of mutualistic symbionts above the percentage generated by simple phenotypic variability. In our following work, we assume that transition occurs when the percentage of mutualistic symbionts rises above the threshold of 10%.

III.2.4 Results

In the following results, the maximum cost of mutualism is 30%, and the other parameters are set to satisfy the viability of the parasitic system (see Table III.1 in appendix III.2.7).

The transition from parasitism to mutualism under restrictive conditions

Our first objective was to investigate whether in the absence of dispersal cost, the transition to mutualism is possible starting from the viable parasitic system without dispersal cost. It represents the most difficult condition for the transition to mutualism. From our simulations, we can compute the transition time when the percentage of mutualistic symbionts rises above 10%, which is our transition threshold.

Without dispersal cost, the transition is more likely to occur under strong competition than weak competition (see the probability of transition in Figure III.5a)). Moreover, when the transition succeeds, it occurs more rapidly under strong competition (median transition time around 7.10^4) than under weak competition (median transition time around $2.5.10^4$). However, with a large dispersal cost ($d = 0.45$), the transition occurs systematically (the probability of transition is 1) and quickly (the median transition time is divided by a hundred 7.10^2), regardless of whether the competition is weak or strong (see Figure III.5a).

The transition is characterised not only by an increase in mutualistic symbionts but also by an increase in host and parasitic symbiont densities (see Figure III.5b and c). During the transition, we also observe an increase in the mean interaction trait of mutualistic symbionts toward 1 (see curve colour in Figure III.5c). Thus, the transition is initiated by weakly mutualistic symbionts, which then rapidly increase their mutualistic interaction. In contrast, the increase in the average host interaction trait is delayed in response to the symbionts' transition (see curve colour in Figure III.5b). Moreover, the transition does not occur at the expense of parasitic symbionts. The latter benefits from the increase in host density created by the mutualistic symbionts. As a result, their density increases so that the parasitic symbionts remain dominant (Figure III.5c).

Note that if the cost of mutualism is sufficiently low (e.g., a maximum cost of only 10% instead of the 30% of the previous results), the transition to mutualism occurs even in the absence of host competition (details not shown).

The evolutionary branching resulting from the transition is accompanied by coevolution with the dispersal trait (see Figure III.6a). As a result, we obtain two classes of symbionts: parasitic global dispersers ($\alpha_s \ll 1$ and $\epsilon \sim 1$) and mutualistic local dispersers ($\alpha_s \sim 1$ and $\epsilon \ll 1$). Conversely, the host trait distribution is more aggregated, and coevolution with the dispersal trait leads to a negative correlation between global dispersal and mutualism intensity (Figure III.6b, $R^2=0.102$, $p\text{-value}=0$). Moreover, we observe that very few hosts exhibit a weak interaction trait ($\alpha_h < 0.2$). The low density of very weak mutualistic hosts results from the apparent competition between hosts due to a high density of symbionts. In this situation, a host is frequently associated with a symbiont. Strong mutualistic hosts will benefit more from parasitic symbionts than weak mutualistic hosts. Indeed, a parasitic symbiont will benefit from a strong mutualistic host by increasing its number of offspring, which eventually reduces the host density and thus host competition.

To investigate whether the transition to mutualism is associated with the emergence of a spatial structure, we measured an index of assortment (see appendix III.2.7 for details). A positive index indicates that on average, individuals with similar phenotypes are closer than individuals with different phenotypes when compared to a random spatial distribution of the individuals in the space (Figure III.7a). The intraspecific assortment quantifies the similarity of agents in a local neighbourhood (8 cells), and the interspecific assortment quantifies the similarity between host and symbiont in the same cell.

Positive assortment indices demonstrate that the agents are locally similar and that hosts and symbionts in the same location also have the same interaction behaviour. As a result, we show

that the transition to mutualism occurs along with the emergence of a spatial structure (see clusters of hosts and mutualistic symbionts Figure III.7b and c). The intraspecific spatial structure is stronger than the interspecific structure. This is not surprising since the formation of the intraspecific spatial structure simply requires that a sufficient proportion of the dispersal is local. However, for an interspecific spatial structure to emerge, a phenotype must have a sufficiently local dispersal, and it must interact with a similar phenotype that also exhibits a local dispersal.

Effect of competition We have shown that competition between hosts promotes the transition to mutualism. We next investigated its quantitative effect on the percentage of mutualistic symbionts. The following results were obtained using a large dispersal cost ($d = 0.45$) to reduce the mean time of transition and thus save computational time. We also discuss the effect of dispersal cost in the next section.

Competition strength increases the percentage of mutualistic symbionts after the transition when competition is global over the landscape, i.e., hosts compete with all the hosts in the landscape (Figure III.8a). However, when competition is more local, individuals compete only with their neighbours (see appendix III.2.7 and Figure III.11 for details), and the percentage of mutualistic symbionts decreases drastically (Figure III.8b). When the competition is too local, the average percentage of mutualistic symbionts eventually drops below the transition threshold, and no transition occurs.

Finally, we showed that mutualism persists only because of strong competition. Indeed, if we reduce the competition after a transition to mutualism, we observe that the population evolves towards the parasitic system (see Figure III.8c and Figure III.12 in the appendix for more details).

Another way to reduce density-dependent competition is to reduce the density of the host. In this case, we show that mutualism still persists (Figure III.13a in appendix). Thus, temporal perturbations in host density tend to enhance the proportion of mutualism. Indeed, the perturbation itself does not change the proportion of mutualistic symbionts because the different symbionts are fairly evenly distributed throughout the space. Then, the space vacated by the perturbation is recolonised mostly by parasitic symbionts due to their more global dispersal (Figure III.13b). However, due to the relaxation of global competition, the probability of host establishment is better, and the mutualistic clusters outside the perturbation zone gain in size, which explains why the proportion of mutualistic symbionts increases slightly despite the recolonization of the centre by parasites. In the end, once recolonization is complete, the system returns to an equilibrium state close to before the perturbation. In terms of trait distribution, the new state is similar to the previous state before the perturbation (details not shown).

The same experiment but with a perturbation that causes the death of 50% of uniformly occupied cells leads to the same results.

Mortality and dispersal cost can induce host dependency in emerging mutualistic systems. Competition is a major process leading to mutualism. However, mortality and dispersal cost also play important roles in shaping the mutualistic system. Thus, for the results below, the competition is both strong and global.

We demonstrated that dispersal cost and mortality promote mutualism (Figure III.9). Although the mutualistic system emerges in a wide range of parameters where the parasitic system is viable, the transition is more likely to occur when the system is close to extinction. We demonstrated that the transition is less likely to occur when the dispersal cost is low.

In particular, for the parameter pair in the area indicated by the grey star, we have shown previously that the probability of transition is very low around 0.086 (see Figure III.5). In addition, we show that the transition is unlikely to occur if the mortality is too low, which tends to demonstrate that the time of emergence increases if the mortality decreases.

The dispersal cost also modifies the characteristics of the system by reducing the average dispersal trait of both species (Figure III.14 and Table III.2 in the appendix). This reduction is associated with more pronounced branching of the symbiont due to the increase in the percentage of mutualistic symbionts. We observed that even in response to a strong dispersal cost, the mean dispersal trait of parasitic symbionts is higher than the mean dispersal trait of mutualistic symbionts.

Under favourable conditions leading to the transition to mutualism, the population of mutualistic hosts always persists in the absence of the population of mutualistic symbionts. Therefore, in our model, the transition to mutualism does not exhibit an absolute dependency between host and symbiont populations. However, *ecological dependency* may occur. The transition to mutualism cooccurs with an increase in host density and thus an increase in intraspecific competition. If this increase in competition is sustainable only in the presence of mutualistic symbionts, we say that the hosts are *ecologically dependent* on the symbionts. To test this dependence, we measured the global competition between hosts in a population at equilibrium after a transition to mutualism. Then, we used this competition as a fixed non-density-dependent competition to test whether a host population with all individuals having the same trait as the mean trait of a population at equilibrium can survive in the absence of mutualistic symbionts and mutation. We show that this dependency occurs when the system evolves toward a mutualistic system in which the percentage of mutualistic symbionts is sufficiently large (Figure III.9 hatched area).

III.2.5 Discussion

The mechanism underlying the transition to mutualism. In relation to our primary question, our results indicate that the transition from parasitism to mutualism occurs when mutualistic efforts coevolve with dispersal, despite the absence of vertical transmission or partner control. Before the transition, the host performs better when alone; therefore, it has no interest in increasing its mutualistic effort; in fact, it is selected to keep it as low as possible. In contrast, the symbiont population is limited by the number of available hosts, which increases when the symbiont becomes mutualistic. If by chance mutations produce a mutualistic symbiont dispersing locally and interacting with a host dispersing locally as well, its offspring will benefit from the increased density of hosts in their neighbourhood and will form a mutualistic cluster (question Q1, Figure III.7c). The cluster will be rapidly invaded by parasitic symbionts dispersing globally, which can lead to its extinction if competition between hosts is weak. Under such conditions, the transition to mutualism rarely occurs (Figure III.5a), and when it does, the percentage of mutualistic symbionts remains low (Figure III.8a). Conversely, when hosts strongly compete for resources, the ecological conditions change dramatically. The formation of mutualistic clusters (Figure III.7a) increases population densities (Figures III.5b and III.5c), which enhances competition between hosts. Areas dominated by parasitic host/symbiont pairs were initially viable, but their population growth rate became negative following the increase in competition. This creates empty space that can be colonized by mutualists, which still disperse globally from time to time. Therefore, contrary to our expectation, the transition is not directly caused by the higher fecundity of mutualistic clusters but only indirectly by the increase in host competition. However, this only occurs when competition between hosts

is partly global (Figure III.8b); if it is purely local, mutualistic clusters cannot influence the viability of parasitic regions. Although areas dominated by parasitic host/symbiont pairs become unsuitable, parasitic symbionts can still invade mutualistic clusters and overcome them. This results in a dynamic equilibrium between mutualism and parasitism (question Q2, Figure III.5c). Coevolution with dispersal results in a negative correlation between mutualism intensity and global dispersal (80% of mutualists disperses locally, Figure III.6), which mirrors the link between altruistic behaviour and local dispersal (Hochberg et al., 2008; Koella, 2000; Le Galliard et al., 2005; Mullon et al., 2018; Purcell et al., 2012). Empirical work has shown that the outcome of interactions between hosts and symbionts depends not only on the traits of the protagonists, but also on the ecological conditions (Bronstein, 1994). For instance, plants take advantage of seed-eating pollinators in the absence of alternative pollinators but not in their presence (Thompson and Cunningham, 2002). Mycorrhizae are beneficial for plants when soil resources are scarce while they are detrimental when resources are abundant (Johnson et al., 1997). In the above cases, the outcome of the interaction depends on both biotic and abiotic factors that are external to the host-symbiont system. Our model showed that the association with symbionts remains parasitic when host competition is low, while it evolves towards mutualism when host competition increases. In that case, the outcome of the interaction depends on intrinsic features of the interactions that are constructed by the eco-evolutionary dynamics of the system, as the emergence of mutualists increases host density.

The transition needs some time to occur because several obstacles must be overcome (simultaneity of the mutations, demographic stochasticity, susceptibility to invasions by parasites) before the mutualists are numerous enough to induce the shift in host competition. For this reason, the dispersal cost was introduced to speed up the transition (Figure III.5a) without affecting the overall behaviour of the model. Dispersal cost induces a selection pressure at the individual level in favour of local dispersal, which increases the likelihood of the formation of mutualistic clusters.

In addition to dispersal cost, mortality enhances the probability of transition. Mortality pushes the parasitic system towards its viability boundary and promotes the eco-evolutionary feedback loop involving host competition. The facilitation of mutualistic symbiosis in harsh environmental conditions has already been observed theoretically and empirically (Callaway et al., 2002; Maestre et al., 2003; Travis et al., 2006). However, explaining mutualistic behaviour it is not always a significant process (Werner et al., 2015). Moreover, in the context of altruism, an inverse relationship is observed (Taylor and Irwin, 2000).

The role of quasi-vertical transmission Although mutualistic symbionts are environmentally acquired, their local dispersal, together with mutualistic hosts, produces a similar effect as vertical transmission (as for mycorrhizae, (Wilkinson, 1997)), which we term "quasi-vertical" transmission. However, local dispersal (even 100%) is not equivalent to vertical transmission because host and symbiont offspring can disperse to any of the 8 neighbouring cells. Vertical transmission due to specific reproductive and physiological adaptations would have produced transitions to mutualism more easily. Moreover, the colonization of empty space by a mutualistic pair requires the simultaneous long-distance dispersal of both species, whereas in the case of vertical transmission, this always occurs. In addition, the need to colonize empty space constitutes an important selection pressure, which partly counteracts the necessity of quasi-vertical transmission. Indeed, mutualistic phenotypes retain their ability to disperse globally ($\sim 20\%$ for symbionts and $\sim 40\%$ for hosts, Figure III.6), which cannot be due to mutations alone. Colonization ability comes along with the avoidance of local overpopulation

generated by mutualism. Similarly, although the evolution of altruism is favoured by kin selection (itself induced by local dispersal (Hamilton, 1964b)), it can also be limited by kin competition (Akdeniz and Van Veelen, 2020; Alizon and Taylor, 2008; Wilson et al., 1992).

A mixed strategy combining both dispersal modes takes advantage of kin selection and simultaneously maintains the opportunity to escape kin competition. Figure III.8b shows that purely local competition between hosts prevents the transition to mutualism because kin competition overcomes kin selection in that case with respect to the evolution of cooperation (Akdeniz and Van Veelen, 2020). In nature, global competition between hosts may arise when plants compete for water present in the same groundwater, while competition for light is more local. Thus, the evolution of mutualism may depend on the dominant form of competition for resources between hosts.

The interplay between three levels of organization The mechanism by which parasitic symbionts and hosts can invade mutualistic clusters is a two-species version of the tragedy of the commons (Feeny et al., 1990; Garrett, 1968; Hardin, 1998), which can be bypassed by local dispersal in the case of altruism (Mitteldorf and Wilson, 2000) as well as in the present case. Indeed, there is no transition to mutualism when dispersal is primarily global ($\epsilon > 0.55$), mutualists and parasites coexist for mixed dispersal strategy ($0.55 > \epsilon > 0.1$), and mutualists almost outcompete parasites when dispersal is mainly local ($\epsilon < 0.1$, details not shown). In the context of altruism, the resolution of the tragedy of the commons involves two levels of organization, the individual-level favouring cheaters and the group-level favoring altruism (Van Baalen and Rand, 1998). In the context of mutualism, parasites are selected at the individual level and mutualists at the host/symbiont pair level, resembling the tit-for-tat strategy where cooperators are selected at the pair level. However, this is not the end of the story because in the absence of dispersal cost, mutualism rarely invades when host competition is weak (Figure III.5a), despite the occasional formation of mutualistic pairs. For the transition to occur, competition between hosts at the global scale is necessary (Figure III.8b), which constitutes a third level of organization involved in the coevolutionary process.

Host dependency and irreversibility of the transition Major transitions in evolution are characterized by the irreversibility and the interdependence between the agents (Estrela et al., 2016; Szathmáry and Smith, 1995). Our model does not include any physiological dependence of the host on its symbiont or any loss of functions in the host due to gene transfers, assuming that this generally occurs during later stages of the evolution of mutualism. Instead, we have defined dependence from a population dynamics perspective: the host is "ecologically dependent" when its population growth rate is negative in the absence of its symbiont, even though it can produce offspring (question Q3). We found that mutualistic hosts deprived of their symbiont exhibit a negative growth rate when the host density after the transition to mutualism becomes sufficiently large (Figure III.9). In our model, this ecological dependency resulted from the density-dependent competition between hosts and the assumption that mutualism is costly for the host, even when its symbiont is absent (e.g., the unconditional production of extrafloral nectaries (Bronstein, 1998)). However, this dependency is not absolute. Indeed, once the density becomes sufficiently low, the mutualistic hosts alone are viable. The dependency may become absolute for a sufficiently high cost of mutualism, but in these conditions, the transition to mutualism will not occur.

If host competition strength decreases permanently, e.g., following the continuous supply of extra resources, the reverse transition back to parasitism occurs (Figure III.8c). This reversion

occurs because host dependency relies on the ecological conditions that change when the host competition strength is modified. However, if host competition decreases punctually, e.g., following a perturbation of a fraction of the landscape, mutualism persists (Figure III.13) because mutualistic clusters take advantage of the reduction of global host competition to colonize free cells around them. This leads to an increase in host competition; in that case, mutualism can restore the ecological conditions, allowing its own persistence, as in a niche construction process (Laland et al., 2016; Lewontin, 1982, 1983; Odling-Smee et al., 2003). Niche construction is generally understood as the improvement of abiotic conditions. In the context of mutualism, it is due to the improvement of host densities, which induces an increase in host competition. This also occurs at the beginning of the transition, when the first mutualistic clusters trigger an increase in global host density.

Conclusion In the present paper, we aim to understand the mechanisms promoting the transition from parasitism to mutualism. To tackle this issue, we develop an agent based model on a lattice. In our general model, we only assume that the mutualistic interactions influence the fecundity of both partners and that hosts face density-dependent competition. In addition, we ensure that the antagonistic system is stable in absence of mutations. We show that in the absence of vertical transmission or partner control mechanisms, the coevolution between mutualistic effort and local dispersal can trigger the transition from parasitism to mutualism, provided that intraspecific competition between host is sufficiently global and that either dispersal cost or competition strength is large enough.

Unexpectedly, we found that mutualistic clusters invade the antagonistic system thanks to their ability to increase the population densities of both partners, thereby triggering global competition between hosts and rendering regions dominated by parasitic host/symbiont pairs unsuitable. In contrast, the higher fecundity of mutualists is not advantageous enough to compensate for the ability of parasites to invade mutualistic clusters. Thus, our results suggest that the eco-evolutionary feedback involving competition between hosts might promote the transition from parasitism to mutualism in a wide range of biological systems, such as plant-fungi, plant-ant and plant-seed-eating pollinator interactions.

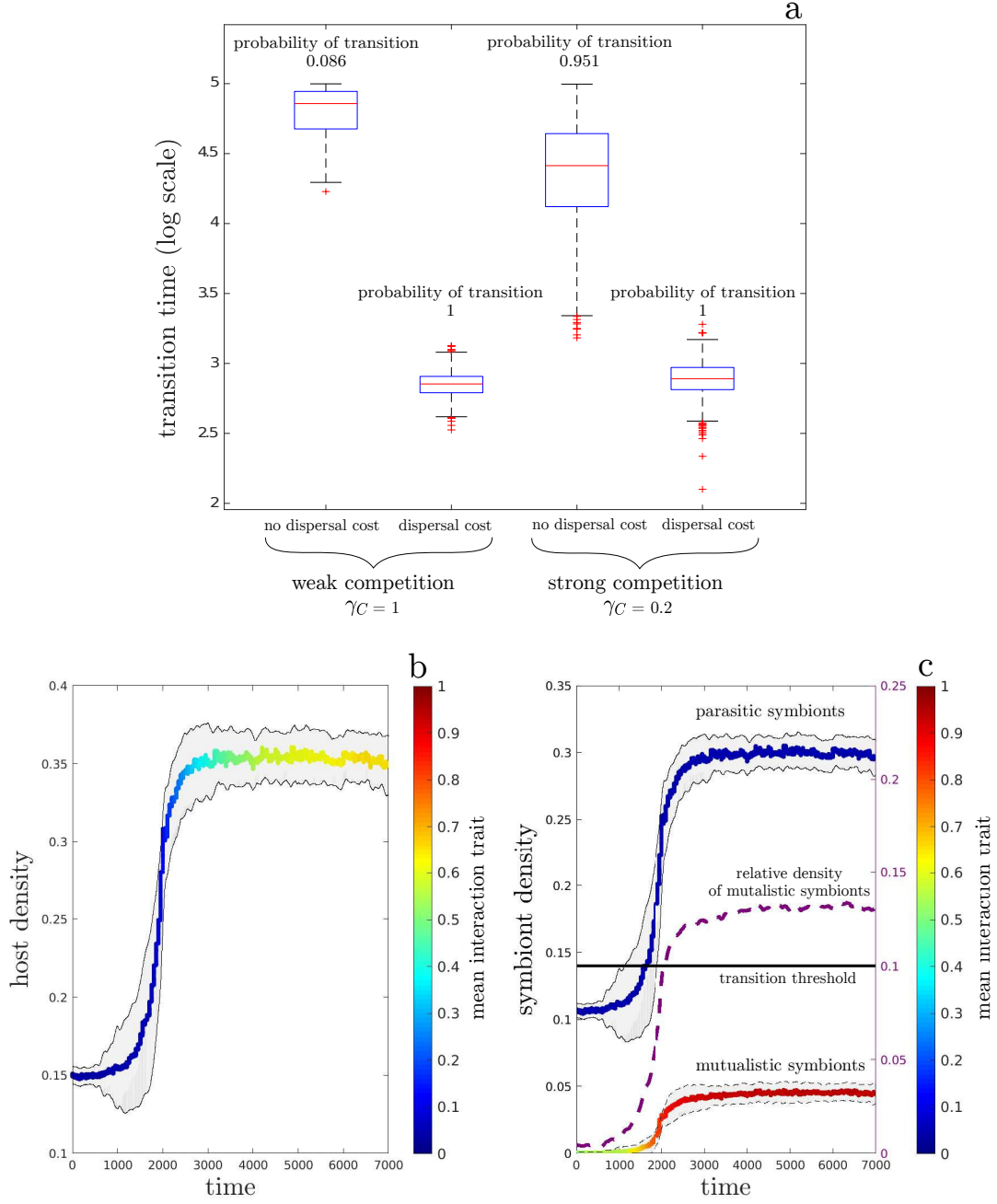


Figure III.5 – a) Transition time as a function of competition strength γ_C and dispersal cost d . Boxplots representing the transition time when the percentage of mutualistic symbionts increases above 10% when starting from the parasitic system. We ran 1000 replicates per parameter pair with a maximum projection time of 10^5 . The probability of transition corresponds to the frequency of transition over the 1000 simulations. In panels b) and c), coloured plain curves represent the host and symbiont densities over time averaged over 100 simulations under strong competition $\gamma_C = 0.2$ and no dispersal cost $d = 0$. The time series are adjusted so that all simulations have a transition time $t = 2000$. The colour gradient corresponds to the mean interaction trait α , and shaded regions correspond to the standard deviation for densities. In panel c), the purple dotted line and the right y-axis show the relative density of mutualistic symbionts, and the black line indicates the 10% transition threshold.

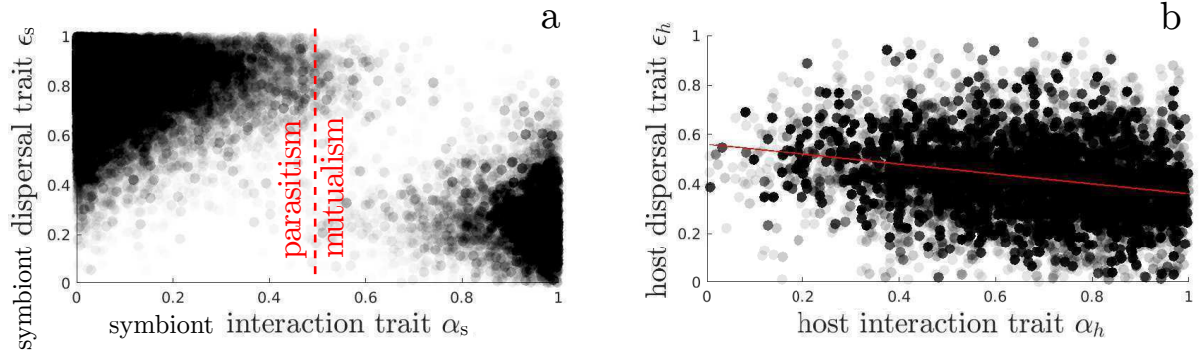


Figure III.6 – Distribution after transition to mutualism in traits domain (ϵ, α) of symbionts (panel a) and hosts (panel b). Plain red line (panel b) shows the linear regression between host traits ($R^2=0.102$, p-value=0). Distributions corresponds to 100 simulations with strong competition $\gamma_C = 0.2$ and no dispersal cost $d = 0$.

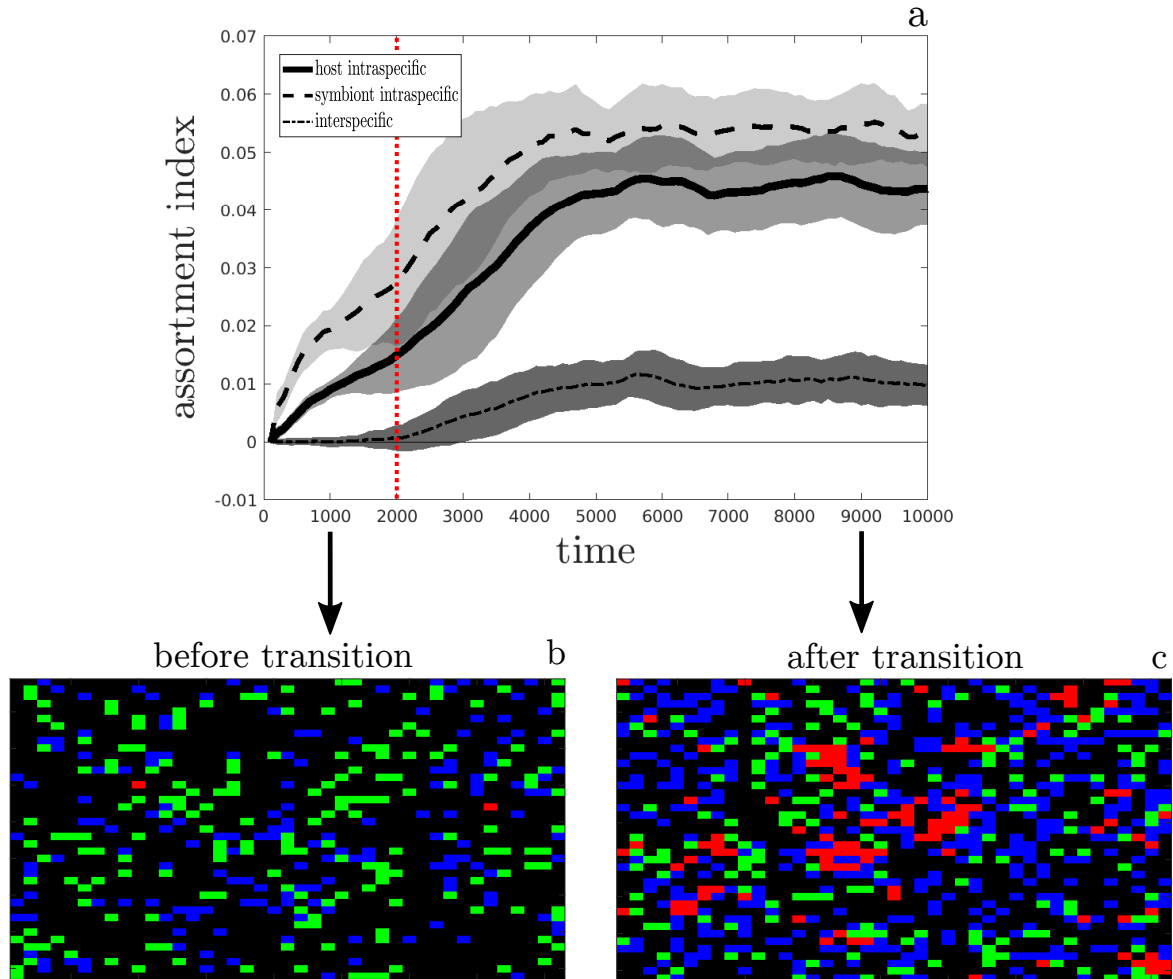


Figure III.7 – a) Spatial structures are described by the assortment index measuring the intraspecific assortment between hosts (plain line), the intraspecific assortment between symbionts (dashed line) and the interspecific assortment between hosts and symbionts (dash-dot line). Results are averaged over 100 simulations with strong competition $\gamma_C = 0.2$ and no dispersal cost $d = 0$. The time series are adjusted so that all simulations have a transition time $t = 2000$ (red dotted line). Grey areas show the standard deviation. b)-c) Snapshots of a region of 40x40 cells before (panel b) and after (panel c) the transition to mutualism. Coloured cells represent host alone (green), host with parasitic symbiont (blue), host with mutualistic symbiont (red), empty (black).

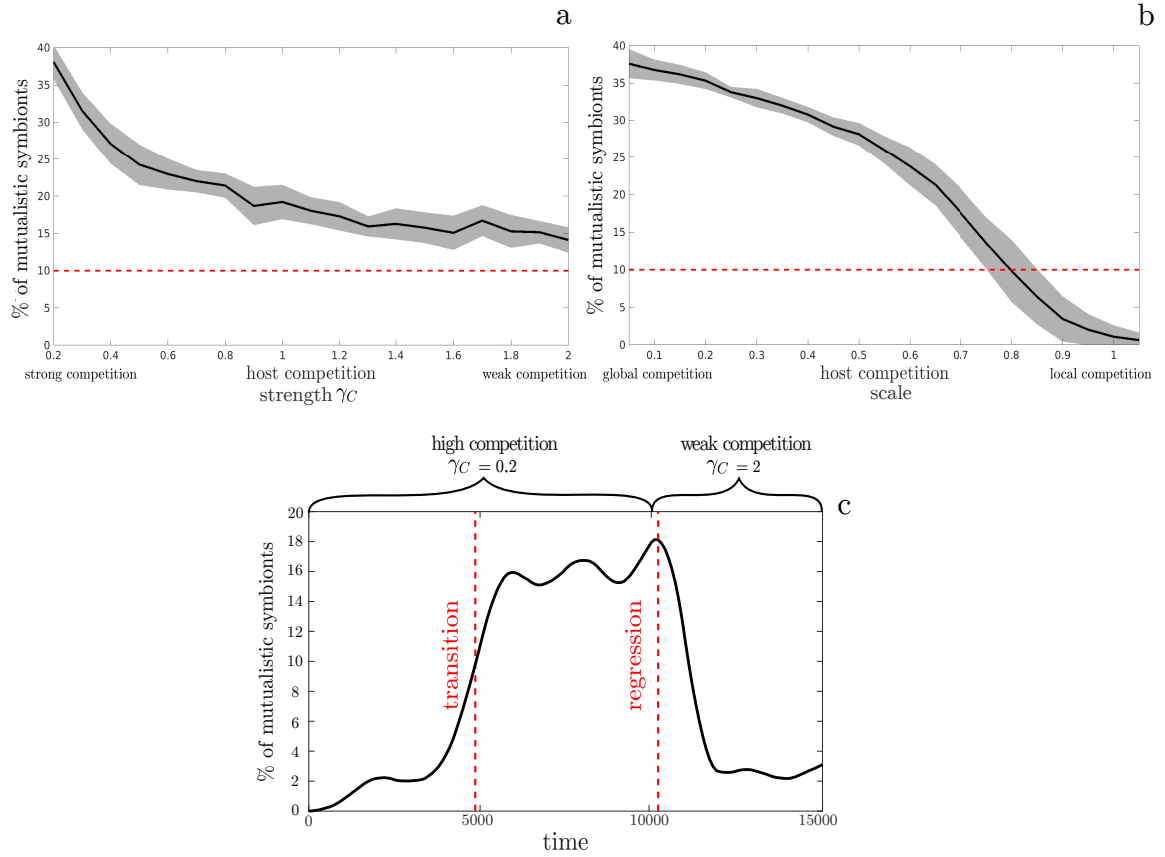


Figure III.8 – The role of host competition in the transition to mutualism. a) The effect of the competition intensity (defined by the competition shape parameter γ_C) on the transition to mutualism (global competition). b) The effect of the spatial scale of the competition (strong competition $\gamma_C = 0.2$). c) The effect of competition on the transition and on the maintenance of mutualism (simulation without dispersal cost). Panels a and b show the results averaged over 50 simulations with a maximum projection time of 10^4 steps, and grey areas give the standard deviation. The red dotted line is the threshold of 10% of mutualistic symbionts above which transition to mutualism occurs.

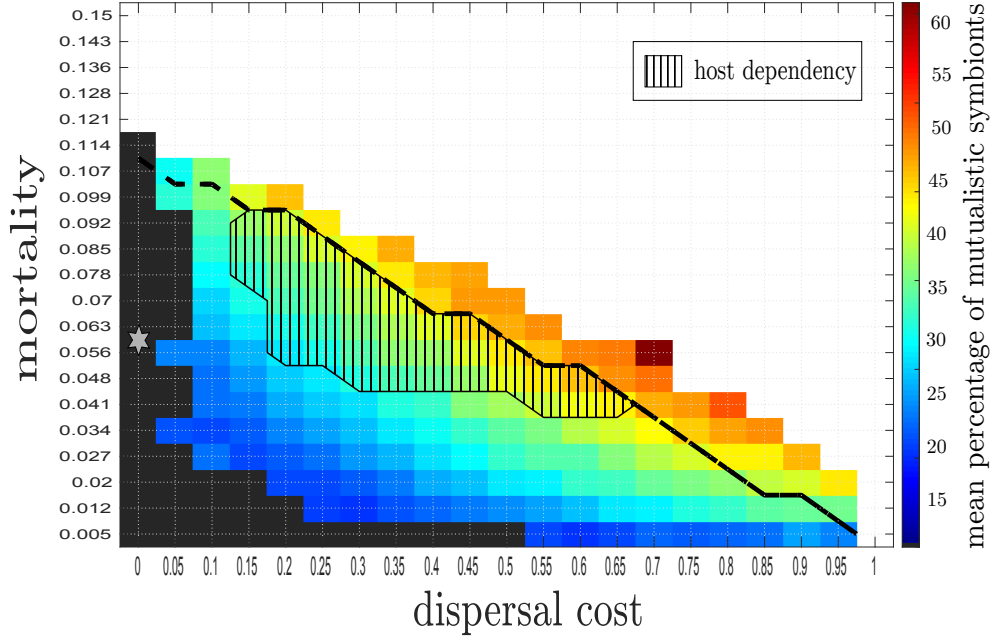


Figure III.9 – The percentage of mutualistic symbionts when there is transition to mutualism as a function of intrinsic mortality and dispersal cost. We performed 50 simulations per parameter with strong global competition $\gamma_C = 0.2$. The percentages are averaged over the simulations that lead to transition, if any occur. The white cells correspond to the nonviability domain for the system with evolution, and above the black dotted line, the parasitic system is not viable. The dark grey area corresponds to no transition for all simulations. The evolution of host ecological dependency occurs in the hatched area. Ecological dependency means that the average host from a population where mutualism has emerged cannot survive the competition experienced by that population (i.e. the ecological conditions) if the mutualistic symbionts are removed. The grey star corresponds to the restrictive conditions of Figure III.6; note that under these conditions, a transition is possible but rare (probability of transition is 0.086), so with only 50 simulations per parameter no transition occurs here.

III.2.6 Acknowledgements

We are grateful to Jean-François Arnoldi, Cédric Gaucherel and Sébastien Lion for their thoughtful comments and discussion on this work.

III.2.7 Appendix

Mathematical and numerical details of the model

We present here the mathematical underpinnings of the model as well as some details of the numerical computation.

Algorithm Our model follows the cycle presented in Figure III.10:

- Host and symbiont die with fixed probability $m \in (0, 1)$.
- They produce offspring, possibly with different traits from them due to mutation. The fecundity of the parents depends on their two traits $(\alpha, \epsilon) \in [0, 1]^2$ and on their interactions with their possibly cell-sharing partner.
- The offspring are dispersed according to the parents' dispersal traits ϵ .
- The offspring of the hosts may establish only in empty cells, while the offspring of the symbionts can only establish in cells already occupied by a solitary host. If several individuals arrive in the same cell, a lottery determines which one will establish, while the others die.

In our numerical computations, mutations occurred only after the descendant was successfully established in a cell. This procedure saves computational time and did not influence our results because offspring dispersal and establishment do not depend on their traits but only on their parent traits. Furthermore, the mortality process was applied to both types of agents simultaneously, while the reproduction and dispersal processes were applied consecutively to the hosts and then to the symbionts. We confirmed that the order of the algorithm did not qualitatively affect our results.

Fecundity rate The fecundity rate f of an agent depends on its mutualistic interaction trait α as well as the interaction trait of its cell-sharing partner. This continuous trait ranging between 0 and 1 determines the intensity of the agent investment in the mutualistic relationship.

We assumed a positive interaction trait dependence between agents. A mutualistic agent tends to increase the fecundity of its cell-sharing partner. The interaction fecundity $f_I^i(\alpha_j)$ of an individual of type $i \in \{h, s\}$, (h = host, s = symbiont) interacting with an individual of type $j \in \{s, h\}$ with trait α_j was defined by

$$\begin{aligned} f_I^h(\alpha_s) &= f_{I,min}^h (1 + c_f^h f_{I,min}^h \alpha_s^{\gamma_f}) \\ f_I^s(\alpha_h) &= f_{I,min}^s (1 + c_f^s f_{I,min}^s \alpha_h) \\ \text{with } c_f^h &= \frac{f_{I,max} - f_{I,min}^h}{f_{I,min}^h} \quad \text{and} \quad c_f^s = \frac{f_{I,max} - f_{I,min}^s}{f_{I,min}^s} \end{aligned} \tag{III.2}$$

The coefficient γ_f allows us to set the influence of trait α_s on fecundity. Using a coefficient $\gamma_f < 1$, we create a convex function allowing a transition from parasitism to mutualism for a central value of the symbiont interaction trait. However, note that modifying the shape of this fecundity curve (from concave to convex via linear) does not qualitatively change our results.

On the other hand, a mutualistic agent has an intrinsic cost reducing its fecundity. The mutualism cost $c_m(\alpha_i)$ of an individual of type $i \in \{h, s\}$ (h = host, s = symbiont) ranges

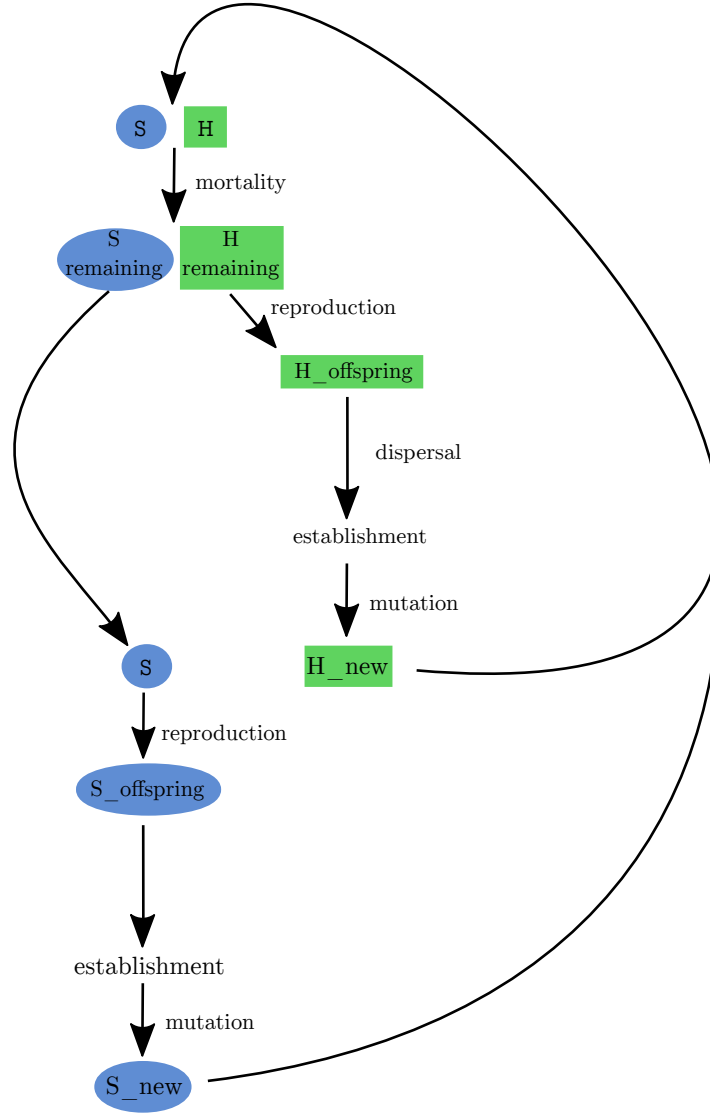


Figure III.10 – Diagram of the numerical algorithm. The host population (H) and the symbiont population (S) undergo intrinsic mortality, then reproduction, dispersal, establishment, and finally mutation. The mortality step is simultaneous for the host and the symbiont, while the other steps occur first for the host and then for the symbiont.

between 0 and 1, and it increases with interaction trait α_i of the agent. It is defined by

$$c_m^i(\alpha_i) = 1 - c\alpha_i \quad (\text{III.3})$$

where c is the maximal cost of mutualism.

Thus, for the host as for the symbiont, the fecundity f_i of an individual i interacting with an individual j is the product of the interaction fecundity $f_I(\alpha_j)$ defined by (III.2) and the cost of mutualism $c_m(\alpha_i)$ defined by (III.3).

$$\begin{aligned} f_h &= c_m^h(\alpha_h) f_I^h(\alpha_s) \\ f_s &= c_m^s(\alpha_s) f_I^s(\alpha_h) \end{aligned} \quad (\text{III.4})$$

When a host agent is alone in a cell, its fecundity is defined by its intrinsic host fecundity

f_a^{max} weighted by its mutualism cost $c_m(\alpha_h)$: Fecundity of the solitary host:

$$f_a = c_m^h(\alpha_h) f_{max}^a. \quad (\text{III.5})$$

Fecundity still depends on the interaction trait of the host but we replace the interaction fecundity $f_I^h(\alpha_s)$ with an intrinsic fecundity f_{max}^a . We therefore consider that the cost of mutualism is a developmental cost that is paid regardless of whether the interaction is realized. It can therefore be said that the mutualism modelled here is a "strong mutualism" in the sense that there is no direct return on investment for the partner with a mutualist effect, and the cost of mutualist behaviour is always paid.

The fecundity rates produced by our process were rarely integers, yet the number of offspring in our model can only be represented by an integer. Thus, in the numerical algorithm, the fecundity was rounded down to the lower integer, and then the decimal part is used as a parameter of a Bernoulli trial to determine whether a descendant was added.

Mutualism/parasitism threshold In our model, the presence of a host always produced a net benefit for the symbiont. However, the presence of the symbiont might be detrimental for the host. Indeed, the fecundity of a host h interacting with a symbiont s is $f_I(\alpha_s) c_m(\alpha_h)$, while the fecundity of the same host h without a symbiont is $f_a^{max} c_m(\alpha_h)$. Thus, the host has net benefit only if its fecundity in association with a symbiont is larger than its fecundity alone. Therefore, mutualism only occurs when $f_I(\alpha_s) > f_a^{max}$. Otherwise, the interaction is parasitic. This criterion does not depend on the host mutualism trait α_h because the hosts always pay the same mutualism cost. Thus, we can define the mutualism/parasitism threshold α_s^* such that $f_I(\alpha_s^*) = f_a^{max}$; thus, we obtain

$$\alpha_s^* = \left(\frac{f_{max}^a - f_{I,min}^h}{c_f^h f_{I,min}^h} \right)^{1/\gamma_f} \approx 0.475 \quad (\text{III.6})$$

with the parameters set in Table III.1.

Competition To test the effect of the spatial scale of the competition, we introduced a scale parameter $c_s \in [0, 1]$ that weighs the effect of local ρ_h^{local} and global ρ_h^{global} host density on the competition. The establishment probability thus satisfies

$$P_I = 1 - \left((1 - c_s) \rho_h^{local} + c_s \rho_h^{global} \right)^{\gamma_C} \quad (\text{III.7})$$

The local host density ρ_h^{local} corresponds to the host density in the 8 neighbouring cells surrounding the implantation cell of the host, while the global density ρ_h^{global} corresponds to the host density all over the landscape (see Figure III.11 for a schematic representation).

These competition scales may have various ecological explanations. For instance, plants sharing the same water table face global competition for this resource. Conversely, the competition for light between plants is an example of local competition. Thus, our competition scale model allows us to describe the competition for several different resources that may appear at different scales. Following our previous examples, if the water supply represents 90% of the competition and light supply represents only 10%, then the competition scale c_s is $c_s = 0.9$ (90% global competition and 10% local competition).

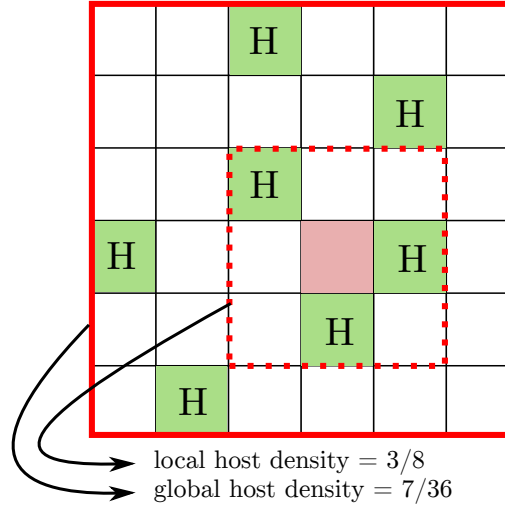


Figure III.11 – Local and global host densities influence the probability of establishment in the focus cell (pink filled square). The global density corresponds to the host density in the whole 36-cell landscape. The local density corresponds to the density in the eight cells vicinity around the focus cell.

Assortment index To compute the assortment index, we measured the similarity between spatially neighbouring phenotypes for the space resulting from the transition to mutualism and for a space containing the same phenotypes but whose distribution in space was randomised. The assortment index corresponds to the difference between the measurement made on the space resulting from the transition to mutualism and the measurement on the randomly rearranged space. If the index shifts positively (resp. negatively) from zero, it means that similar phenotypes are closer (resp. more distant) than different phenotypes compared to random spatial distribution. This methodology is similar to that used in [Pepper and Smuts \(2002\)](#) and [Pepper \(2007\)](#).

In practice, for the intraspecific assortment index, we utilized the following algorithm for each species: i) for each occupied cell by the target species, we measured the difference between the interaction trait present in the cell and the average of the interaction traits present in the neighbouring cells (a maximum of 8 neighbours can be present), and then we averaged these measurements to obtain an average similarity S at the scale of the whole space; ii) this operation was repeated on 1000 spaces containing the same interaction traits but randomly redistributed between the occupied cells to obtain the average similarity corresponding to a random spatial distribution S_r ; iii) finally, the assortment index corresponds to $S - S_r$.

For the interspecific assortment index, the first step was different: i) for each cell occupied by a host-symbiont pair, we measured the difference between their interaction traits, and then we averaged all of these measurements to obtain an average similarity S . Steps ii and iii follow the same methods as described above.

Competition strength, perturbation and mutualism persistence

Competition strength determines mutualism persistence In the main text, we show that competition is essential for the transition to mutualism, but it is also important for its persistence, as shown here. In this section, we explored the effect of a sudden variation in competition strength γ_C on the persistence of mutualism. We started with a strong competition $\gamma_C = 0.2$. As expected from our previous results, a transition to mutualism occurred (see

Parameters	Values
mortality m	0.06
mutualism cost c	0.3
upper limit of host and symbiont interaction fecundity $f_{I,max}$	8
lower limit of host interaction fecundity $f_{I,min}^h$	0.1
lower limit of symbiont interaction fecundity $f_{I,min}^s$	2.5
upper limit of solitary host fecundity f_{max}^{sh}	0.5
shape coefficient of the host interaction fecundity γ_f	4
maximum mutation distance d	0.5

Table III.1 – Fixed parameters used for results unless otherwise specified.

Figure III.12a), c) and d)). Then, around $t = 10^4$, we suddenly switched the competition strength to $\gamma_C = 2$, corresponding to weak competition. We observed regression of mutualism due to the proportion of mutualistic symbionts decreasing from 20% to less than 5% (see Figure III.12a) and e)). We observed that the regression of mutualism due to a weakening of the competition corresponded with an increase in host and symbiont densities. This increase is due to the reduction of competition, which determines densities more than the presence or absence of mutualism does.

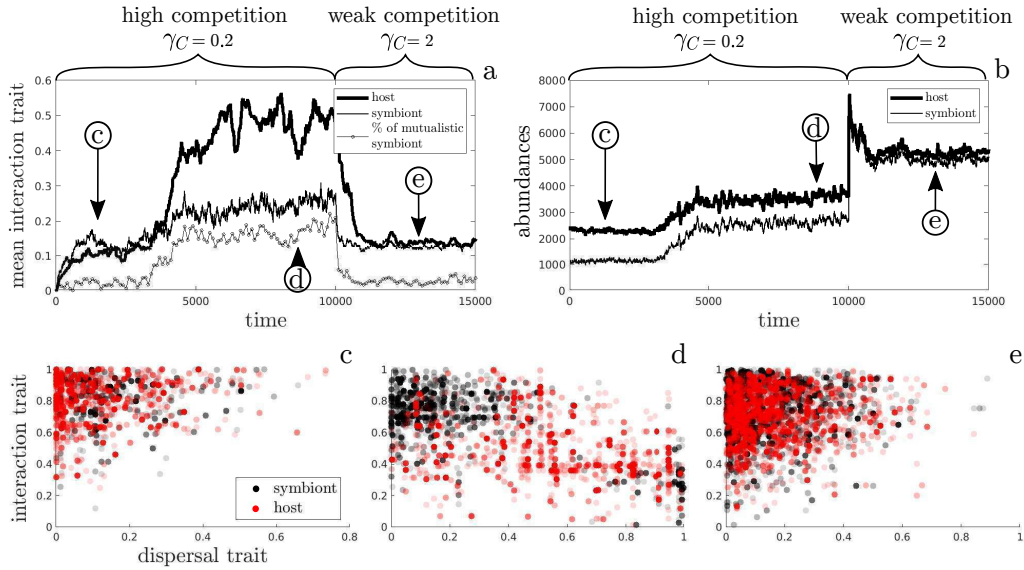


Figure III.12 – The transition to mutualism and collapse of mutualism depending on competition. a) Host and symbiont average interaction traits and the percentage of mutualistic symbionts over time. b) Host and symbiont abundance. There is high competition from $time = 0$ to $time = 10000$ and weak competition from $time = 10001$ to the end. c) Dispersal and interaction traits domain before the transition to mutualism. d) Dispersal and interaction traits domain during mutualism persistence. e) Dispersal and interaction traits domain after mutualism collapse.

Density perturbation does not affect mutualism persistence Next, we tested how mutualism responds to a decrease in competition due to eradication of hosts and symbionts

in a large homogeneous region of space (Figure III.13). While previously we demonstrated that mutualism regresses when competition is set to be weak, we show here that mutualism persists in the face of decreased competition due to decreased host density.

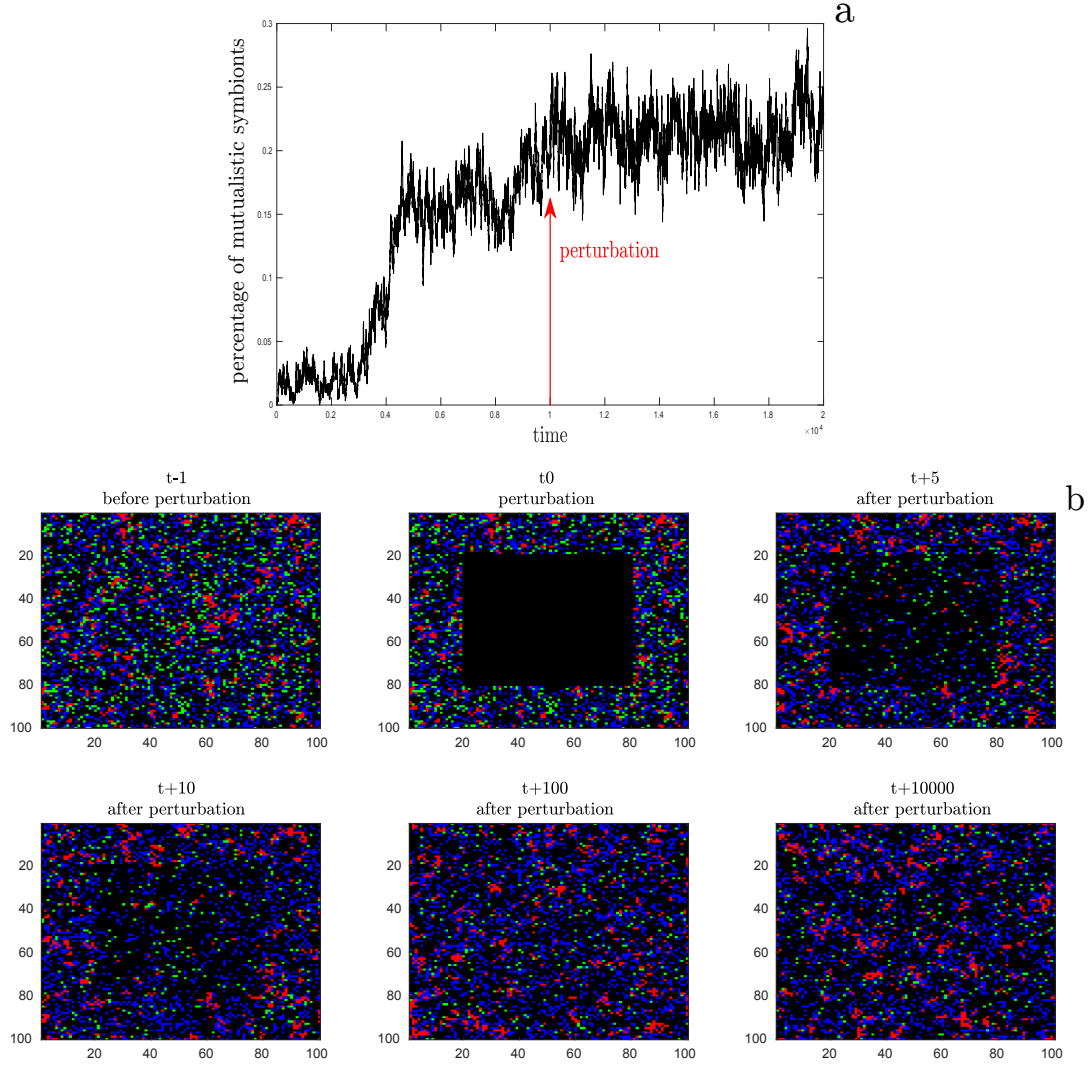


Figure III.13 – Maintenance of mutualism in the face of a reduction in competition caused by a perturbation creating a large square of free cells. a) The proportion of mutualist symbionts, showing from t_0 to t_{10000} the transition to mutualism and the eco-evolutionary equilibrium, then until t_{20000} the response following the perturbation. b) Snapshot at several times: $t - 1$ is the eco-evolutionary equilibrium with mutualism just before the perturbation, then at t_0 the perturbation, and then $t + 5$, $t + 10$, $t + 100$ and $t + 10000$ after the perturbation. In black, the free cells; in green, the hosts alone; in blue, the couples with parasitic symbionts; and in red, the couples with mutualist symbionts.

Mortality and dispersal cost can induce host dependency in emerging mutualistic systems.

In the main text, we focused on the effect of mortality and dispersal cost on the transition to mutualism and host dependency. Here, we present in more detail the effect of dispersal cost on the distribution of hosts and symbionts in trait space for three values of dispersal cost and fixed mortality rate (Figure III.14). In addition, the table III.2 shows the features of the clusters in the trait distribution.

We demonstrated that the dispersal cost favours the transition to mutualism. Moreover, even when the cost was high, the features of the clusters revealed that parasitic symbionts maintained a more global dispersal than mutualistic symbionts.

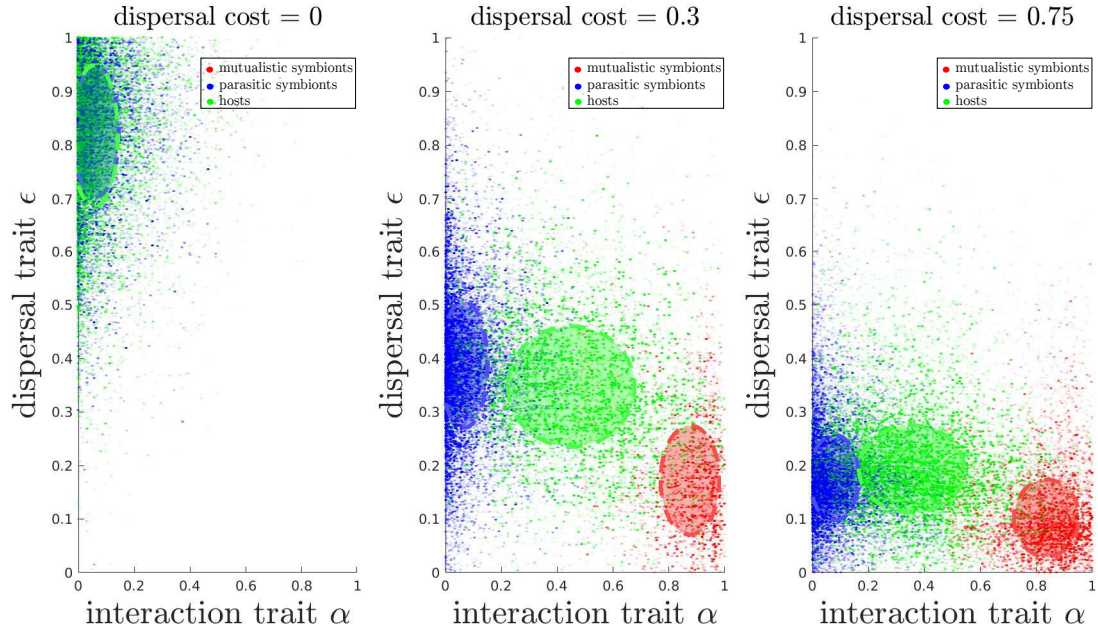


Figure III.14 – Joint distribution of the host (green), the parasitic symbiont (blue) and the mutualistic symbiont (red) populations in the traits domain for mortality $m = 0.03$ and an increasing dispersal cost $d \in \{0, 0.3, 0.75\}$. The ellipses correspond to the standard deviation. The 48 runs averaged in Figure III.9 are plotted together.

dispersal cost	species	mean interaction trait	mean dispersal trait
$d = 0$	hosts	0.074	0.81
	parasitic symbionts	0.06	0.82
	<i>mutualistic symbionts</i>	<i>* (density < 2%)</i>	<i>* (density < 2%)</i>
$d = 0.3$	hosts	0.45	0.35
	parasitic symbionts	0.07	0.39
	mutualistic symbionts	0.88	0.17
$d = 0.75$	hosts	0.36	0.19
	parasitic symbionts	0.08	0.18
	mutualistic symbionts	0.84	0.10

Table III.2 – Features of the clusters in the traits domain

CHAPITRE IV

CAUSALITÉ RÉCIPROQUE ENTRE INDIVIDUS, NIVEAUX TROPHIQUES ET COMMUNAUTÉ

IV.1 Introduction et synthèse des résultats

Dans ce dernier chapitre nous explorons la causalité réciproque entre dynamique écologique et évolutive à travers un modèle de communauté ressources-consommateurs dans lequel plusieurs traits évoluent. Le trait déterminant les stratégies d'acquisition des ressources (Adaptive Foraging, noté AF) par les consommateurs est notamment pris en compte. Dans ce contexte, la causalité réciproque écologie-évolution se matérialise par les effets que l'évolution de l'AF chez les consommateurs peut avoir sur les propriétés de la communauté (diversité, productivité, biomasse, stabilité), propriétés qui à leur tour influencent les dynamiques évolutives des ressources et des consommateurs.

Cet intérêt pour les propriétés de la communauté fait écho au programme de recherche "Biodiversity and Ecosystem Functioning" (BEF) qui cherche à conceptualiser les relations entre les différentes propriétés des écosystèmes, notamment les relations entre la diversité et la biomasse, la productivité et la stabilité (Hector et al., 1999; Loreau and De Mazancourt, 2013; Loreau et al., 2002; Tilman et al., 2014). Ce cadre BEF considère la relation diversité-stabilité comme généralement positive grâce à un effet "d'assurance". En effet, plus la diversité est grande plus il y a de chances que parmi les espèces constitutives de l'écosystème certaines soient résistantes et continuent d'assurer les fonctions de l'écosystème face à une perturbation. Cette relation positive a été en particulier explorée expérimentalement (Tilman and Downing, 1994; Tilman et al., 1997, 2006) et théoriquement (Loreau, 2010b; Loreau and De Mazancourt, 2013; Wang et al., 2021).

Cependant, la corrélation positive de la relation diversité-stabilité (ou sa notation équivalente complexité-stabilité) n'est pas universellement reconnue et fait toujours l'objet de débats et controverses (voir la méta-analyse de (Landi et al., 2018)). Les résultats non concordants obtenus ont été attribués à de multiples facteurs, comme la diversité des modèles utilisés ou encore le caractère flou inhérent à la notion de stabilité (Nikisianis and Stamou, 2016). La stabilité peut en effet être définie par des propriétés à l'échelle de l'écosystème (travaux propres au cadre BEF), mais également en se fondant sur des métriques centrées sur les extinctions d'espèces (Chen and Cohen, 2001; May, 1973). Ainsi, alors que des extinctions d'espèces ne vont pas forcément influencer les métriques de stabilité dans le cadre BEF grâce à l'effet d'assurance, elles vont générer de l'instabilité dans d'autres contextes.

Cependant, la prise en compte de l'AF - c'est-à-dire la capacité pour les consommateurs de

choisir activement comment ils dispensent leurs efforts de consommation entre les différentes ressources disponibles - dans des modèles où la mesure du nombre d'extinctions suggérerait une relation complexité-stabilité négative, inverse la nature de la relation qui devient positive (Beckerman et al., 2010; Heckmann et al., 2012; Kondoh, 2003a, 2006, 2010). L'AF intègre dans ce cas le fait que les consommateurs se détournent des espèces dont les densités deviennent très faibles, prévenant ainsi l'extinction de ces espèces. L'AF peut donc jouer un rôle important dans les propriétés des écosystèmes, au-delà des spécificités liés à la structure des modèles et des méthodes de mesure de la stabilité.

Or, la plupart des travaux du cadre BEF n'intègrent pas ce processus d'AF, et ceux cités précédemment comportent des faiblesses qui nous semblent importantes. En effet, les modèles utilisés ne considèrent pas la dynamique évolutive ni des traits déterminant les interactions entre les individus, ni de l'AF lui-même qui est simplement considéré comme étant présent et fixe chez toutes les espèces. Pour dépasser ces limites, nous proposons d'inclure l'évolution de l'AF par sélection naturelle. Ceci pourrait éventuellement conduire à la disparition de ce trait, notamment à cause des coûts entraînés, qu'ils soient métaboliques ou en temps de recherche des proies préférées ; ce qui ne peut pas se produire dans les modèles pré-cités. De plus, ces modèles écologiques déterminent a priori le nombre d'espèces et la connectivité du réseau généré (méthode en modèle de niche (Williams and Martinez, 2000)) et ne peuvent donc accéder à la relation entre AF et complexité (diversité). En fait, ces travaux proposent une relation complexité-stabilité positive en présence de l'AF, mais si on imagine une relation négative entre l'AF et la complexité alors la relation globale devient incertaine. Si l'AF réduit la complexité, et donc la stabilité, alors la conclusion devient l'inverse de celle proposée lorsque la complexité est fixée a priori, c'est-à-dire une déstabilisation des réseaux par l'AF.

Nous proposons ici de pallier ces faiblesses grâce à un modèle éco-évolutif ressources-consommateurs permettant d'explorer les interactions et causalités réciproques, au sein de la triade AF-diversité-stabilité. Dans ce modèle les ressources et les consommateurs ont la possibilité de se diversifier selon un trait de niche. Le trait de niche des ressources détermine leur capacité de charge, et peut prendre une valeur optimale. La compétition avec les autres ressources est également prise en compte selon le scénario suivant : plus des ressources ont des traits de niche similaires plus elles entrent en compétition entre elles. Le trait de niche des consommateurs détermine leur adaptation à l'exploitation des ressources. Plus un consommateur a un trait de niche similaire à celui d'une ressource, plus il est physiologiquement capable d'exploiter efficacement cette ressource. De plus, les consommateurs sont caractérisés par un second trait déterminant la manière dont ils organisent leur temps d'exploitation des différentes ressources. Ce trait définit le compromis entre un comportement d'AF et un comportement aléatoire (défini par une exploitation des ressources proportionnellement à leurs densités). Ainsi, notre modèle considère une dynamique évolutive de l'AF, ce qui nous évite de tirer des conclusions sur l'effet de l'AF dans des conditions où il n'évoluerait pas. Ainsi, l'AF influence la communauté (diversité, biomasse, productivité, stabilité) à condition qu'il ait pu évoluer par sélection naturelle dans cette communauté. Notre modèle permet également d'empêcher l'évolution de l'AF (en ne considérant pas de mutation), ce qui permet de comparer les propriétés d'une communauté selon que l'AF soit libre d'évoluer ou qu'il soit bloqué. De plus, notre modèle permet l'émergence de communauté, c'est-à-dire que nous ne définissons pas a priori le nombre d'espèces et la connectivité. Ces propriétés émergent de l'histoire évolutive de la communauté. Plus précisément, les conditions initiales fixent une seule ressource et un seul consommateur, ensuite la dynamique éco-évolutive permet la diversification de chaque niveau trophique par la mutation des traits de niche. Ainsi, l'évolution de l'AF peut avoir un effet sur la diversité de la communauté qui a son tour peut avoir un effet sur les pressions de

sélection en faveur ou au détriment de l'AF formant une causalité réciproque.

La plupart des modèles s'intéressant au cadre BEF et la relation diversité-stabilité sont des modèles écologiques, sans évolution. De ce fait, ils explorent les interactions des parties (les individus, ou les espèces) vers le tout qui est l'écosystème. Avec un modèle éco-évolutif nous explorons les interactions des parties sur le tout mais également les interactions inverses, du tout vers les parties, l'ensemble formant une causalité réciproque. Nous répondons ainsi aux incitations à développer une approche éco-évolutive du programme BEF (Fussmann et al., 2007; Thuiller et al., 2013).

Nos résultats montrent que la triade AF-diversité-stabilité est étroitement inter-connectée à travers une causalité réciproque entre écologie et évolution (Figure IV.1). Un premier résultat concerne l'évolution non systématique de l'AF, ce qui questionne son rôle dans la relation diversité-stabilité lorsque les conditions ne permettent pas son évolution. Nous montrons entre autre que l'évolution de l'AF dépend des interactions entre les consommateurs (notamment la compétition), ainsi que des caractéristiques de la communauté de ressources (notamment sa diversité). Par exemple, lorsque les conditions permettent une grande diversification des ressources, l'évolution de l'AF est favorisée. Effectivement, l'exploitation des ressources éloignées de l'optimum de niche et à faibles densités imposent un choix actif par les consommateurs d'aller exploiter ces ressources.

Nous montrons également que l'AF a un effet positif sur la diversité. En effet, les consommateurs ont besoin de l'AF pour exploiter les ressources éloignées de l'optimum de niche. Ainsi, ces consommateurs chez lesquels l'AF évolue vont exploiter ces ressources et exercer une pression évolutive qui va les forcer à s'éloigner d'autant plus de l'optimum de niche. Il se crée un équivalent de la "course à l'armement" dans laquelle d'une part les ressources sont sélectionnées pour avoir un trait de niche de plus en plus éloigné de l'optimum et d'autre part les consommateurs doivent accroître leur efficacité dans l'exploitation de ces ressources et sont sélectionnés en conséquence en faveur de l'AF. Le modèle admet une limite à cette course puisque la niche a une taille limitée au-delà de laquelle les ressources ne peuvent plus se développer. Donc la diversification des ressources, quand les conditions le permettent, entraîne l'évolution de l'AF, qui elle-même stimule la diversification des ressources de sorte qu'au final l'AF augmente la diversité qui renforce l'AF selon une causalité réciproque. Lié à cet effet sur la diversité, l'évolution de l'AF augmente aussi la complémentarité entre les consommateurs, mesurée par l'inverse du chevauchement de leur régime alimentaire. Effectivement lorsque les consommateurs ont un comportement d'exploitation des ressources aléatoire, ils consomment les ressources proportionnellement à leurs densités. Ainsi, tous les consommateurs passent la même durée à exploiter chaque ressource, et la différence entre leurs régimes alimentaires provient de leurs différences d'efficacité sur chacune. Avec l'AF non seulement les consommateurs choisissent activement l'organisation de leur temps mais en plus ils augmentent la diversité des ressources ce qui offre plus de choix à la constitution de régimes différents.

L'AF a également un effet sur la biomasse. Elle augmente la biomasse des consommateurs au détriment de la biomasse des ressources. Elle a aussi un effet non linéaire sur la productivité. Par ailleurs, nous observons une forte corrélation entre la variabilité des propriétés de la communauté et l'augmentation de l'AF moyen dans la communauté. Lorsque l'AF devient fort dans la communauté, la productivité peut aussi bien être plus forte que plus faible par rapport à celle d'une communauté caractérisée par les mêmes conditions mais pour laquelle l'AF est inhibée.

En outre, l'effet de l'AF sur la stabilité dépend de la perturbation subie. Nous avons considéré trois types de perturbation : une augmentation graduelle de la mortalité des consommateurs, un déplacement de l'optimum de niche à une vitesse croissante et un déplacement brutal de

l'optimum de niche à une distance croissante. Pour ces trois perturbations nous augmentons graduellement leur intensité jusqu'à extinction du niveau trophique des consommateurs. La mesure de stabilité se fait à partir de l'intensité maximale de la perturbation qu'une communauté peut supporter. Face à l'augmentation de la mortalité l'AF n'a pas d'effet notable, c'est-à-dire que les deux communautés réagissent de façon similaire : celle où l'AF a évolué et celle partageant les mêmes conditions mais sans évolution de l'AF (pas de mutation du trait). Le point important est cependant la régression de l'AF avec l'accroissement de la perturbation, lorsque ce dernier a la possibilité d'évoluer, de sorte que face à la perturbation maximale supportable, les deux communautés - avec et sans évolution de l'AF - sont pratiquement similaires car l'AF a pleinement régressé là où il avait évolué. Nous soulignons ici qu'avec une approche écologique où l'AF n'aurait pas de dynamique évolutive le résultat serait différent et conclurait à un effet négatif de l'AF car celui-ci n'aurait pas pu régressé. C'est grâce à sa capacité d'évolution, et en l'occurrence de régression, que l'AF n'a pas d'effet sur la stabilité face à cette perturbation.

Face à la deuxième perturbation pour laquelle l'optimum de niche dérive à une vitesse croissante l'AF a un effet négatif sur la stabilité. À cause du déplacement de la niche, la communauté de ressources est contrainte de suivre l'optimum de niche entraînant une diminution de la diversité, de sorte que l'AF est défavorable pour les consommateurs. L'AF régresse avec l'augmentation de la perturbation mais il ne régresse pas assez vite et finalement a un effet négatif sur la stabilité de la communauté.

Pour la dernière perturbation, consistant également en un déplacement de l'optimum de niche mais cette fois-ci par un "saut" brutal de plus en plus distant, l'AF a un effet positif sur la stabilité. De manière inattendue, l'effet est direct et indirect au travers de l'effet sur la diversité. En transposant la diversité de la communauté avec évolution de l'AF à la communauté sans AF, cette dernière a une stabilité équivalente à la communauté avec AF. Autrement dit, l'effet positif de l'AF s'explique en premier lieu par son effet positif sur la diversité. En fait, la plus grande diversification de la communauté permet une plus grande proximité des ressources et des consommateurs (dans l'espace des traits de niche) par rapport à l'optimum de niche après perturbation, et ainsi de supporter un saut de l'optimum de niche à une distance supérieure par rapport à une diversification moindre. Cependant, en effectuant la manipulation inverse, c'est-à-dire en attribuant la faible diversité de la communauté sans AF à la communauté avec AF, cette dernière atteint une stabilité intermédiaire entre les deux communautés. L'AF a donc également un effet positif direct, indépendant de la diversité, face à cette perturbation.

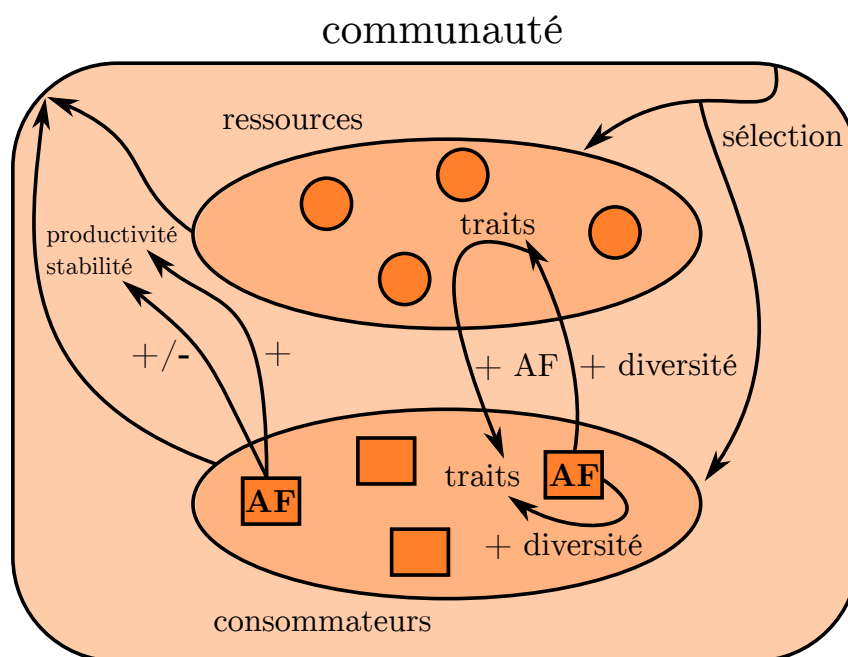


Figure IV.1 – Synthèse des interactions multiples, et causalités réciproques, liées au couplage entre l'évolution de l'AF et la dynamique écologique entre ressources et consommateurs. Nous renvoyons le lecteur vers le corps de texte pour les détails.

IV.2 Article : The evolution of adaptive foraging mitigates the biodiversity-ecosystem functioning relationships

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IV.2.1 Abstract

Diversity among ecosystems generally enhances their productivity, stability and more generally their functioning. This positive relationship between biodiversity and ecosystem functioning (BEF) may result from various mechanisms such as interspecific complementarity or the greater use of limiting resources through Adaptive Foraging (AF). However, those mechanisms may be absent in some ecosystem or they can evolve by natural selection under environmental disturbance. In this paper, we first investigate under which conditions the AF behavior evolves within ecosystems. Furthermore, we aim to disentangle the impacts of AF on diversity and stability of ecosystems under environmental disturbances. To tackle those issues, we develop an eco-evolutionary model of resource-consumer community. Resources and consumers can diversify within a niche and consumers can modify their foraging strategy from random foraging to adaptive foraging. We first show that AF emerges by natural selection only when the environment allows for high resource diversity. When the AF evolves, we show that it promotes diversity among all trophic levels. However, it has a mixed effect on biomass and productivity. Although it enhances consumer biomass, it reduces resources biomass. And a strong AF behavior reduces productivity while a moderate AF increases it. Finally, we show that the nature of the disturbance modifies the effect of AF on stability. Under sudden environmental disturbances, the evolution of AF directly enhances stability or indirectly through its positive effect on diversity. However, under gradual changes, the AF has detrimental effects on stability and it is not stable because it disappears among the community as the intensity of change increases.

Keywords: biodiversity ecosystem functioning, stability-diversity relationship, adaptive foraging, eco-evolutionary dynamics

Author contributions: SI, JG and LL originally formulated the project; SI, JG and LL developed the model; LL and OG performed the numerical analyses; all authors participated in writing the manuscript

IV.2.2 Introduction

In a context of global change and biodiversity loss, knowledge of ecosystem properties and their relationship with biodiversity is a major issue, particularly the relationship between biodiversity and ecosystem stability. It is in this context that the "Biodiversity Ecosystem Functioning" (BEF) research program has been deployed to describe the interactions between biodiversity and ecosystem properties ([Hector et al., 1999](#); [Loreau, 2010a](#); [Loreau and De Mazancourt,](#)

2013; Loreau et al., 2002; Tilman et al., 2014).

The BEF framework proposes that diversity and stability are positively related, i.e. greater diversity leads to greater stability. Indeed, the insurance hypothesis, or portfolio effect, suggests that when an ecosystem faces a disturbance, a high diversity of species ensures a greater chance that some of them will be resistant to this disturbance and will continue to ensure the ecosystem's functions (Figge, 2004; Tilman, 1996). Conversely, when diversity is poor, it is enough for the disturbance to affect the few species present for the whole ecosystem to be strongly impacted.

Prior to the BEF framework, the relationship between diversity and stability was already the source of considerable debate. In particular, (May, 1973, 1972) proposed a negative relationship based on a modelling approach, whereas the classic studies were rather in favour of a positive relationship (Elton, 1958; MacArthur, 1955). Ever since, many studies have focused on the diversity-stability relationship with contrasting results, see (Landi et al., 2018) for a review. Besides, the relationship with diversity, the food web stability has been widely explored. In particular, many studies have focused on the disturbance propagation along a food web (Dunne et al., 2002; Eklöf and Ebenman, 2006; Sole and Montoya, 2001). Indeed, if within a food web a species sees all the species it consumes disappear, then it will also disappear, which constitutes a secondary extinction.

However, these works generally use fixed interaction food webs, i.e. the interactions are defined at the generation of the food web and do not change afterwards, according to the niche model method (Williams and Martinez, 2000). This lack of possible variability in the system prevents any adaptation in the system, which is a strong assumption. Indeed, it is thus considered that if a species sees its resources or its prey disappear, then it will also disappear without being able to redirect its interactions towards other species. However, it is clear in behavioral ecology that a large diversity of species show adaptive foraging (AF) abilities, i.e., an active adjustment of their foraging efforts to the various resources available (Dill, 1983; Owen-Smith, 2008). In a food web model this means the ability of species to actively modulate the intensity of their interactions with other species.

Indeed, many studies highlight the importance of AF in the relationship between diversity and stability (Beckerman et al. (2010); Heckmann et al. (2012); Kondoh (2003a,b); Mougi (2016); Uchida and Drossel (2007)). Using the robustness (number of species extinction) as a measure of stability, they show a positive effect of diversity on stability once AF is present. The same type of ecological models admit a negative relationship between stability and diversity in the absence of AF (Chen and Cohen, 2001; May, 1973). Thus, AF has an effect on stability. However, those works do not allow to explore possible effects of AF on diversity, because in those models diversity is defined a priori. Since there is a relationship between diversity and stability, it seems that not taking into account the possible role of AF on diversity could bias the results. For example, one can imagine that if AF has a negative effect on diversity, and the diversity-stability relationship is positive, then one could conclude that AF has a negative effect on stability, which is the opposite of what is established by (Beckerman et al. (2010); Heckmann et al. (2012); Kondoh (2003a,b); Uchida and Drossel (2007)).

A way to disentangle this issue is to use eco-evolutionary models which capture the food web properties, including diversity, emerging from species interactions and evolution processes (Allhoff et al., 2015; Aubree et al., 2020; Girardot et al., 2020; Loeuille and Loreau, 2005). However, only few of those studies take into account adaptive foraging (Drossel et al., 2001; Guill and Drossel, 2008).

In addition, up to our knowledge no ecological or eco-evolutionary models on food web allows AF to evolves. In those studies, AF is fixed in the sense that there are no evolutionary dynamics

of this trait. Those studies implicitly assume that AF is an evolutionary advantageous and stable strategy. However, AF implies actively searching and selecting resources, at the expense of time and energy. Thus, it is not certain that AF evolves systematically by natural selection under all conditions.

Therefore, these considerations call for re-exploring the relationships between diversity and stability in an eco-evolutionary context where AF has a true evolutionary dynamics and diversity is an emergent property of the eco-evolutionary dynamics. This need to include eco-evolutionary dynamics in the development of the BEF framework has already been advocated (Fussmann et al., 2007; Loreau, 2010b; Thuiller et al., 2013). Indeed, primarily to question the relationship between diversity and ecosystem properties one can ask how diversity emerges and what feedbacks may exist between diversity and other properties when evolution is taken into account. Indeed, evolution can be fast enough to share a time scale close to that of ecological dynamics, so that feedbacks exist between evolutionary and ecological dynamics (Hairston Jr et al., 2005; Thompson, 1998). Thus, we propose an eco-evolutionary context where the evolutionary and ecological dynamics interact in order to understand the links within the AF-diversity-stability triangle. In particular, we seek to answer the following questions (Figure IV.2):

- To what extent is AF evolutionary adaptive ?
- When AF evolves, what are its effects on the emergent properties of the community: biomass, productivity and diversity ?
- What is the effect of AF on stability ? Furthermore, after exploring its effect on diversity, is its effect on stability direct or indirect (i.e. through diversity)?

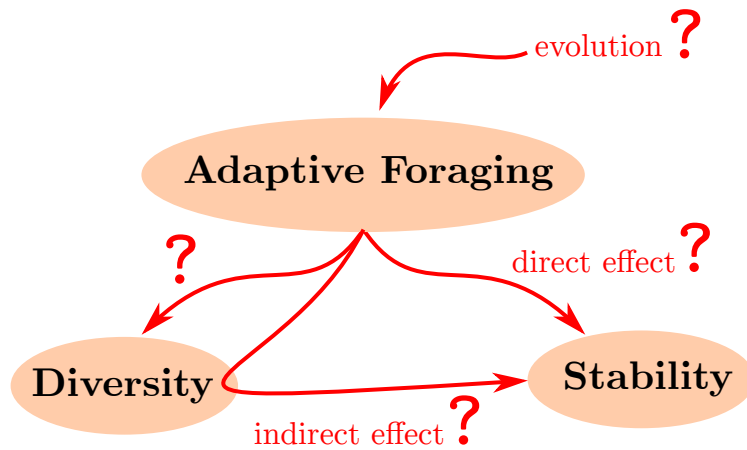


Figure IV.2 – The main interactions explored by the study. We question the evolution of AF through natural selection, and then its effect on community diversity and stability. We distinguish whether the effect of AF on stability is directly related to AF or whether it is related to the effect of AF on diversity.

IV.2.3 Model and methods

Consumer-resource model

We focus on a system consisting of resources and consumers characterised by a niche trait and foraging strategies characterized by a foraging trait. Resources can diversify in the ecological niche thanks to mutation, natural selection and competition. Consumers need resources to survive in the ecological niche. Their consumption depends on their niche trait as well as their foraging strategy ranging from random foraging to adaptive foraging. Our deterministic model describe the evolution in time and trait space of the resources density (r), the consumer density (c) and the foraging strategy (ϕ) of the consumers under mutations, selection and interactions. We write:

$$\partial_t r = r \left(\overbrace{g \left(1 - \frac{r_{eff}}{K(y)} \right)}^{\text{resource growth}} - \overbrace{F_r[r, c, \phi]}^{\text{resource consumption}} \right) + \overbrace{\mathcal{M}_y(r)}^{\text{niche trait mutations}} \quad (\text{IV.1})$$

$$\partial_t c = c \left(\overbrace{F_c[r, \phi]}^{\text{resource absorption}} - \overbrace{(d + I\rho_c(t))}^{\text{maintenance cost competition}} \right) + \overbrace{\mathcal{M}_x(c)}^{\text{niche trait mutations}} + \overbrace{\mathcal{M}_z(c)}^{\text{AF trait mutations}} \quad (\text{IV.2})$$

The components of the model and the foraging strategy model for ϕ are described below.

Resource-consumer interactions and niche traits. In the absence of consumers, resources grow logistically depending on their niche trait y which defines their carrying capacity $K(y)$. We fix the centre of niche at $y_0 = 0$, the optimal trait where the carrying capacity is maximal K_0 . The carrying capacity follows a Normal distribution of variance σ_K which describes the niche width (see Figure IV.3a). Inside the niche, the resources face competition with resources in their trait neighbourhood $r_{eff}(t, y) = \int C(|y - y'|)r(t, y')dy'$ (Dieckmann and Doebeli, 1999). The competition strength $C(|y - y'|)$ between two resources of trait y and y' only depends on the distance between their niche traits $|y - y'|$. The competition kernel C is a centered Normal distribution with variance σ_C characterizing the average neighbourhood around each trait (see Figure IV.3b).

In the presence of consumers, resources are exploited at a rate $F_r(r, c, \phi)$ while consumers density increases thanks to the resource absorption $F_c(r, \phi)$. The interactions between resource of trait y and consumer of trait x also depend on the resource-consumer affinity described by the interaction kernel $\Delta(x, y)$. The interaction strength only depends on the distance between traits and it follows a centered normal distribution of variance σ describing the generalist degree of consumers (see Figure IV.3c). We choose a Holling type II functional response to describe those interactions. We write

$$F_r[r, c, \phi](t, x, y) = \iint \frac{b\phi(t, x, y, z)\Delta(x, y)c(t, x)}{1 + s(z)b \int \phi(t, x, y, z)\Delta(x, y)r(t, y)dy} dx dz \quad (\text{IV.3})$$

$$F_c[r, \phi](t, x, y, z) = \alpha \int \frac{b\phi(t, x, y, z)\Delta(x, y)r(t, y)}{1 + s(z)b \int \phi(t, x, y, z)\Delta(x, y)r(t, y)dy} dy \quad (\text{IV.4})$$

where α is the conversion coefficient, b the extraction coefficient and $s(z)$ the searching time which depends on the foraging trait z as explained below.

Moreover, consumer density decreases due to mortality d and the competition between all consumers at a rate $I\rho_c$ where $\rho_c(t) = \iint c(t, x, z)dx dz$ is the total consumer biomass.

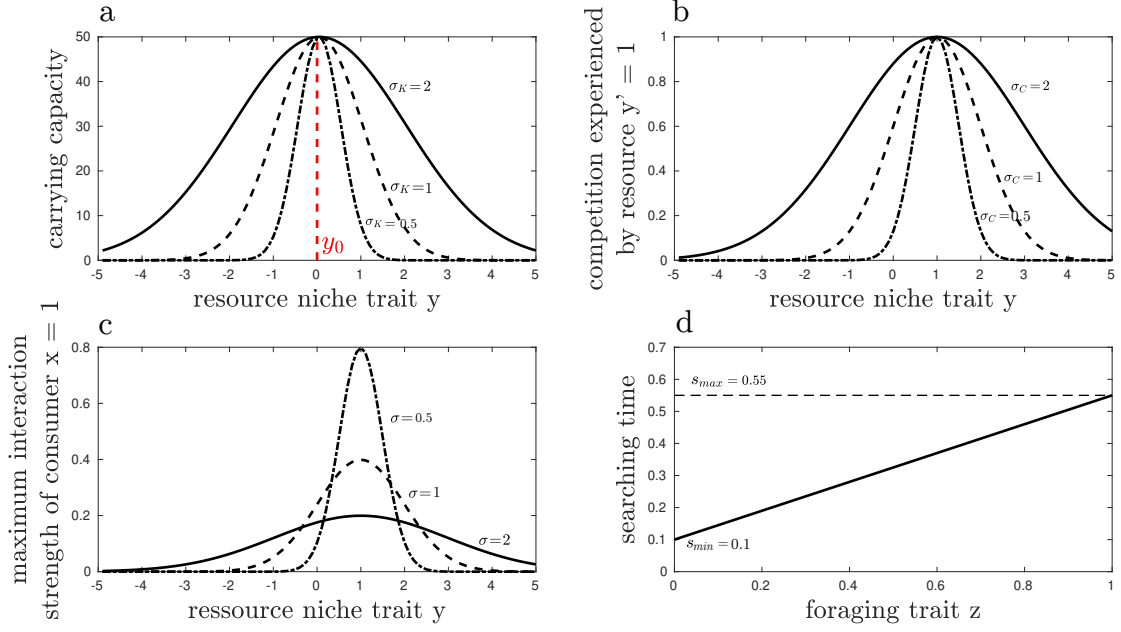


Figure IV.3 – a) Carrying capacity $K(y)$ of resources for various niche width $\sigma_K = \{0.5, 1, 2\}$. The niche centre fixed at $y_0 = 0$ corresponds to the maximal carrying capacity. b) Competition kernel K_C for various neighbourhood sizes $\sigma_C = \{0.5, 1, 2\}$ between a focal resource $y' = 1$ and all resources according to their niche trait y . c) Interactions kernel for various generalist degree $\sigma = \{0.5, 1, 2\}$ between a focal consumer $x = 1$ and all resources according to their niche trait y . d) Searching time according to the foraging trait z . For panels a-c, the values of -5 and 5 as niche trait limits are arbitrary. The choice of negative and positive values on either side of the niche centre is for clarity.

Foraging strategies and adaptive foraging trait The interaction between consumers and resources not only depends on the match between their niche traits but also on the way consumers distribute their foraging efforts. Since consumers have a finite time available for resources acquisition, they share this time between the different resources available. Consumers can choose different strategies to organize their foraging efforts $\phi(t)$: i) Random Foraging (ϕ_{RF}), the consumer randomly forages its environment without selecting resources or ii) Adaptive Foraging (ϕ_{AF}), the consumer uses adaptive foraging by actively searching for the resources maximizing its energy gain. The consumer foraging strategy depends on its foraging trait $z \in [0, 1]$ which corresponds to the proportion of its foraging time spend using AF strategy. Thus, the resulting consumer efforts are

$$\phi = z\phi_{AF} + (1 - z)\phi_{RF}.$$

The RF effort ϕ_{RF} is directly proportional to the resource density

$$\phi_{RF}(t, x, y) = \frac{r(t, y)}{\int r(t, y') dy'} \quad (\text{IV.5})$$

While the AF effort ϕ_{AF} evolves over time according to the following dynamics

$$\begin{aligned} \partial_t \phi_{AF}(t, x, y, z) = l_\phi c(t, x, z) & \left(\int r(t, y) \phi_{AF}(t, x, y', z) [u(t, x, y, z) - u(t, x, y', z)]_+ dy' \right. \\ & \left. - \int r(t, y') \phi_{AF}(t, x, y, z) [u(t, x, y', z) - u(t, x, y, z)]_+ dy' \right) \end{aligned} \quad (\text{IV.6})$$

where $u(t, x, y, z)$ represents the potential gain of a consumer of trait (y, z) on a resource of trait x , i.e. if the foraging efforts are only on this resource:

$$u(t, x, y, z) = \frac{b\Delta(x, y)r(t, y)}{1 + s(z)b \int \phi(t, x, y, z)\Delta(x, y)r(t, y)dy} \quad (\text{IV.7})$$

The AF dynamics assumes that a consumer is able to compare the gains received from exploiting resource y with the gains received from other resources y' according to the effort it puts into each resource. For instance, if the potential gain u is greater on resource y than on resource y' , the consumer increases its foraging effort on resource y . Moreover, the increase is weighted by the density of resource y and the effort it has put on resource y' up to now. The more effort the consumers puts into a resource that is not optimal, the faster it will adjust its effort to the better resource.

However, we consider that the comparison between resources takes time for the consumer, so the adjustment of its efforts is not instantaneous. The parameter l_ϕ describes the speed at which it adapts its effort.

Moreover, the adaptive foraging induces an increase on the searching time, $s(z) = s_{min} + z(s_{max} - s_{min})$, because the consumer has to search for the targeted resources (Figure IV.3d).

Mutation of traits and diffusion In our model, we assume that the ecological and evolutionary dynamics occurs at the same time scale. Thus, the niche traits and the foraging traits evolves due to mutations. Unlike the adaptive dynamic framework where a mutant phenotype is introduced only if its invasive fitness is positive (Geritz et al., 1998), we constantly introduce mutants through niche trait diffusion $\mathcal{M}_y(r)$ and $\mathcal{M}_x(c)$ as well as AF trait diffusion $\mathcal{M}_z(c)$ when AF evolves

$$\mathcal{M}_x(c)(t, x, z) = \frac{U\sigma_m^2}{2}\partial_x^2 c(t, x, z), \mathcal{M}_y(r)(t, y) = \frac{U\sigma_m^2}{2}\partial_y^2 r(t, y) \text{ and } \mathcal{M}_z(c)(t, x, z) = \frac{U\sigma_m^2}{2}\partial_z^2 c(t, x, z)$$

where U is the frequency of mutation and σ_m^2 is the mean effect of a mutation. The ecological dynamics selects for the mutants that persist. Thus, we assume that foraging traits and niche traits evolve separately, there are only additive effects of mutations, no epistasis.

Numerical analysis of the model

Community emergence The eco-evolutionary dynamics of the model allows for the diversification of resources and consumers, thanks to mutation, until a community emerges (Figure IV.4a). In the initial condition, we consider a single resource placed in the centre of the niche ($y = y_0$) and a consumer at the same position ($x = y$). Since one of the objectives is to evaluate whether adaptive foraging can evolve by natural selection, the initial consumer has a purely random foraging strategy ($z = 0$).

Note that although we consider continuous traits, the numerical analysis requires them to be discretised. Therefore, community emergence takes as input parameter the maximum number of niche trait values and foraging trait values. Typically the numerical simulations are performed with 31 values of niche trait and 11 values of foraging trait.

Community proxies To assess the effect of adaptive foraging on the community we measure community-level proxies: biomass, productivity and diversity. Biomass proxies are the total biomass of resources and the total biomass of consumers. For diversity we use functional diversity indices: the functional dispersion FDis (Laliberté and Legendre, 2010) and the functional regularity FRO (Mouillot et al., 2005). The productivity is measured as the

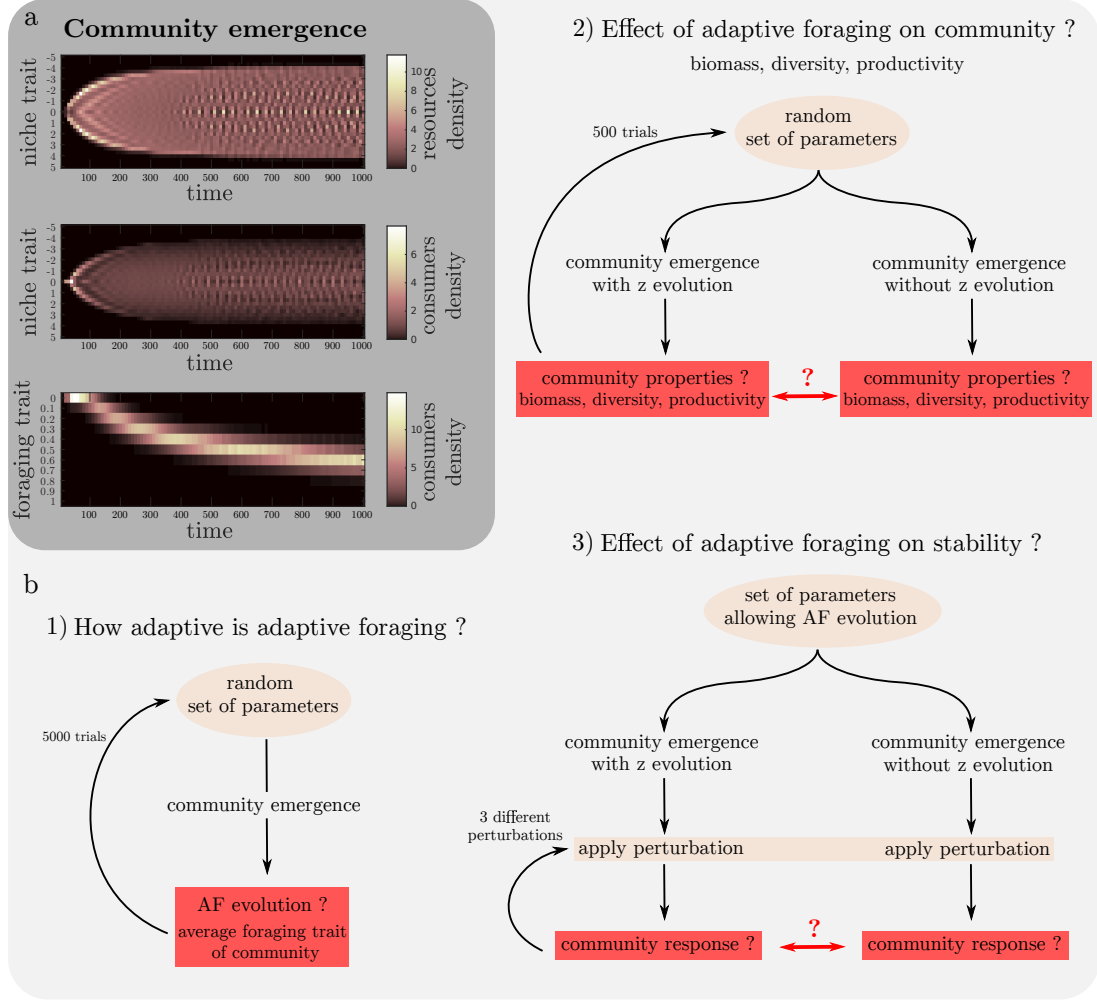


Figure IV.4 – a) Eco-evolutionary dynamics of a resource-consumer community starting from an initial condition with a resource and a consumer at the niche centre, and a purely random foraging strategy. Resource density ($r(t, y)$) (top panel), consumer densities according to niche trait $\int c(t, x, z) dz$ (centre panel) and foraging trait $\int c(t, x, z) dx$ (bottom panel). b) General structure of the study. 1) To what extent adaptive foraging can evolve through natural selection, 2) what are the effects of the evolution of adaptive foraging on community biomass, diversity and productivity and 3) what is the effect of the evolution of adaptive foraging on stability.

total flow of biomass from resources to consumers.

Overall scheme Our numerical analysis is threefold (Figure IV.4b). First, we test how adaptive foraging can be adaptive from the perspective of natural selection. We generate 5000 communities associated to different set of parameters ($\sigma, \sigma_K, s_{max}, d, I, g$) and then we perform a global sensitivity analysis by Partial Rank Correlation Coefficients (PRCC, [Saltelli et al. \(2004\)](#)) on this sample. We focus on the mean value of the foraging trait in the community $\bar{z}$ defined as

$$\bar{z}(t) = \iint z \frac{c(t, x, z) dx dz}{\iint c(t, x', z') dx' dz'} \quad (\text{IV.8})$$

In this way, we highlight the influence of each parameter on the evolution of adaptive foraging, and thus the conditions that allow or prevent its evolution. Secondly, we choose 500 parameters values leading to persistence of resource-consumer community but with various mean trait foraging in the community. We compare those emerged communities with a community resulting from our model without foraging evolution ($\mathcal{M}_z(c)$ is set to 0 in (IV.1) and the fixed foraging trait in the community is $z = \bar{z}$, the mean trait of the compared community). We then compare proxies of the communities to measure the effect of adaptive foraging evolution. The final step is to assess the effect of the evolution of adaptive foraging on the stability of the community. We use a single set of parameters to ensure the evolution of strong adaptive foraging (mean foraging trait $\bar{z} \approx 0.9$) and compare the responses to perturbations between the community with adaptive foraging evolution and the community with inhibited evolution.

Adaptation to changing environment Because of the eco-evolutionary dynamics induced by our model, we cannot use classical stability metrics of ecological studies (Domínguez-García et al., 2019). For instance, the robustness metric is based on the number of species that disappear after a disturbance (Kondoh, 2006, 2010). This metric is not suitable for our model because evolution can produce a constant turnover of species and can quickly replace a species that would become extinct. To maintain our community point of view, we investigate three type of perturbations: a) gradually increasing consumer mortality, c) brutally changing niche centre and b) gradually moving niche centre at constant speed. For each perturbation, we measure the critical perturbation intensity leading to extinction of consumers.

In the first perturbation, we measure the maximal mortality rate d the community can withstand (Figure IV.5a).

In the second, we induces a shift of the niche centre y_0 at constant speed $c > 0$, $y_0(t) = ct$. We measure the critical speed above which the community cannot keep pace with the niche shift (Figure IV.5b).

The last perturbation is an abrupt displacement of the niche centre from y_0 to $y_0 + \delta$, $\delta > 0$. We measure the maximal jump size of the niche centre above which community cannot adapt (Figure IV.5c).

IV.2.4 Results

How adaptive is adaptive foraging

To investigate under which conditions adaptive foraging (AF) is evolutionary adaptive we conduct a PRCC analysis on the six main parameters influencing the evolution of AF (Figure IV.6a). If the PRCC is positive, the parameter tends to promote AF, while it tends to inhibit AF for negative PRCC.

We show that all six parameters can play a significant role in the evolution of adaptive foraging (Figure IV.6a), so that depending on the conditions AF will not necessarily evolve. Thus, the conditions inhibiting the evolution of AF are: intrinsically specialised consumers (small σ), a narrow niche (small σ_K), a strong searching time trade-off (large s_{max}), a low intrinsic consumers mortality d , low inter-consumer competition (small I) and low resource growth (small g).

The effect of the intensity of the trade-off is rather obvious, but the effects of the other parameters require a little more thought. For instance, the promotion of AF when consumers are intrinsically generalists (large σ) is not intuitive. However, when consumers are intrinsically

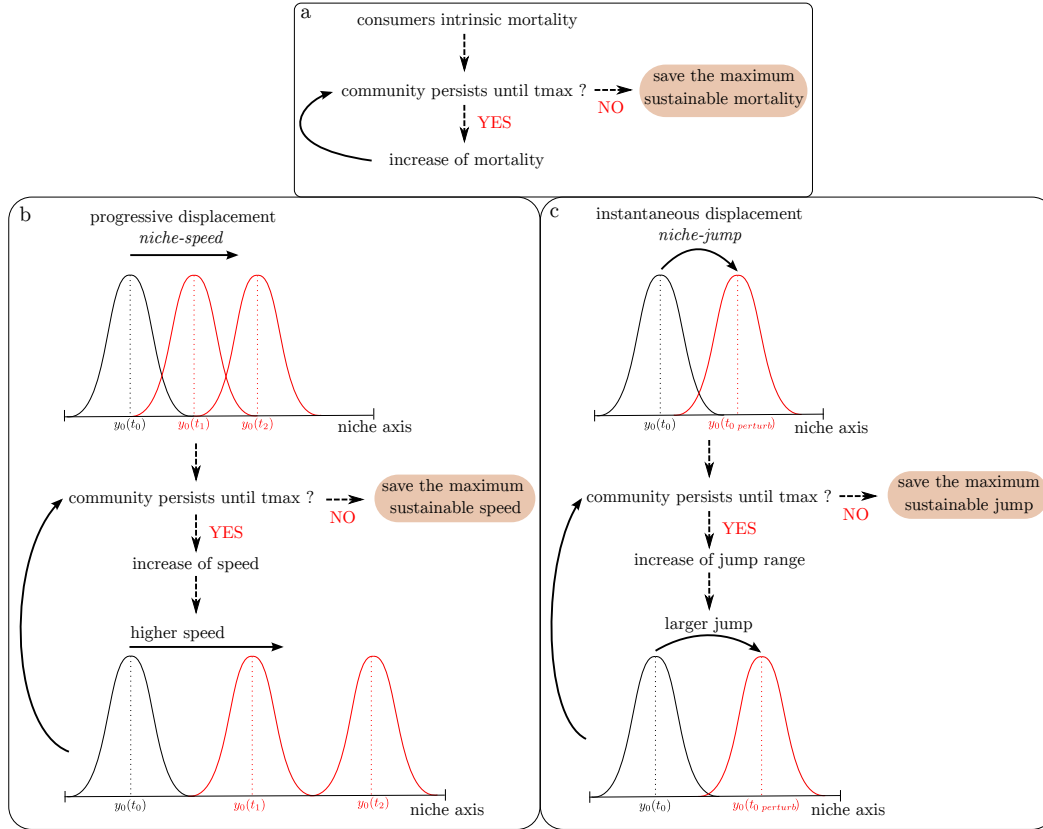


Figure IV.5 – Schematic representation of the three perturbations: a) Gradually increasing mortality perturbation consists of successively increasing the mortality of consumers until all consumers are extinct. b) Niche-speed perturbation consists of a progressive displacement of the niche. The speed is gradually increased until all consumers are extinct. c) The niche-jump perturbation consists of an instantaneous displacement of the niche centre to a certain range. The range of the jump is gradually increased until the consumers are extinct.

generalists they have a high capacity to extract all resources, so if they simply focus on resource abundance they will quickly over-exploit the most abundant resources. Thus, when consumers have an intrinsic generalist capacity they actually benefit more from being each specialised on a few resources through AF.

The effect of the size of the niche could be anticipated, as when the niche is narrow (small σ_K) there is little diversity with only a few resources and a few consumers, all with close niche traits. Thus, there is no interest in considering the match between the niche traits of resources and consumers, therefore the AF is detrimental.

Regarding the mortality of consumers (d), as well as their competition, it is possible to conclude that the more difficult the conditions are for consumers, the more the AF is favoured. In general, it can be assumed that when conditions are difficult consumers can no longer simply exploit resources in proportion to their abundance (but see further that this is no longer true when conditions reach the limits of viability).

Finally, when resources grow rapidly (large g), those that are far from the niche centre become interesting to exploit for adapted consumers. These consumers then use AF to exploit these resources (see Figure IV.6b). Indeed, since the densities of these resources are lower than those of resources close to the niche centre, AF is essential in order to focus foraging efforts on them.

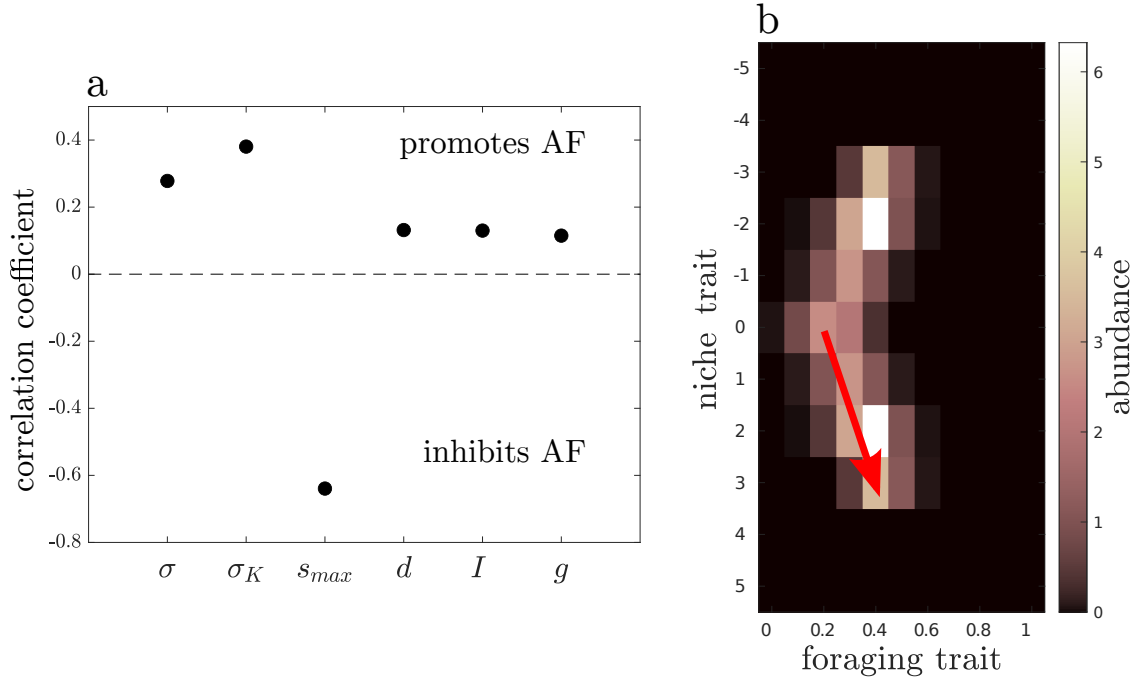


Figure IV.6 – a) PRCC analysis on the mean foraging trait of the community for the six main parameters: σ , σ_K , s_{max} , d , I and g . The proxy targeted by the analysis is the evolution of adaptive foraging, expressed by the average value of the foraging trait at the community level. b) Example of a community with a diversity of foraging trait values. The red arrow indicates the propensity of consumers to adopt a foraging strategy with higher proportion of adaptive foraging when they are far from the niche centre.

Moreover, not all consumers in a community have the same adaptive foraging intensity (Figure IV.6b). In fact, the position of consumers in the niche determines their foraging strategy. Consumers furthest from the niche centre use AF while consumers in the centre of the niche have a more random foraging strategy, and therefore focus on the most abundant resources in the niche centre.

Effect of adaptive foraging on community

First, we show that in general the evolution of AF is accompanied by a gain in consumers biomass on average, at the expense of a decrease in resources biomass (Figure IV.7a). By measuring the niche overlap between consumers we show that the gain in biomass of consumers is explained by a complementarity effect (Figure IV.12). Indeed, the presence of adaptive foraging in the community decreases the niche overlap between consumers (Figure IV.12a), i.e. consumers use resources differently, thus increasing the complementarity between them. Moreover, the diversity of foraging strategies, i.e. different values of foraging trait, increases complementarity even more (Figure IV.12b).

However, some communities where AF evolves have lower consumer biomass than communities where AF is inhibited. Indeed, the variability of biomass increases with the mean foraging trait of the community.

Secondly, AF has a positive effect on consumer and resource diversities, both on functional dispersion (Figure IV.7b) and functional regularity (Figure IV.13). Although the variability of diversity increases with mean foraging trait, the difference of communities without AF is

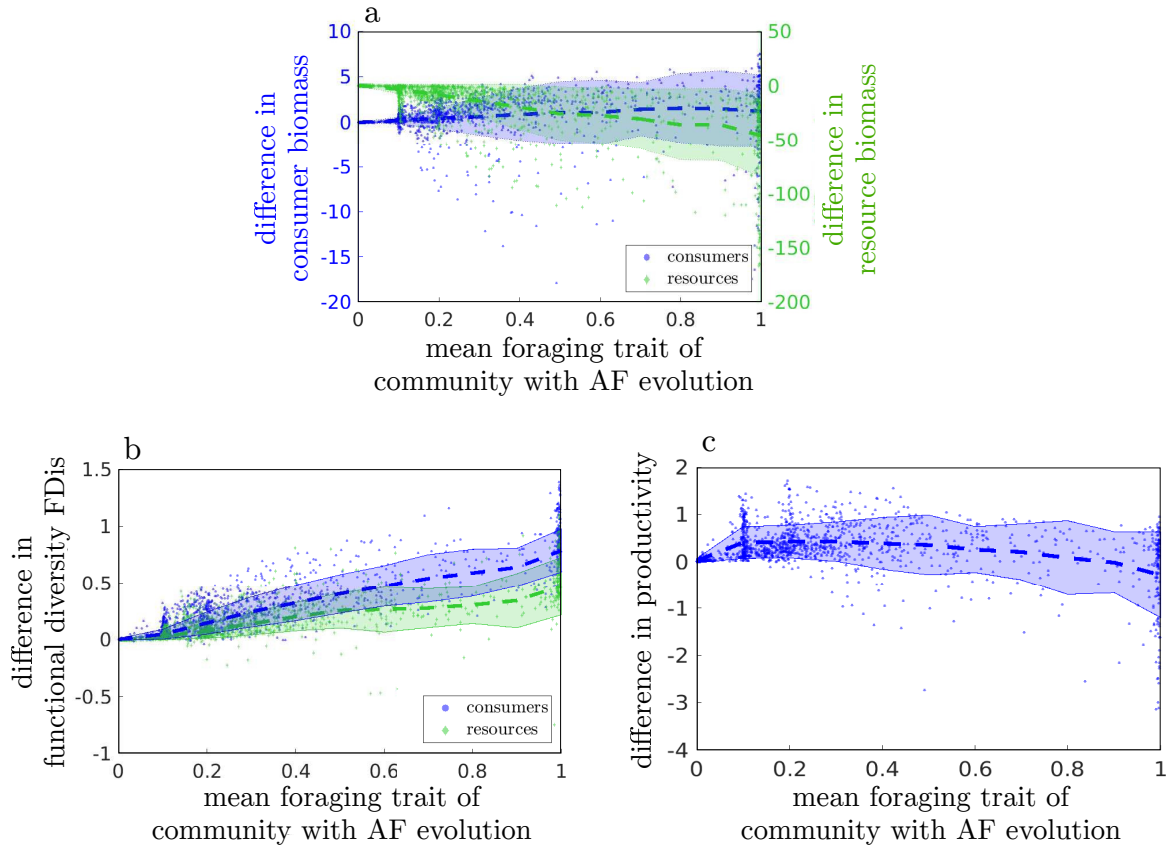


Figure IV.7 – Difference in the three proxies (biomass, diversity, productivity) between communities where the evolution of AF is allowed by the diffusion of the foraging trait and communities where the evolution of AF is inhibited. a) Difference in biomass. b) Difference in functional dispersion. c) Difference in productivity. For all panels, differences are made from 500 pairs of communities that emerged with 500 different parameter sets. The dotted lines represent the mean and the areas the standard deviation

almost always positive with rare exceptions. Thanks to AF, consumers have the ability to impose a superior consumption pressure on resources that are far from the centre of the niche than consumers without AF. This consumption pressure leads to an eco-evolutionary dynamics comparable to an arms race where resources have a selection pressure to grow towards the limits of the niche to escape the consumers. Moreover, the consumption of resources that are far from the niche centre reduces the competition between them, which allows the growth of resources even further from the centre.

Finally, the relationship with productivity (i.e the flow of biomass from resources to consumers) seems more complex because non-linear (Figure IV.7c). Thus, when the community with AF evolution has a rather low mean foraging trait, although higher than 0, there is a consequent productivity gain compared to the community without AF. However, above a mean foraging trait of about 0.4, the increase in AF within communities results in a productivity gain that becomes smaller, until it is slightly negative on average for mean foraging trait close to 1. Interestingly, with strong AF there is an increase of variability of productivity. Thus, although the negative effect on average, among the communities with strong AF some have a great gain in productivity and others a great deficit.

Relationship between diversity, adaptive foraging and stability

Now, we aim to understand the effect of AF on the stability of community. Since Stability and diversity are often linked, we aim to disentangle the direct effect of AF on stability from its indirect effect through diversity.

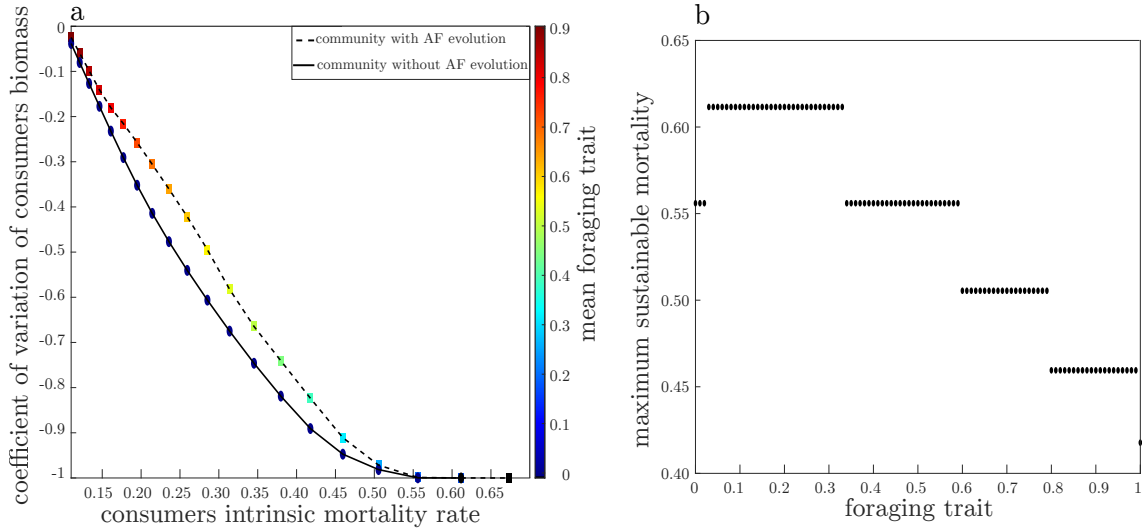


Figure IV.8 – Communities with and without AF evolves similarly under consumer mortality increase. a) Responses of both communities (with and without the AF evolution) expressed as the coefficient of variation of consumer biomass. A negative coefficient of variation indicates a decrease in biomass, the threshold value of -1 corresponds to an extinction of all consumers. The coloured gradient indicates the mean foraging trait inside the community. b) Response of the monospecific community according to the value of the single foraging trait allowed. In this case the evolution of the foraging trait is inhibited.

Regression of AF prevents the direct negative effect of AF on the stability of community facing mortality increase

By applying the perturbation of increasing mortality until consumers extinction we show that the community with AF evolution reacts similarly to the community without AF evolution. Both communities lose their consumers at close mortality values (Figure IV.8a). After each increase in consumers mortality the two communities reach a new equilibrium with a lower and lower consumers biomass. Thus the coefficient of variation of the biomass follows a monotonic decrease until it reaches the limit value of -1 corresponding to a zero consumers biomass. Moreover, under this mortality perturbation, consumers in the community with AF evolution gradually reduce their foraging trait.

However, by examining the response of monospecific communities in terms of foraging trait and without evolution, we show that the greater the foraging trait of consumers the smaller the maximum mortality they can sustain (Figure IV.8b). When the mortality increases the consumers cannot persist far from the niche centre where resources have a low growth rate. This leaves only consumers close to the niche centre, where it is better to have a random foraging strategy. Thus, when consumers are forced to do AF in a niche centre they pay the trade-off due to AF while having no gain from AF and eventually the maximum mortality they can sustain is lower than consumers not using AF. Hence, we show a direct negative effect of

AF.

In fact, this negative effect explains why under a critical increase of mortality the community with AF evolution is very similar to the community without AF evolution. As mortality increases, consumers gradually reduce their adaptive foraging until an average foraging trait close to 0 (Figure IV.8a, color gradient). Thus, AF has a direct negative effect on community stability in the face of increase mortality, but with AF evolution the negative effect only causes AF regression and community stability with evolution is not impacted.

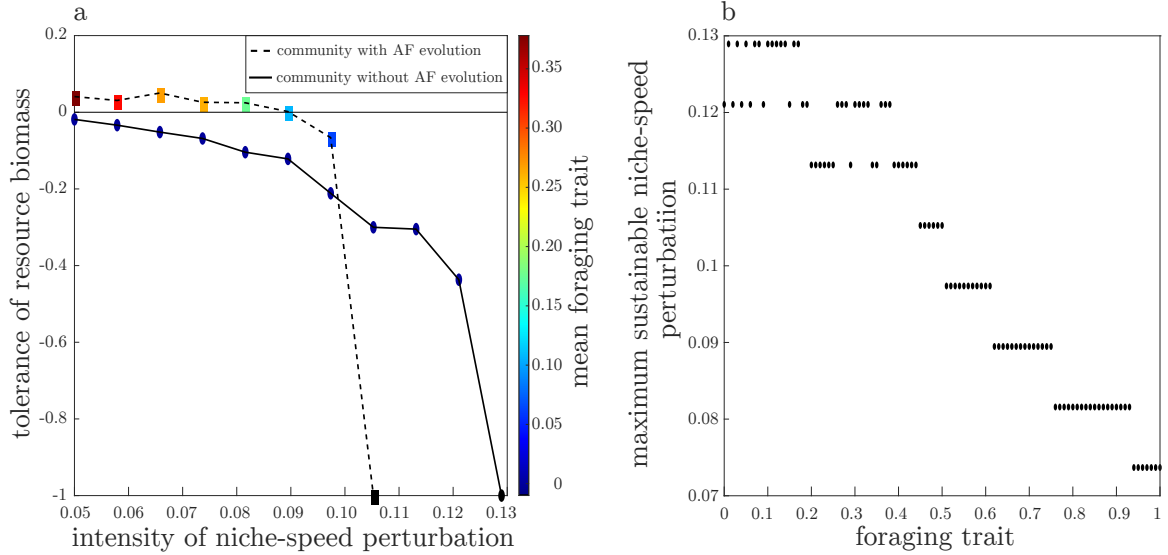


Figure IV.9 – Results of the niche-speed perturbation. a) Responses of both communities (with and without the AF evolution) expressed as the coefficient of variation of consumer biomass. A negative coefficient of variation indicates a decrease in biomass, the threshold value of -1 corresponds to an extinction of all consumers. The coloured gradient indicates the value of the average foraging trait at the community level. b) Response of the monospecific community according to the value of the single foraging trait allowed. In this case the evolution of the foraging trait is inhibited.

AF enhances lag load under shifting niche

We then investigate the impact of resource niche perturbations on the community stability. We start with a niche shifting its centre at a constant speed.

We show that the community with AF evolution suffers the disappearance of its consumers for a maximum speed of niche displacement lower than the maximum speed sustainable by the community without AF evolution (Figure IV.9a). In fact, we see that with the increase in the speed of niche displacement, i.e. the intensity of the perturbation, the AF regresses in the community with evolution. While in the initial community the average foraging trait is about 0.9, at the first perturbation intensity it drops to 0.4. And at the maximum perturbation that the community can sustain the average foraging trait is about 0.05. Thus, although the AF is detrimental face of this perturbation, its evolution allows its regression. However, when the speed of niche displacement is too fast, consumers do not have time to evolve towards a reduction in AF and become extinct. This is why the community with AF evolution, and initially a strong AF, does not withstand as much perturbation as the community without AF can.

By testing the response of monospecific communities, we validate the direct negative effect of

AF on the stability of the community in the face of this disturbance (Figure IV.9b). When the niche shifts, the diversity of resources is reduced and only those resources that follow the shift of the niche centre have abundances that are attractive to consumers. A random foraging strategy will mostly exploit these resources and there is no possible advantage to increase foraging effort on other resources since their abundances are too low. Thus, the use of AF by consumers does not bring any advantage in the exploitation of resources, and on the contrary consumers pay the trade-off of searching time.

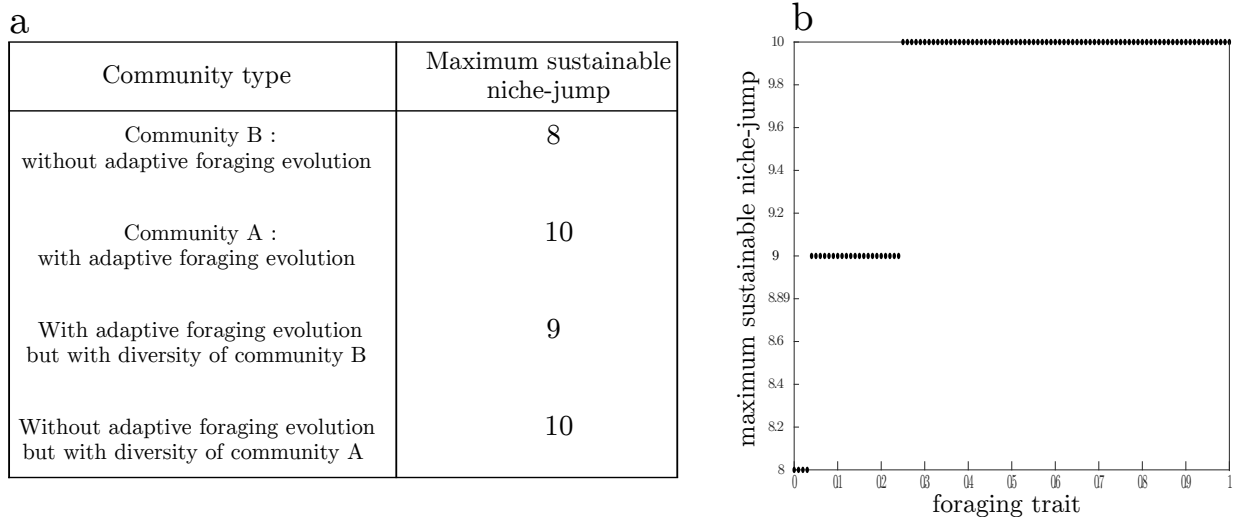


Figure IV.10 – Results of the niche-jump perturbation. a) Responses of four types of community: the two classic communities (with and without AF evolution) named A and B, and two other communities corresponding to the classical communities but whose diversity has been exchanged. b) Response of the monospecific community according to the value of the single foraging trait allowed. In this case the evolution of the foraging trait is inhibited.

Direct and indirect stability enhancement by AF under niche-jump perturbation

The second perturbation of the niche is the niche-jump, i.e. sudden shift of the niche centre to a certain distance from the initial centre. Following a niche-jump if the community persists it will rebuilt a similar community around the new niche centre and reach an equilibrium similar to the one before the perturbation. Thus it is impossible to use the coefficient of variation of biomass as a proxy for the response to the perturbation. We only look at the maximum magnitude of the niche-jump that the community can sustain as a proxy for stability. We show that the community with AF evolution can manage a larger maximum niche-jump than the community without AF evolution (Figure IV.10a, first and second rows). This effect suggest that a greater diversity leads to greater stability through a selection effect. We test the effect of diversity by applying the diversity of the community without AF evolution to the community with AF evolution, i.e. a decrease in diversity. The maximum niche-jump sustained by this community falls between the two values of the previous community (Figure IV.10a, third row). This means that there is a positive effect of diversity, which is lost by reducing diversity, but also a positive effect directly related to the use of AF by consumers. Conversely, by applying the diversity of the community with AF evolution to the community without AF evolution, the maximum sustainable perturbation is the same as that supported

by the community with AF evolution (Figure IV.10a, last row). Thus, diversity in itself is sufficient to sustain this disturbance without the help of AF.

By testing the response of monospecific communities in terms of foraging trait, we find the positive effect of adaptive foraging on stability in the face of niche-jump perturbation (Figure IV.10b). Moreover, we see that when consumers make little use of adaptive foraging, the maximum sustainable perturbation corresponds to an intermediate value. We know that AF has a positive effect on diversity (Figure IV.7b), so the monospecific community with low AF has an intermediate diversity compared to diversity without AF and diversity with high AF, and therefore an intermediate stability.

IV.2.5 Discussion

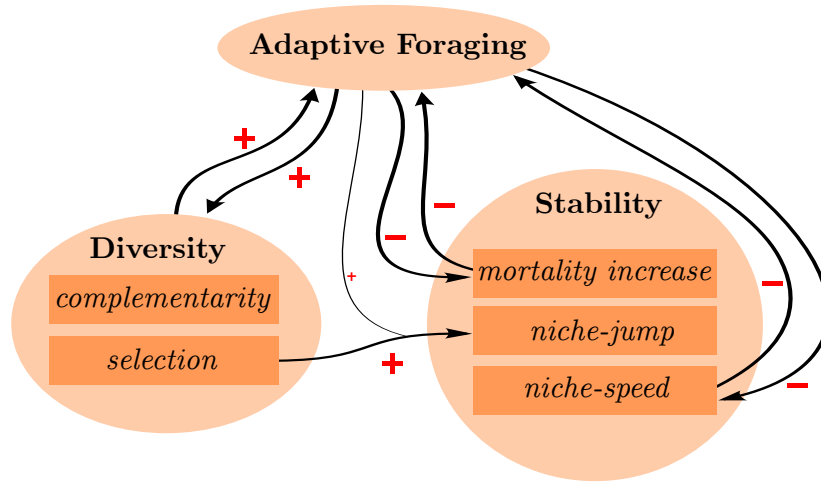


Figure IV.11 – Caption

The present work explores the threefold interactions between Adaptive Foraging, diversity and stability in an eco-evolutionary context (Figure IV.11). We show that AF is an important process within the BEF framework because its evolution have direct and indirect effects on both diversity and stability of communities composed of primary producers and consumers.

Evolution of adaptive foraging

Previous models exploring the effect of AF on community characteristics assumed that AF was a fixed trait of equal intensity for all consumers (Beckerman et al., 2010; Heckmann et al., 2012; Kondoh, 2003a,b; Uchida and Drossel, 2007). However, its intensity may vary between consumers and this behavior may be absent in some ecological contexts. In our study, we first investigate under which conditions the AF can emerge. We show that AF does not evolve systematically by natural selection. In stressed ecosystems where the diversification of primary producers is constrained by a narrow niche, the evolution of AF is limited, due to the low diversity of resources. Furthermore, when the cost of AF is too large compared to the size of the niche (for instance small σ_K and high s_{max}), the AF does not emerge (see Figure IV.6a for a full representation of the unsuitable condition for the AF to emerge). In those unfavorable cases, consumers diversify according to their niche trait but all maintain a minimal foraging trait corresponding to random foraging.

Moreover, even under ecological conditions for which AF can evolve, this does not occur with

the same intensity for all consumers. Consumers adapted to resources that are far away from the niche optimum are selected for strong AF, because their resources occur at low density. Conversely, consumers adapted to abundant resources growing at the center of the niche do not need to be choosy, since by feeding randomly they often encounter their optimal resource. Thus, evolution does not simply lead to either the presence or the absence of AF at the community level, but to a diversity of strategies among the community. The foraging strategy truly depends on the position of consumers in the niche.

Effects of adaptive foraging on biomass, productivity and diversity of community

The evolution of AF, measured by the mean foraging trait across consumers, has several effects on community properties in comparison with communities emerging in the same conditions except that consumers cannot become choosy. The evolution of AF increases the biomass of consumers and decreases the biomass of resources (Figure IV.7a). Indeed, AF induces a reduction of the niche overlap between consumers (Figure IV.12). In other words, it promotes interspecific complementarity. With AF, consumers have more diversified diets and therefore use more resources. Its effect on productivity is non-linear (Figure IV.7c). When AF intensity is from low to moderate, community productivity increases, whereas intense AF induces on average a slight decrease in productivity. In fact, it seems that when the AF becomes too strong, the gain in biomass of the consumers is too much at the expense of the biomass of the resources. Thus the productivity corresponding to the flow of the resources to the consumers, is reduced. Finally, the evolution of AF also enhances the functional diversity of both consumers and resources (Figure IV.7b). Indeed, this positive effect of AF is due to an eco-evolutionary loop between resources and consumers that resembles the Red Queen hypothesis (Van Valen, 1973). In the absence of AF, the resources standing far away from the niche centre are subject to a small consumption pressure, because the consumers cannot specialize on them. These resources exert interspecific competition in the vicinity of their niche, which prevents the emergence of other resources further away from the niche centre. In contrast when AF evolves consumers can consume these resources more heavily, reducing their density. Thus, it decreases competition among resources allowing for the emergence of new resources among the niche. therefore, resource diversity increases. The evolution of new resource species triggers the diversification of consumers which are also further away from the niche centre, and so on. This process stops when the limits of the exploitable niche are reached by the resources.

Moreover, the evolution of AF in the first place occurs when the diversity of resources is high enough, which occurs in relatively unstressed environments (large resource niche width, σ_K). Causation is therefore circular: AF both promotes and is promoted by resource diversity.

However, the evolution of AF increases the variability of each of these community properties, which may blur the overall trends. When AF does not evolve the emerging communities have similar properties across simulations. However, when AF emerges, the resulting communities can show contrasting biodiversity and productivity characteristics, even if the mean foraging trait among consumers are similar. Beside some rare exceptions, AF always increases diversity. However, the gain of diversity can vary a lot, from a slight increase to a doubling increase (Figure IV.7b). However, the impact of AF on biomass and productivity is more complex. Although biomass and productivity are often positively correlated (Balvanera et al., 2006; Cardinale et al., 2006; Loreau, 2010b; Tilman, 1996; Tilman et al., 1997), the evolution of AF can mitigate this relationship.

Community stability

Previous theoretical studies have reported a positive effect of AF on community stability (Beckerman et al., 2010; Heckmann et al., 2012; Kondoh, 2003a,b; Uchida and Drossel, 2007), based on ecological niche-model and measures of food web robustness. In parallel, several experiments (Schläpfer and Schmid, 1999; Tilman, 1996; Tilman and Downing, 1994; Tilman et al., 1996) and models (May, 1973; Thibaut and Connolly, 2013; Van Altena et al., 2016; Yodzis, 1981) have established a causal relationship between diversity and stability. Given the bidirectional relationship between AF and diversity, the effect of AF on community stability may therefore be direct, indirect, or both. This question can be tackled by the present work because, contrary to previous studies, diversity was not fixed but instead emerged during the eco-evolutionary dynamics.

We show that, after a sudden environmental change (niche-jump perturbation), communities with AF were more stable (Figure IV.10a). AF increases diversity of both producers and consumers, in particular it favors the emergence of species standing far away from the niche center. In a sense, those extreme species were already adapted to the niche jump perturbation and therefore persisted, unlike the central species. The positive effect of diversity on stability was therefore due to a selection effect (Loreau and Hector, 2001), since the higher diversity triggered by AF allows for "selection" of perturbation-resistant species. We also found that AF increased the complementarity between species (Figure IV.12), since it reduced their niche overlap, but this had no effect on stability at least with respect to the different perturbations tested.

We also show that there is a positive direct effect of AF in the face of this pressure, although weaker than the indirect effect through diversity. This effect is certainly explained by the delay in the evolution of consumers towards the new niche optimum compared to resources. After the abrupt change in environment, resources evolve towards the new optimum so that resources with high densities are quickly distanced from consumers in trait space. Consumers with a random foraging strategy continue to exploit these resources even though they are no longer sufficiently adapted to them. On the contrary, thanks to AF, consumers can focus on resources to which they are better adapted despite their lower densities. Because of its positive effect, and the punctual nature of the disturbance, the AF is not affected by the disturbance, and when the community shifts on the new niche optimum it is similar to before the disturbance. In contrast, in the cases of ecosystem disturbance or constant environmental change, AF had a negative direct effect on stability. This occurred because AF is costly; choosy consumers went extinct prematurely in comparison to random consumers. This time, diversity had no effect on stability, which precluded any indirect positive effect of AF. This non-effect of diversity is due to the gradual and persistent nature of these disturbances that destroy diversity, thereby depriving it of a possible positive effect. Finally, the evolution of AF was hampered by these two ecosystem pressures (Figure IV.11), intense disturbances even led to its complete disappearance. In the case of mortality increase AF regressed quickly, so that its potential negative effects were not perceived. A purely ecological model without evolution would have found a negative effect of AF on stability, missing the fact that AF can regress during the course of the ecosystem pressures. The same process was at work with the niche-speed pressure but the regression of AF was not fast enough, so that the direct negative effect of AF was apparent for intense pressures.

Conclusion In communities harboring primary producers and their consumers, diversity and ecosystem properties such as biomass, productivity and stability are often positively related (Schläpfer and Schmid, 1999; Tilman, 1996; Tilman and Downing, 1994; Tilman et al., 1996). This can be explained by a complementarity effect between species when they are

diverse, which also increases the chances of resisting a disturbance since some species will probably be insensitive to it (Griffin et al., 2009; Loreau and Hector, 2001; Poisot et al., 2013; Vanellander et al., 2009). Greater diversity also increases the probability of having a few species that perform well under certain conditions, this is the selection effect (Loreau and Hector, 2001). However, since consumers often modify their foraging activities in function of the abundance distribution of the resources (Bergman et al., 2001; Hassell and Southwood, 1978; Whiten et al., 1991), theory should incorporate the evolution of adaptive foraging (AF) to the evolutionary diversification of producer-consumers communities.

We show that the emergence of diversity can be favored by the evolution of AF, and reciprocally that diversity can promote AF evolution. In the case of sudden environmental change, this bidirectional process between AF and diversity enhances community stability through the selection of species at the edge of the environmental niche. In the case of constant environmental change or of ecosystem disturbance, AF can instead destabilize the communities because of its intrinsic cost. However, in such cases AF becomes itself counter-selected, which ultimately cancels out its negative effect on stability.

Furthermore, we show that the evolutionary diversification of resources and consumers shaped by AF produces a wider array of communities, with biomass and productivity characteristics much more heterogeneous than communities without AF. As a result, the relationships between diversity and biomass, and between diversity and productivity can be positive, negative or unimodal. Although the evolution of AF always promotes diversity, it also leads to a more complex picture than the standard positive relationship between diversity, biomass and productivity.

The multi-directional causal mechanisms involved in our study emphasize that the relationships between ecosystem characteristics, in particular adaptive foraging, productivity and stability, are not necessarily fixed for a given ecosystem, and that the existence of eco-evolutionary feedback loops can turn these relationships dynamics and historical.

IV.2.6 Appendix

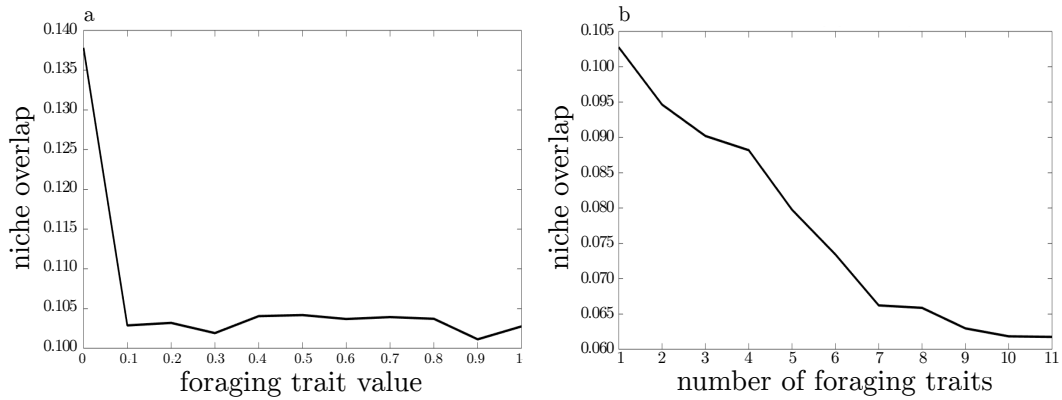


Figure IV.12 – Relationship between niche overlap and adaptive foraging. a) Niche overlap according to foraging trait value. For each foraging trait value, there is a community with a single foraging trait value and no evolution of that trait. b) Niche overlap as a function of foraging strategy diversity. The niche overlap is measured for a community with a single maximum foraging trait value ($z = 1$), then the measure is repeated with a community with two foraging traits ($z = 1, 0.9$), and so on until a community with all possible foraging trait values is reached.

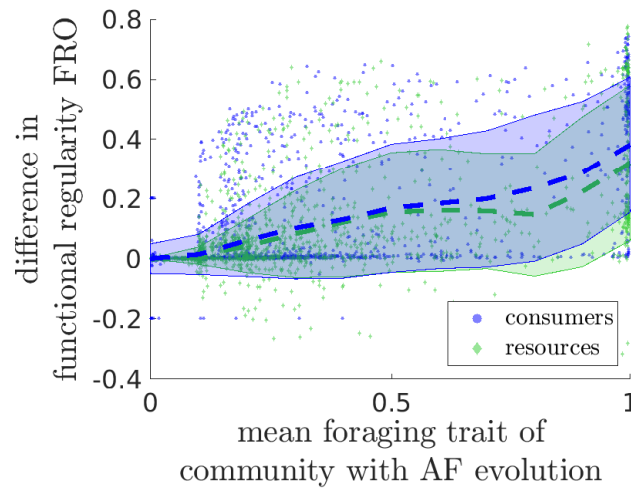


Figure IV.13 – Difference in functional regularity between communities where the evolution of AF is allowed by the diffusion of the foraging trait and communities where the evolution of AF is inhibited. The difference is made from 500 pairs of communities that emerged with 500 different parameter sets.

CHAPITRE V

CONCLUSION GÉNÉRALE ET PERSPECTIVES

Dans ce dernier chapitre notre objectif est de dépasser les discussions détaillées incluses à l'issue de chacun des chapitres pour créer, à l'image de ce qui a été fait dans l'introduction générale, des liens conceptuels entre ces trois chapitres.

Causalité réciproque

L'élément fondamental qui émerge de l'ensemble des travaux de cette thèse est l'importance du principe de causalité réciproque dans les systèmes complexes. Nous montrons dans trois contextes biologiques différents comment peuvent émerger de l'ensemble des interactions parties-parties, parties-tout et tout-parties, des causalités réciproques qui ont un rôle fondamental dans les propriétés de ces systèmes complexes. Pour rappel, dans le chapitre II nous montrons que les propriétés du système buis-pyrale reposent sur la causalité réciproque entre les communautés et la métacommunauté. La dynamique de la métacommunauté émerge des interactions entre les communautés via la dispersion de la pyrale et du buis, tandis qu'en retour les dynamiques locales sont également influencées par la dynamique globale de la métacommunauté, et notamment les extinctions de certaines communautés de buis à cause d'invasions successives de la pyrale. Dans le chapitre III nous montrons que la transition du parasitisme vers le mutualisme du système hôtes-symbiotes dépend de bouclages causaux entre les dynamiques écologique et évolutive ainsi qu'entre trois niveaux d'organisations différents. Ainsi, l'apparition par mutations d'une faible proportion de mutualistes, malgré leur désavantage initial, entraîne une augmentation de la compétition entre les hôtes, qui à son tour change la dynamique écologique des différents couples hôtes-symbiotes, au profit final du phénotype mutualiste. Enfin, dans le chapitre IV nous montrons le rôle de la causalité réciproque entre écologie et évolution dans l'émergence de communautés. Plusieurs bouclages causaux peuvent être décrits, le principal concernant la diversité de la communauté et l'évolution de l'adaptive foraging (AF). L'émergence d'une diversité de ressources suffisante en conditions environnementales favorables, va favoriser l'évolution de l'AF chez certains consommateurs, et l'AF à son tour va induire une pression de sélection sur les ressources se traduisant par une plus grande diversification. Ce premier point mérite d'être remis dans la perspective de notre introduction, qui montrait les limites d'une vision réductionniste, y préférant une vision dialectique. Effectivement, dans les trois contextes biologiques étudiés les propriétés des systèmes complexes ne dépendent pas uniquement des propriétés des parties. C'est l'ensemble des interactions, et les causalités réciproques qui en découlent, qu'il faut considérer pour appréhender ces systèmes. Poussée à l'extrême, la vision dialectique suggérerait que les parties ne puissent même pas être con-

sidérées en l'absence de l'ensemble des bouclages causaux avec le tout, puisque leurs propriétés sont constamment remodelées par ces bouclages. Néanmoins, l'usage de la modélisation nécessite de définir des parties, en incluant deux catégories : les variables d'état et les relations qui existent entre elles. Pour être plus concret, nous pouvons développer l'exemple du modèle de métacommunauté du système pyrale-buis qui nécessite que les communautés soient numériquement définies en l'occurrence sous forme de cellules de matrice. A l'opposé l'approche dialectique décrirait la métacommunauté plutôt comme un ensemble d'interactions plus ou moins fortes, aux contours mouvants. Cependant, nous tenons à souligner que nos méthodes de modélisation laissent une part importante au principe d'émergence (du mutualisme, de communautés, de structures spatiales), de telle sorte que les parties constitutives des systèmes complexes étudiés ne sont pas définies a priori. Irrémédiablement les parties sont représentées par des objets numériques distincts, mais en revanche le nombre de parties et les interactions entre elles sont des propriétés émergentes de nos modèles. Même dans le modèle de métacommunauté, bien qu'un nombre maximal de parties soit défini en conditions initiales (le nombre de peuplement de buis), les processus d'extinction et recolonisation restructurent ensuite le système en changeant ce nombre et leurs interactions.

Persistance

Le deuxième point de convergence entre les chapitres est la question de la persistance de ces systèmes complexes. Comme décrit dans l'introduction (section I.4) cette question peut être envisagée comme un ensemble de sous-questions : de quoi dépend la persistance d'un système complexe, de ses parties, de son tout ? Mais le prisme de la vision dialectique impliquant que tout système contienne un changement, comment concilier ces notions de changement et de persistance ?

Dans l'introduction, nous avons apporté des éléments de réponse en proposant un cadre dans lequel l'individualité d'un système complexe, c'est-à-dire ce qui persiste, est défini non seulement par ses propriétés mais également par ses interactions, et notamment les causalités réciproques. Nous avons également utilisé comme synonyme la notion de processus. Ce qui définit un système, et donc ce sur quoi la persistance est évaluée, c'est que le système continue à réaliser les mêmes processus au cours du temps. Par exemple la persistance du système buis-pyrale est représentée par le maintien des interactions entre les deux espèces et entre les communautés, ainsi que par la causalité réciproque avec la métacommunauté. Nous suggérons alors la proposition "It's the song, not the singer" ([Doolittle and Booth, 2017](#); [Doolittle and Inkpen, 2018](#)); autrement dit, l'important ce n'est ni les parties, ni le tout, mais l'ensemble des relations causales qui réalisent la "musique" du système et les propriétés qui conditionnent ces relations.

Cet élément de réponse à la question "qu'est-ce qui persiste ?" fournit également une réponse à cette autre question "qu'est-ce qui détermine la persistance d'un système complexe ?". Effectivement, puisque le système qui persiste peut être représenté par l'ensemble des relations causales, alors la persistance ne repose sur aucun élément du système en particulier mais sur l'ensemble des relations causales. Autrement dit, il est imaginable de considérer un système dont des parties changent, mais dont les interactions, et causalités réciproques, seraient inchangées. Cependant, les relations causales du système étant tout de même conditionnées par ses propriétés (par exemple le nombre d'espèces dans le système), un changement trop important des parties induira irrémédiablement un changement des relations causales et donc d'individualité du système. Ainsi, l'individualité ne repose pas uniquement sur la composition en parties, mais celle-ci joue tout de même un rôle.

Une analogie peut-être envisagée avec le mythe du bateau de Thésée raconté par Plutarque

: toutes les planches de ce bateau sont progressivement remplacées au cours du temps, de sorte que la question se pose de savoir s'il s'agit toujours au final du bateau de Thésée. Nous considérons que tant que le bateau flotte, tant qu'il est propulsé par le vent, tant qu'il peut se manoeuvrer dans différentes directions, c'est-à-dire tant qu'il peut réaliser tous les processus normalement réalisés par le système "bateau de Thésée" grâce à ses propriétés (par exemple l'agencement des planches de telle sorte à former une coque), alors il s'agit toujours du même bateau.

Il est important de considérer que la vision de l'individualité et de la persistance des systèmes complexes que nous décrivons ici implique une prise en compte de l'historicité du système. Premièrement par le fait que nous soulignons l'importance des relations causales, dans l'individualité comme dans la persistance. Ces relations causales ne pourront être perçues que si elles s'expriment à travers le temps. Autrement dit, une photo instantanée d'un système, disons une communauté par exemple, ne montrera que les parties du système, pas les relations causales. De plus, nous avons précisé que l'individualité reposait non seulement sur l'ensemble des relations causales, mais aussi sur les propriétés les conditionnant. Ces propriétés qui jouent un rôle dans les relations causales du système ne peuvent être qu'une partie de l'ensemble des propriétés du système et nous pouvons les qualifier de propriétés fondamentales du système. Pour définir ces propriétés il est également nécessaire de considérer l'historicité du système.

Dans chacun des chapitres nous avons testé la persistance du système étudié, selon cette vision "dialectique" de la persistance. Dans le chapitre II cette vision s'exprime par la considération que le système persiste dès lors que les deux espèces coexistent en interaction dans le système complexe formé de la causalité réciproque entre communautés et métacommunauté. Dans le chapitre III, nous nous sommes intéressés à la persistance du mutualisme, non pas sous le prisme de la persistance du phénotype mutualiste, qui lui n'est qu'une partie du système complexe, mais sous le prisme de la persistance des relations causales permettant la formation du système avec une forte proportion de mutualistes. Ce système est constitué des populations d'hôtes et de symbiontes, parasites et mutualistes, qui sont en perpétuel changement. De plus, la structure spatiale change continuellement puisque des clusters s'effondrent alors que d'autres se forment. Malgré ces changements quantitatifs des différentes parties du système, l'ensemble des relations causales persiste de telle sorte que le mutualisme soit sélectionné. Notons que dans ce modèle nous considérons que la transition du parasitisme vers le mutualisme s'est produite à partir du moment où il y a 10% de symbiontes mutualistes dans la population. Le fait que ce critère soit quantitatif peut sembler aller à l'encontre de notre propos. Cependant, ce critère quantitatif, indispensable d'un point de vue méthodologique, cache des relations causales et donc un véritable changement de système selon notre définition. Ainsi, quantité et qualité entretiennent aussi une relation dialectique. Effectivement, le passage d'une proportion de symbiontes mutualistes d'environ 2%, lorsque les mutualistes sont contre-sélectionnés et simplement résultat de la variabilité phénotypique due aux mutations, à une proportion supérieure à 10% lorsque le mutualisme est sélectionné, n'est possible qu'à condition que la causalité réciproque entre le paysage (la compétition globale entre les hôtes), les clusters et les individus devienne suffisamment forte. Ainsi, les deux situations - avant et après transition - correspondent à deux systèmes différents. Lorsque nous perturbons le système avec une extinction des populations d'hôtes et de symbiontes dans une partie de l'espace, au-delà des changements quantitatifs engendrés, nous perturbons en fait la causalité réciproque entre le paysage et les sous-parties. Nous montrons que celle-ci peut néanmoins se reconstituer pour reformer le même système.

Enfin dans le chapitre IV, nous n'avons pas mesuré la persistance de trait ou d'espèces comme le veut la tradition associée à l'exploration de la stabilité de réseaux trophiques ([Dunne](#)

et al., 2002; Eklöf and Ebenman, 2006; Kondoh, 2003a; Sole and Montoya, 2001), mais celle des interactions dans les communautés. Effectivement, le modèle considéré impliquant une dynamique éco-évolutive il n'est pas possible de mesurer des extinctions d'espèces après une perturbation puisque l'évolution va pouvoir recréer ces espèces ensuite. De plus, à cause des causalités réciproques entre les niveaux trophiques et les dynamiques écologique et évolutive, les abondances au sein des communautés sont très dynamiques. Les communautés sont donc des systèmes complexes dont les parties sont en constant changement. Nous avons considéré qu'à travers l'extinction de l'ensemble du niveau trophique des consommateurs le système devenait réellement différent, à cause de la perte de la causalité réciproque non seulement entre les deux niveaux trophiques mais également entre l'AF et les propriétés de la communauté. Nos résultats sur la réponse des communautés face à la perturbation de changement brutal et ponctuel de l'environnement sont les plus explicites par rapport au cadre conceptuel précédemment décrit. En effet, face à cette perturbation, la persistance de la communauté repose sur la causalité réciproque entre l'évolution de l'AF et la diversité de la communauté. La diversité est à l'origine de l'évolution de l'AF qui se traduit par une plus grande diversité, elle-même responsable d'une persistance améliorée.

Ce cas particulier de la perturbation brutale (niche-jump) dans le chapitre IV permet d'illustrer le lien entre relations causales au sein du système et les propriétés assurant une meilleure persistance du système. En synthèse, le système génère les conditions favorables à sa propre persistance.

En fait, cette caractéristique se retrouve également dans les deux autres chapitres. Lorsque le système buis-pyrale du chapitre II est placé dans un espace initialement saturé en buis, la dynamique globale va induire l'extinction de certains peuplements de buis, autrement dit la disparition de certaines parties du système. Cette dynamique d'extinction du buis, et également de recolonisation, va perdurer jusqu'à atteindre un équilibre où l'espace sera constitué de groupements de peuplements de buis répartis à peu près équitablement. Cette structure spatiale favorise la persistance du système par rapport à la structure initiale caractérisée par des oscillations très prononcées de la population de pyrale, et donc sensible à d'éventuelles perturbations stochastiques en période de faible abondance. Pour ce qui est du chapitre III, la création par le système mutualiste des conditions permettant sa persistance selon un processus de construction de niche a déjà été discutée.

Dans le chapitre introductif (section I.3.2) ce phénomène était déjà présent dans notre extension du modèle de [Pepper and Smuts \(2002\)](#). Dans ce modèle l'apparition des consommateurs modérés à partir d'une situation initiale avec des consommateurs gourmands et sans structure spatiale est explorée. Nous montrons que la dynamique entre ressources et consommateurs gourmands génère une structure spatiale à travers la mortalité des ressources lorsqu'elles sont sur-exploitées. Cette structure spatiale permet ensuite l'émergence du phénotype modéré, qui devient même dominant dans la coexistence des deux phénotypes. Si nous considérons que le système est formé de la coexistence des deux phénotypes, dans ce cas celui-ci génère effectivement les conditions favorables à sa persistance. L'originalité tient à l'opposition entre chacune des parties du système - phénotype modéré vs phénotype gourmand - et aux conditions favorables à l'autre phénotype induites par chaque phénotype. Effectivement, le phénotype gourmand entraîne une forte mortalité des ressources créant une structure spatiale favorisant le phénotype modéré. À l'inverse, le phénotype modéré détruit la structure spatiale en entraînant la régénération de ressources non sur-consommées, favorisant ainsi le phénotype gourmand. Cette causalité réciproque positive entre les deux phénotypes, à travers la causalité réciproque avec la structure spatiale, est la source des oscillations des densités de chaque phénotype.

Perspectives

Cette notion de systèmes complexes favorisant sa propre persistance permet maintenant d'aborder les perspectives de cette thèse dans le cadre de sa problématique principale, l'évolution des écosystèmes par sélection naturelle.

Nous avons brièvement évoqué en introduction les verrous conceptuels préalables à toute tentative de réponse à cette question. La théorie de l'évolution par sélection naturelle repose sur le trépied : variabilité (différents phénotypes), sélection (différentes valeurs sélectives), et hérédité (transmission du phénotype du parent au descendant). S'agissant du niveau d'organisation de l'écosystème, le principe de variabilité est facilement adaptable, en revanche les principes de sélection selon la valeur sélective (fitness) et d'hérédité sont plus complexes à envisager. Les travaux empiriques concernant cette question ont pu s'affranchir de ces difficultés grâce à une méthodologie permettant de traiter les écosystèmes comme des organismes (Blouin et al., 2015; Swenson et al., 2000a,b). Dans ces manipulations l'individualité des écosystèmes est créée par leur isolement (par exemple avec des écosystèmes microbiens isolés dans des tubes à essai différents), et la reproduction est assurée par l'expérimentateur en prenant un échantillon de chaque écosystème et en le laissant se développer dans un nouveau milieu. Ces manipulations montrent que l'évolution par sélection artificielle au niveau des écosystèmes est possible. À présent, l'approche conceptuelle et par modélisation cherche à s'affranchir des conditions restrictives de la sélection artificielle pour correspondre à la sélection naturelle.

Nous avons proposé l'idée que la fitness, habituellement mesurée comme la capacité à produire de nombreux descendants, pouvait en fait s'exprimer par la notion de persistance (Bouchard, 2008). La reproduction ne serait alors qu'une des composantes de la fitness, une manière de persister. Ainsi, la difficulté d'imaginer qu'un écosystème puisse se reproduire - en considérant le terme de reproduction dans le même sens que pour des organismes - n'empêche pas de penser qu'il puisse tout de même exprimer une fitness à travers sa capacité à persister (Bouchard, 2011, 2014; Dussault and Bouchard, 2017; Lenton et al., 2021). La persistance des écosystèmes peut elle-même être divisée en deux composantes : la capacité à persister localement et la capacité à se re-produire (ce qui correspond à une variante de la reproduction organismique). La première composante peut s'exprimer comme une capacité à conserver les propriétés et relations causales qui font son identité en tant que système face aux perturbations. La conséquence sera alors sa persistance dans le temps au même titre qu'un phénotype avantageux perdurera grâce à des générations successives de descendants. Le lien est ainsi évident avec le principe de système générant, et préservant, des conditions permettant sa propre persistance. Ce principe s'apparente à une notion d'homéostasie des écosystèmes, ceux-ci se construisant sur des relations causales qui assurent le maintien de conditions permettant leur persistance (Boyd, 1999; Ibanez, 2020). La seconde composante de re-production consiste à accepter que les écosystèmes ne puissent pas se reproduire dans le sens organismique du terme, mais qu'un procédé analogue est concevable (Doolittle and Inkpen, 2018; Ibanez, 2020). La re-production repose sur la manière dont l'individualité des systèmes complexes a été définie plus haut, c'est-à-dire que les propriétés fondamentales et les relations causales sont à prendre en compte tout autant que la composition du système en terme de parties constitutives. (Doolittle and Booth, 2017; Doolittle and Inkpen, 2018; Ibanez, 2020). Ainsi, la dispersion d'organismes depuis un écosystème "parent" peut être comparée à la dispersion de propagules de cet écosystème. Si ces organismes finissent par former un ensemble, dans une localité différente de l'écosystème parent, mais de telle sorte que les propriétés fondamentales et relations causales de l'écosystème parent soient re-produites, alors il est possible de considérer que l'écosystème parent s'est re-produit. Et ceci malgré des différences possibles dans l'assemblage des organismes qui seraient provoquées par des dispersions d'organismes venant d'autres écosystèmes. Nous pouvons remarquer que les deux composantes de la fitness envisagées : persistance et re-production, sont étroitement

liées puisque le principe de re-production nécessite que l'écosystème parent ait une certaine persistance. Cette vision de la fitness des écosystèmes permet de prédire que les écosystèmes qui sont en mesure de générer les conditions favorisant leur persistance seront sélectionnés. Alors que dans les trois chapitres précédents cette capacité des systèmes à générer leur propre persistance est une propriété émergente non-sélectionnée, celle-ci pourrait être une propriété sélectionnée dans un contexte de méta-écosystème soumis à l'évolution par sélection naturelle.

Pour conclure, nous envisageons une approche par modélisation capable d'explorer cette question de l'évolution des écosystèmes par sélection naturelle.

Le principe serait de considérer un méta-écosystème, c'est-à-dire un assemblage d'écosystèmes en interactions à travers des flux biotiques et abiotiques. La différence avec le concept de métacommunauté et communautés résiderait dans la prise en compte supplémentaire du compartiment abiotique, alors que les communautés ne sont constituées que du compartiment biotique. En intégrant ce compartiment, des possibilités supplémentaires de dynamiques de type construction de niche sont créées, dans lesquelles l'écosystème générerait des conditions favorisant sa persistance, par exemple à travers des cycles biogéochimiques (Barot et al., 2016; Doolittle, 2017; Loeuille et al., 2017). Ces écosystèmes émergeraient de sorte que leurs différentes histoires évolutives mènent à une diversité d'écosystèmes. On peut imaginer qu'en conditions initiales l'environnement abiotique soit hétérogène afin de permettre cette diversité initiale à l'émergence. Par exemple Girardot et al. (2020) montrent comment l'environnement, en l'occurrence représenté par le taux de croissance d'une ressource basale, peut permettre la génération de réseaux trophiques aux propriétés variées à travers leur histoire évolutive. Les organismes auraient ensuite la possibilité de remodeler leur environnement selon une vision constructiviste de celui-ci. Les flux biotiques et abiotiques entre les écosystèmes assureraient leur mise en compétition et les écosystèmes les moins persistants pourraient être remplacés par la re-production des plus persistants.

Des travaux récents se plaçant dans le cadre de l'hypothèse Gaia (Lovelock and Margulis, 1974) - mais dans une version moins idéaliste, à l'image de la théorie de sélection multi-niveaux par rapport à la sélection de groupe naïve - ont posé les premières pierres en explorant comment des organismes peuvent rendre leur écosystème plus persistant ou productif (Arthur and Nicholson, 2017; Boyle et al., 2012; Doolittle, 2017; Lenton et al., 2018; zu Castell et al., 2019). Ces travaux amènent des réflexions conceptuelles et des résultats en modélisation intéressants. Cependant, les modèles sont généralement fondés sur des présupposés propres au milieu microbien ou bien formés d'écosystèmes minimalistes. De plus, ils ne considèrent pas systématiquement plusieurs écosystèmes en compétition. Or, au même titre que l'exploitation d'individus altruistes par des individus tricheurs, la question peut se poser de l'exploitation d'écosystèmes de type Gaia par des "écosystèmes tricheurs". Un élargissement de ces résultats à des modèles incorporant des interactions plus complexes et des écosystèmes en compétition dans un méta-écosystème nous semble la prochaine étape.

Enfin, considérer la possibilité de conflit entre niveaux de sélection, par exemple entre le niveau de l'individu et celui de l'écosystème semble une composante importante. Effectivement, si les phénotypes des individus assurent en même temps la sélection de ces individus et la sélection des écosystèmes composés de ces phénotypes alors il est difficile de différencier si la sélection agit uniquement au niveau de l'individu ou également au niveau de l'écosystème. Il est tout à fait possible que la sélection agisse dans la même "direction" aux deux niveaux, ce qui représente alors le versant "facile" de l'exploration de la sélection au niveau des écosystèmes. Idéalement, nous aimerions aborder le versant "difficile", c'est-à-dire lorsque les forces de sélection entre les différents niveaux de sélection sont opposées. Par exemple, la sélection au niveau individuel pourrait favoriser des phénotypes très compétitifs au sein des différents

niveaux trophiques, mais en situation de dominance de ces phénotypes, la persistance de l'écosystème serait fragilisée pour diverses raisons (un recyclage des nutriments moins efficace par exemple). Ainsi, ces individus très compétitifs seraient potentiellement en mesure d'envahir des écosystèmes au sein du méta-écosystème, mais les écosystèmes contenant une proportion trop importante de ces individus verraient leur compartiment abiotique dégradé et serait contre-sélectionné par rapport à d'autres écosystèmes plus persistants et productifs.

Notre contribution à cet édifice grâce à la pierre apportée avec le chapitre III sur l'évolution du mutualisme est ainsi illustrée car la dynamique décrite dans ce chapitre est en plusieurs points similaire à celle imaginée ici. Resterait à dépasser le stade de l'écosystème minimaliste en modélisant un écosystème écologiquement plus riche, par exemple en considérant plusieurs niveaux trophiques avec potentiellement des interactions variées (antagonistes et mutualistes), ainsi qu'un compartiment abiotique avec un cycle des nutriments.

RÉSUMÉ

Les domaines de l'écologie et l'évolution sont constitués de systèmes complexes – organismes, espèces, communautés – qui se prêtent mal à une approche réductionniste. Ces systèmes ont des propriétés émergentes qui dépassent la somme des propriétés de leurs parties. Leur étude demande alors de s'intéresser aux interactions entre les parties et le tout de ces systèmes. Par exemple, l'étude d'une métacommunauté ne peut pas se limiter à l'étude stricte du tout (la métacommunauté) ou l'étude stricte des parties (les communautés composant la métacommunauté). La compréhension de cet système complexe demande de considérer le tout, les parties, et les interactions entre eux. De plus, ces interactions peuvent être multidirectionnelles, elles ne sont pas exclusivement des parties vers le tout, la causalité réciproque est possible, le tout influençant alors les parties. Dans cette thèse nous explorons à travers trois systèmes biologiques distincts comment les interactions entre le tout et les parties définissent ces systèmes. La thèse est donc constitué de trois chapitres. Dans le premier nous explorons un modèle de métacommunauté simulant l'invasion de la pyrale du buis, un insecte herbivore invasif en Europe, et étudions les interactions entre les échelles spatiales locale et globale. Ce modèle écologique de dynamique des populations est calibré à partir de mesures empiriques sur le terrain et à travers une manipulation en mésocosme. Notre modèle reproduit l'instabilité des dynamiques locales. En effet, localement l'insecte s'éteint irrémédiablement à cause de sa sur-exploitation de sa ressource (le buis). Cependant, notre modèle montre que les interactions entre les communautés, grâce à la dispersion de l'insecte, peut mener à la persistance du système à l'échelle de la métacommunauté. De plus, nous montrons que la structure de la métacommunauté émerge des interactions entre les dynamiques locales. Le deuxième chapitre explore dans quelle mesure une interaction mutualiste entre un hôte et un symbionte peut émerger à partir d'une interaction parasitique en coévoluant avec la dispersion. Nous développons un modèle éco-évolutif individu-centré dans un espace spatialisé en 2D et considérons comme condition initiale une population d'hôtes en interaction avec une population de symbiontes parasitiques. Nous montrons que grâce à l'évolution d'une dispersion locale une structure spatiale peut émerger de la dynamique du système hôte-symbionte. L'émergence de cette structure spatiale induit la formation de plusieurs niveaux d'organisation en interactions entre eux : le niveau de l'individu, le niveau du regroupement spatial, et le niveau du paysage. Tandis que le niveau de l'individu favorise l'évolution du parasitisme, les deux niveaux supérieurs du regroupement spatial et de l'ensemble du paysage favorise l'évolution du mutualisme. Nous montrons que selon la force de la structure spatiale, modulée par l'intensité de la compétition à l'échelle du paysage, la transition du parasitisme vers le mutualisme peut se produire. Enfin, le dernier chapitre s'intéresse à l'évolution d'une stratégie d'acquisition de ressource chez des consommateurs dans un modèle éco-évolutif consommateurs-ressources. La littérature montre que la capacité des consommateurs à moduler activement leur manière de consommer les différentes ressources est un processus important dans le fonctionnement des écosystèmes, notamment leur stabilité. Cependant, ces résultats sont obtenus à partir de modèles de communautés fixes ce qui prive l'étude de certaines interactions potentielles entre le niveau de l'individu et celui de la communauté. À partir de notre modèle d'émergence de communautés nous montrons que la stratégie d'acquisition des ressources des consommateurs a un effet sur des propriétés de la communauté, notamment sa biomasse, sa productivité, sa diversité et sa stabilité. De plus, la structure de l'ensemble de la communauté module l'évolution des stratégies des consommateurs.

ABSTRACT

The fields of ecology and evolution are made up of complex systems - organisms, species, communities - that do not lend themselves well to a reductionist approach. Indeed, these systems may have emergent properties that exceed the sum of the properties of their parts. Their study then requires an interest in the interactions between the parts and the whole of these systems. For example, the study of a metacommunity cannot be limited to the strict study of the whole (the metacommunity) or the strict study of the parts (the communities composing the metacommunity). Understanding this complex system requires considering the whole, the parts, and the interactions between them. Moreover, these interactions can be multidirectional, they are not exclusively from the parts to the whole, reciprocal causality is possible, the whole then influencing the parts. In this thesis we explore through three distinct biological systems how the interactions between the whole and the parts define these systems. The thesis therefore consists of three chapters. In the first we explore a metacommunity model simulating the invasion of the boxwood moth, an invasive herbivorous insect in Europe, and study the interactions between local and global spatial scales. This ecological model of population dynamics is calibrated from empirical field measurements and through mesocosm manipulation. Our model reproduces the instability of local dynamics. Indeed, locally the insect is irreversibly extinguished due to its over-exploitation of its resource (boxwood). However, our model shows that interactions between communities, thanks to the dispersal of the insect, can lead to the persistence of the system at the scale of the metacommunity. Furthermore, we show that the structure of the metacommunity emerges from the interactions between local dynamics. The second chapter explores the extent to which a mutualistic interaction between a host and a symbiont can emerge from a parasitic interaction by co-evolving with dispersal. We develop an individual-centred eco-evolutionary model in a 2D space and consider as initial condition a host population interacting with a population of parasitic symbionts. We show that through the evolution of a local dispersal a spatial structure can emerge from the dynamics of the host-symbiont system. The emergence of this spatial structure induces the formation of several interacting levels of organisation: the individual level, the spatial cluster level, and the landscape level. While the individual level favours the evolution of parasitism, the two higher levels of spatial cluster and the landscape favour the evolution of mutualism. We show that depending on the strength of the spatial structure, modulated by the intensity of competition at the landscape level, the transition from parasitism to mutualism can occur. Finally, the last chapter focuses on the evolution of adaptive foraging among consumers in a consumer-resource eco-evolutionary model. The literature shows that the adaptive foraging is an important process in the functioning of ecosystems, especially their stability. However, these results are obtained from models of fixed communities, which deprives the study of some potential interactions between the individual and community levels. From our model of community emergence we show that the resource acquisition strategy of consumers has an effect on community properties, including biomass, productivity, diversity and stability. Furthermore, the structure of the whole community modulates the evolution of consumers' strategies.

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