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Community stability and turnover in changing environments

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Abstract

The question whether communities should be viewed as superorganisms or loose collections of individual species has been the subject of a long-standing debate in ecology. Each view implies different spatial and temporal community patterns. When environment gradually changes in space or in time, the organismic view predicts that species turnover is discontinuous, while the individualistic view predicts gradual changes in species composition. The main objective of this thesis is to understand the theoretical conditions under which these various types of community response can occur. First, I study the role of interspecific competition can play in the emergence of various spatial community patterns. I investigate the theoretical conditions in competition under which smooth or discrete spatial patterns can emerge. Then, I study how interactions between species and their environment can lead to various community patterns in space. I notably show how ecological niche construction can lead to the emergence of abrupt changes in species composition and in the environment, and the role biodiversity plays therein. Finally, I focus on the role biodiversity can play against ecosystem collapse. In this section, I illustrate how diversity loss, through its effects on total biomass, can lead to ecosystem collapse.

Résumé

Les communautés d'êtres vivants peuvent elles êtres considérées comme des organismes complexes, ou au contraire comme de simples groupes d'espèces, individuelles ? Cette question est à l'origine de nombreux débats en écologie, ces deux visions impliquant notamment des prédictions très différentes dans les patrons spatiaux et temporels de communautés. Lorsque l'environnement change graduellement dans l'espace ou dans le temps, la vision individualiste implique des changements graduels dans la composition des communautés, tandis que la vision du "super-organisme" prédit des changements davantage abrupts. L'objectif principal de cette thèse est de comprendre et déterminer sous quelles conditions ces différents types de réponse des communautés aux changements de l'environnement peuvent advenir. Dans une première partie, nous étudions le rôle que la compétition inter-spécifique peut jouer dans l'émergence de différents patrons spatiaux de communautés. Nous étudions notamment les conditions théoriques sous lesquelles la compétition peut faire apparaitre des patrons graduels ou discontinus dans la composition des espèces. Dans une deuxième partie, nous étudions l'influence des interactions entre les espèces et leur environnement sur les patrons spatiaux de communautés. Nous montrons notamment comment des phénomènes de construction de niche peuvent mener à l'émergence de changements brutaux dans la composition des communautés, mais également dans les conditions de l'environnement. Enfin, dans une dernière partie, nous illustrons le rôle que peut jouer la biodiversité dans la protection des écosystèmes face à des effondrements écologique, et notamment le rôle que peut jouer la biomasse dans cette protection.

Remerciements

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Contents

Introduction générale

"Je ne sais comment font ceux qui du même coup-d'oeil aperçoivent; saisissent et jugent. Ce qui frappe mes regards pour la première fois, est rarement vu en même tems des yeux de l'esprit."
Louis Ramond de Carbonnière

Contexte historique

Les communautés écologiques sont composées de différentes espèces qui interagissent entre elles et avec leur environnement. La façon dont les communautés réagissent aux changements des conditions abiotiques dans le temps et dans l'espace constitue une thématique de recherche ancienne en écologie. Notamment, les modalités selon lesquelles la composition spécifique change lorsque l'environnement varie graduellement sont toujours sujettes à débat. Au XIXe siècle, le naturaliste Alexandre de Humbolt fut parmi les premiers à décrire les changements de végétation le long d'un gradient altitudinal des Andes équatoriales (Bonpland and von Humboldt, 1805). Le savant fondateur de la "phytogeographie", discipline qui s'intéresse à la distribution géographique des plantes, décrit notamment différentes "régions" aux compositions floristiques distinctes et facilement identifiables. En montant en altitude, se succèdent par exemple la "région des plantes alpines" et la "région des lichens". En revanche, il ne donne que peu d'informations sur la vitesse à laquelle ces changements de composition floristique s'opèrent dans l'espace. La façon dont les espèces apparaissent ou disparaissent lorsque la température, les conditions du sol, ou la pluviométrie changent va par la suite donner lieu à de nombreux débats entre écologues (Egerton, 2015). Et c'est à nouveau au sujet des communautés végétales qu'une des plus grandes controverses voit le jour au début du XXe siècle. Frederic Clements, botaniste américain, avance que les changements de composition spécifique dans l'espace se font de manière discrète lorsque l'environnement change : une communauté en remplace une autre. A l'opposé, Henry Gleason (1926) avance que ces changements sont graduels, et que l'on ne saurait distinguer des entités discrètes dans la composition des communautés dès lors que la variation des facteurs environnementaux est graduelle. Cet argument de la gradualité des changements spécifiques sera qualifiée par la suite "d'hypothèse du continuum".

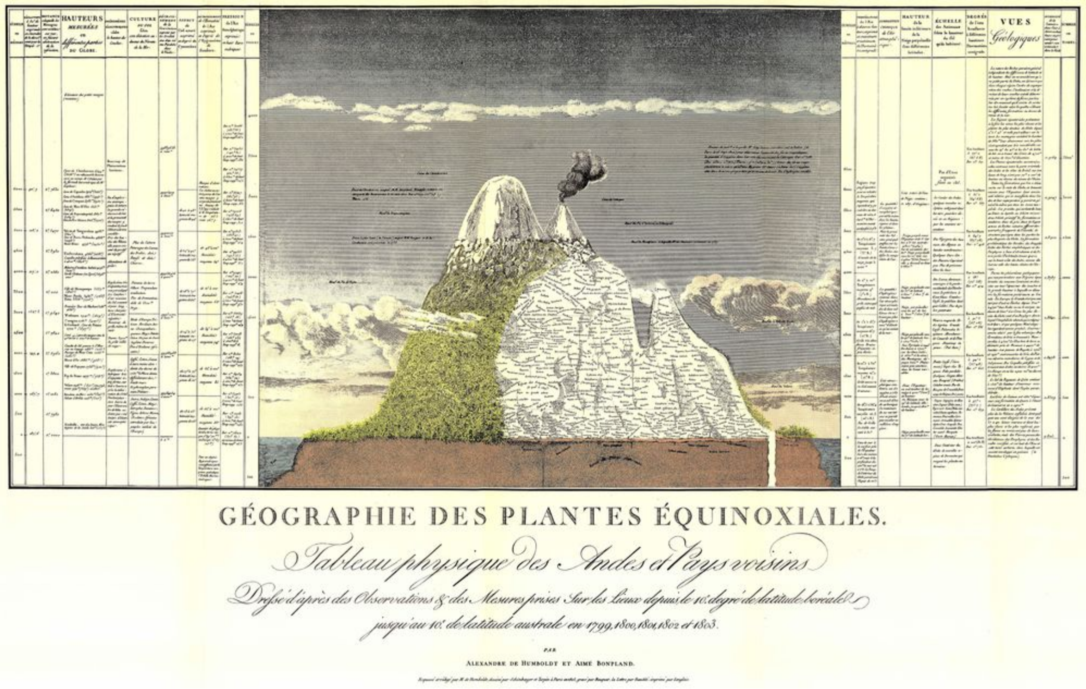

Figure 1: Carte de la distribution des végétaux le long d'un gradient altitudinal des Andes par Alexandre de Humbolt. (Bonpland and von Humboldt, 1805)

En même temps que se développe une vaste littérature concernant les variations d'abondances des espèces dans l'espace, l'étude des successions temporelles se développe (Egerton, 2015). Les premières observations de ces dynamiques de succession sont relativement anciennes, comme en attestent les observations de William King (1685) sur les tourbières irlandaises. Dans son essai "Oeconomia naturae", Linné décrit déjà des dynamiques de succession menant à la formation d'un couvert forestier à partir d'un sol licheneux pratiquement nu (Von Linne, 1972). Au début du XXe siècle, Frederic Clements développe dans son ouvrage "An analysis of the development of vegetation" l'idée selon laquelle la dynamique de succession s'effectuerait en plusieurs étapes ("stages"), se terminant par l'installation d'une association végétale terminale nommée "climax" (Clements, 1916). Henri Gleason marque à nouveau son opposition sur ce point, considérant que la délimitation de communautés discrètes dans le temps est souvent impossible (Gleason, 1926).

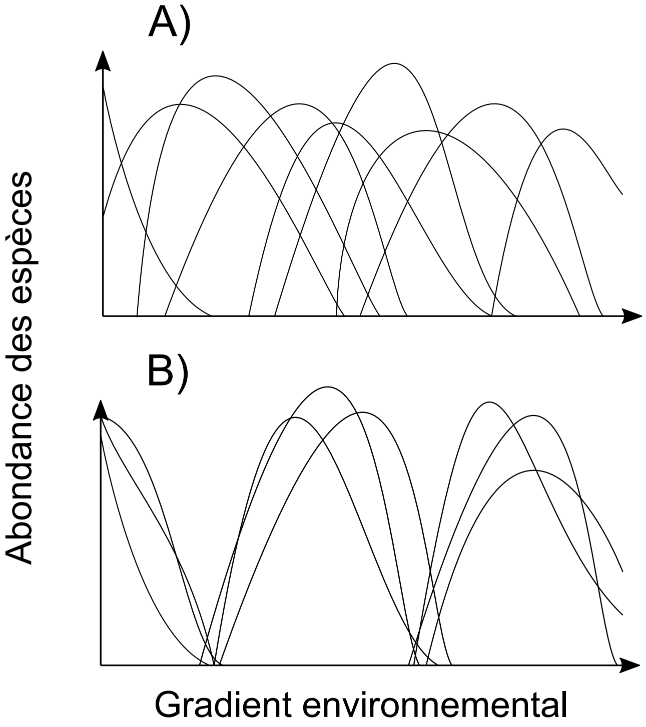

Figure 2: Patrons de communautés le long d'un gradient environnemental spatial ou temporel : A) Selon l'hypothèse du continuum, les changements d'abondance et de composition sont graduels dans l'espace ou dans le temps. B) Selon la vision Clementsienne, les communautés forment des ensembles discrets, qui se succèdent dans le temps ou dans l'espace, délimités par d'étroites zones (espace) ou brèves périodes (temps) dans lesquelles un important changement de composition spécifique est observé.

Ce débat, au delà d'une opposition concernant des variations de la composition spécifique dans le temps ou dans l'espace, soulève des questionnements plus profonds quant à la nature des communautés d'être vivants. La dynamique de succession menant au climax est notamment décrite par Clements comme similaire à celle du développement d'un organisme complexe: *"The developmental study of vegetation necessarily rests upon the assumption that the unit or climax formation is an organic entity. As an organism the formation arises, grows, matures, and dies."*(Clements, 1916). En adoptant cette vision, il réunit les processus de succession temporelle et les patrons spatiaux de communautés au sein d'un même phénomène de "développement". Dans l'espace, en présence d'une variation des facteurs environnementaux, les zones de végétation sont interprétées par Clements comme étant des stades de développement distincts : *In the case of water, for example, the bare area of excess is the starting-point for the series of zones, as it is for the series of stages. In short, zones are stages.* Cette vision de la communauté-organisme est rejetée par Tansley (1935), qui reconnait cependant un niveau d'organisation important au sein de certaines communautés végétales, allant jusqu'à les qualifier de "quasi-organisme". Une opposition plus franche aux concepts de communauté-organisme est apportée par Gleason (1926), qui considère que la dynamique d'une communauté dépend avant tout des espèces, individuellement, qui la composent : *every species of plant is a law unto itself, the distribution of which in space depends upon its individual peculiarities of migration and environmental requirements. Its disseminules migrate everywhere, and grow wherever they find favorable condition.* C'est l'hypothèse individualiste, qui s'oppose au concept de communauté-organisme formulé par Clements.

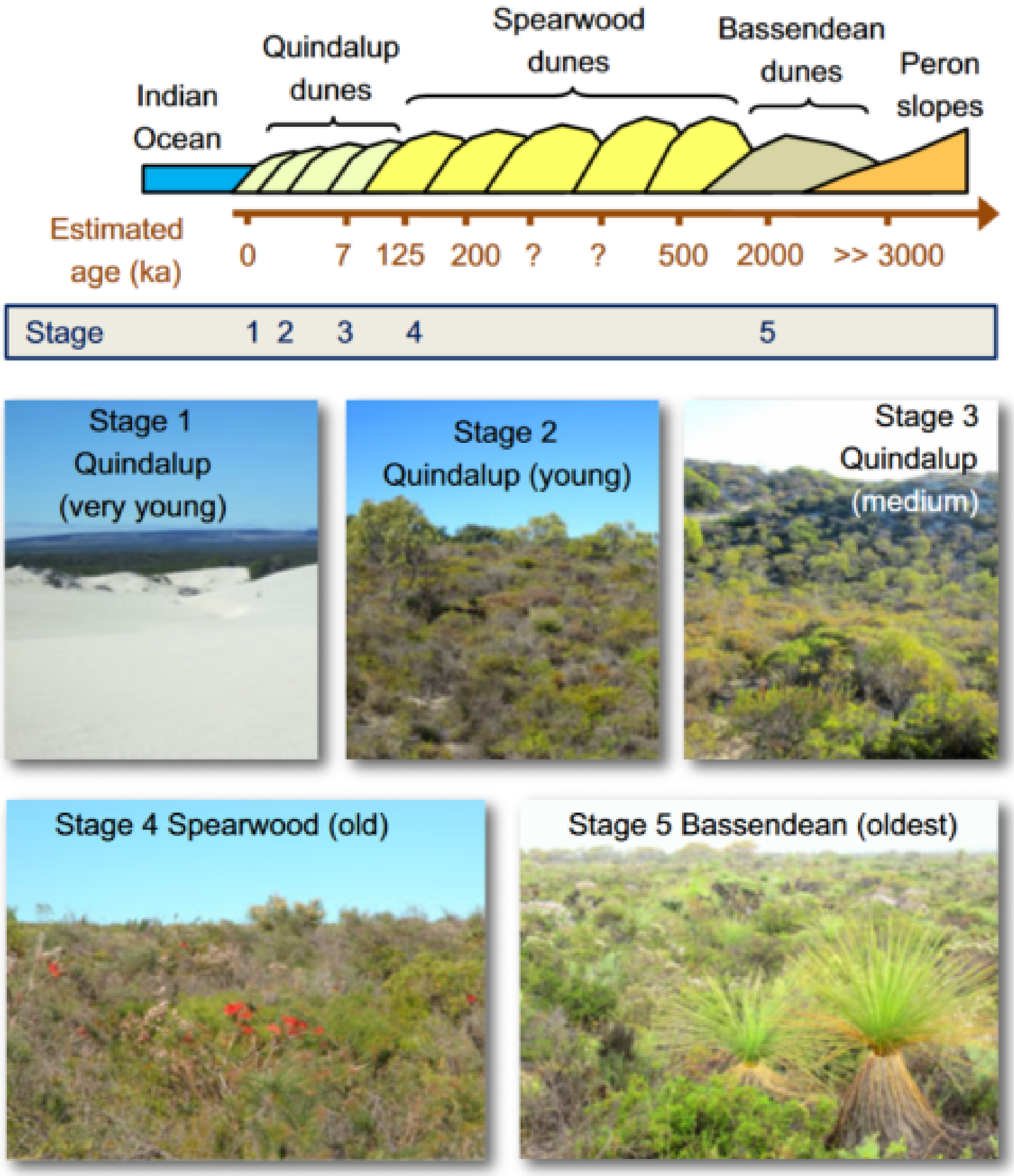

Figure 3: Chronoséquence de végétation. Sur cet exemple d'un ecosystème côtier australien, on peut apprécier différents stades d'une dynamique de succession. L'âge de formation des dunes augmente au fur et à mesure que l'on s'éloigne de la côte. Près de la mer, le processus de succession est peu avancé,(formation des dunes entre 0 et 125 000 ans pour les stades 1 à 3). Plus on s'éloigne de la côte, plus ce processus est avancé (formation des dunes entre 125 000 ans et 2 millions d'années pour les stades 4 et 5). La composition spécifique ainsi que le type de formation végétale varient en fonction du stade dans la dynamique de succession. Illustration : (Laliberté et al., 2012)

Interactions et distribution spatiale des espèces

Ces controverses du début du XXe siècle se sont cependant avant tout portées sur des observations de patrons, sans pour autant en déterminer leurs causes. La nature des interactions entre les espèces, leurs intensités, la relation des espèces avec leur environnement sont autant de processus pouvant influencer la distribution des espèces dans l'espace.

La reconnaissance d'interactions inter-spécifiques est actée depuis longtemps dans les disciplines de la botanique, dont sont issues les controverses entre visions organismique et individualiste. En 1820, l'existence de la compétition est déjà envisagée par le botaniste suisse De Candolle : "*toutes les plantes d'un pays, toutes celles d'un lieu donné, sont dans un état de guerre les unes relativement aux autres*" (de Candolle, 1820). Les premiers fondements de la théorie de la compétition s'appuient sur les travaux de Vito Volterra (1926) et Alfred James Lotka (1926), dont sont issues les équations de compétition de Lotka-Volterra. Ces équations se basent elles-mêmes sur l'équation logistique de Verhulst (Verhulst, 1838), mais introduisent des coefficients de compétition entre espèces qui réduisent leurs taux de croissance. Ces equations constituent actuellement un des modèles les plus utilisés en dynamique des populations. De nouveaux développements théoriques vinrent s'ajouter à ces travaux pionniers, qu'il s'agisse de compétition par exploitation des ressources (Tilman, 1982; MacArthur, 1969), ou d'interférences entre espèces (Case and Gilpin, 1974).

La compétition entre espèces fut notamment désignée comme un des facteurs explicatifs de leur distribution spatiale. Dans son ouvrage "Geographical ecology", Robert MacArthur (1972) fait par exemple l'hypothèse que le Martin-pêcheur *Megaceryle alcyon* voit son aire de répartition contrainte au sud, non pas par des facteurs environnementaux, mais par la présence de deux autres espèces de martins pêcheurs, *Chloroceryle americana* et *Megaceryle torquata*, avec qui il entre en compétition pour les ressources. La question de l'influence de la compétition dans la distribution spatiale des espèces donna cependant lieu à plusieurs controverses notoires. En 1975, Jared Diamond postule notamment que la composition des communautés dans l'espace est principalement influencée par la compétition inter-spécifique (Diamond, 1975). Il propose que certaines espèces ne peuvent coexister en présence d'autres, avec pour résultante un patron de communauté en échiquier (checkerboard pattern), comme il l'observe dans les îles d'Océanie au sujet de communautés d'oiseaux. Ses résultats, qui s'appuient sur des observations empiriques et des éléments théoriques, furent cependant vivement contestés par Simberloff et Connor. Ces derniers reprochaient notamment à Diamond l'absence d'hypothèse nulle permettant de tester l'influence de la compétition sur la distribution des espèces (Connor and Simberloff, 1979), et avançaient que des différences dans la capacité de dispersion des espèces pouvaient expliquer les patrons observés. A de larges échelles spatiales, la question du rôle joué par les interactions spécifiques reste encore débattue.

A une échelle géographique plus restreinte, en revanche, davantage d'éléments permettent de mettre en évidence l'influence de la compétition sur la répartition des espèces (Robertson, 1996; Tilman, 1982). Terborgh and Weske (1975) font notamment le constat que les interactions compétitives peuvent restreindre la distribution de certaines espèces d'oiseaux, comme il l'ont observé le long d'un gradient altitudinal des Andes Péruviennes. Ces résultats sont conformes à ceux d'études récentes, qui démontrent que la compétition contraint la colonisation de certaines espèces de plantes le long d'un gradient altitudinal (Choler et al., 2001).

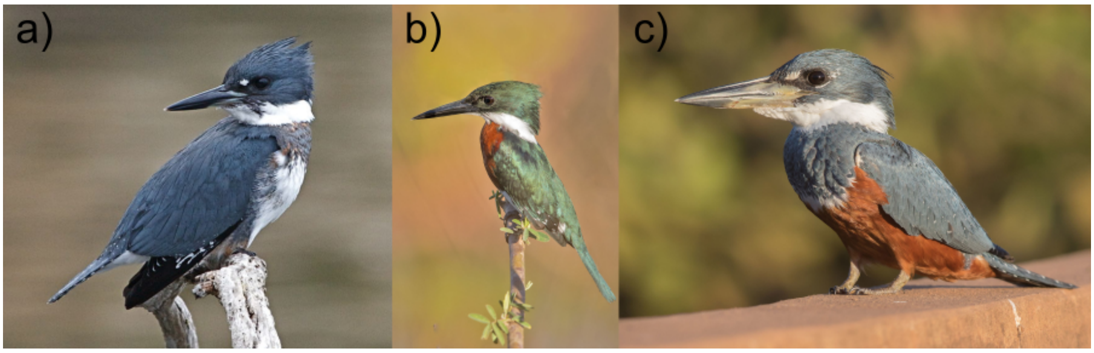

Figure 4: Robert MacArthur fait l'hypothèse que la distribution du martin pêcheur *M.alcyon* (a) est contrainte au sud de son aire de répartition par la présence de deux autres espèces compétitrices : *C. americana* (b) et *M.torquata* (c). Crédits : a) Teddy Llovet , b) & c) : Andreas Trepte.

Des interactions positives peuvent également conditionner la distribution spatiale des espèces. Un des premiers cas décrit en écologie fut celui du cactus *Carnegiea gigantea* "Cactus Saguaro", dont la survie est facilitée lorsqu'il pousse à proximité immédiate d'une espèce "nourrice" comme *Parkinsonia microphylla* (Niering et al., 1963). Il a également été montré que des interactions positives entre plantes permettaient à certaines espèces d'étendre leur distribution vers de plus hautes altitudes le long d'un gradient altitudinal (Choler et al., 2001).

Dans des milieux aux conditions environnementales contraignantes, l'interaction des espèces avec leur environnement abiotique est également susceptible de créer différents types de patrons dans la distribution des espèces. C'est notamment le cas en présence d'espèces "ingénieures de l'écosystèmes", capables de modifier leur environnement abiotique. Ceci peut s'observer en particuler dans les milieux arides, dans lesquels des patrons en patchs, réticulés ou en bandes peuvent émerger dans l'espace du fait d'intéractions entre des espèces ingénieures et leur environnement (Meron et al., 2004; Gilad et al., 2004; von Hardenberg et al., 2001). Dans cet exemple, la présence d'un couvert végétal améliore les conditions micro-climatiques, tout comme la rétention d'eau ou de nutriments. Ceci favorise en retour la survie et le développement des végétaux (von Hardenberg et al., 2001; Kéfi et al., 2007). L'amélioration des conditions environnementales en présence d'un couvert végétal peut également faciliter l'installation d'autres espèces végétales, comme décrit dans le paragraphe précédent. En revanche, lorsque le sol est à nu, les conditions ne permettent pas l'installation d'un couvert végétal (Kéfi et al., 2007).

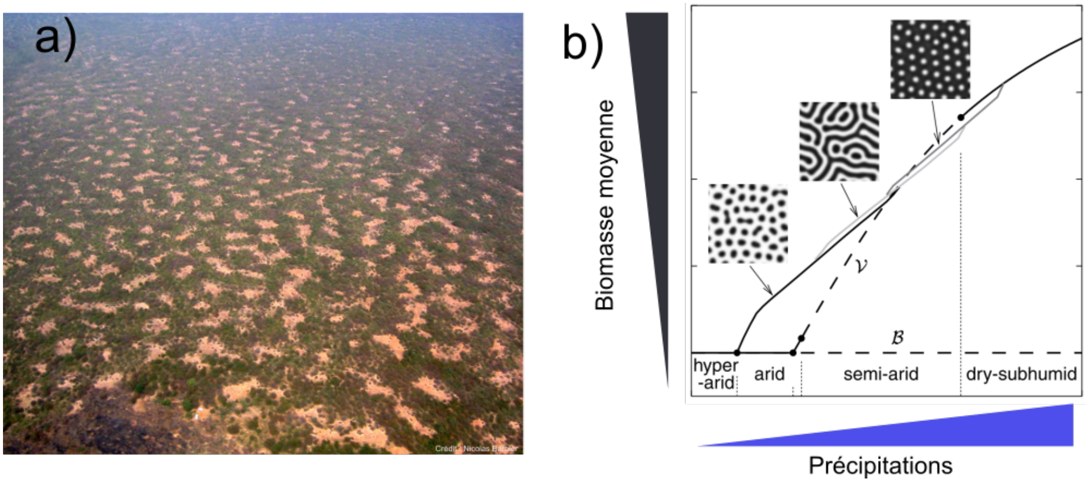

Figure 5: A) Patrons de végétation dans une zone aride du Niger. b) Patrons de végétation prédits théoriquement en fonction du taux de précipitation. Modifié d'après von Hardenberg et al. (2001)

Degré d'intégration des communautés : de l'individu au super-organisme

Le degré d'intégration d'une communauté correspond au niveau d'interdépendance des espèces entre elles. Dans le cas de l'hypothèse individualiste, le degré d'intégration d'une communauté est par définition faible, voire nul. La dynamique d'une communauté peut alors être comprise en étudiant tous ses éléments - *i.e* ses espèces - considérés séparément. Aucun comportement collectif émergent n'est attendu. L'hypothèse de la communauté-organisme stipule le contraire : chaque entité est en interaction avec d'autres, et il en résulte des phénomènes collectifs à l'échelle du groupe que l'on ne peut comprendre en étudiant séparément chacune de ses entités. Ces deux visions des communautés sont encore largement débattues en écologie, qu'il s'agisse des conséquences évolutives associées à la considération des communautés en tant que "super-organismes" (comme la sélection de groupe, Wilson and Sober (1989)) , ou des patrons spatiaux de communautés (McIntosh, 1998).

L'existence de hauts degrés d'intégration entre espèces est reconnue depuis longtemps en écologie, notamment en présence d'un faible nombre d'espèces. Ces associations hautement intégrées se basent sur la présence d'interactions positives entre espèces, qu'elles soient directes ou indirectes. Les interactions mutualistes directes constituent un exemple dans lequel l'association d'au moins deux organismes est bénéfique pour chacun d'entre eux, voire même obligatoire. Ces associations d'organismes - aussi qualifiées "d'holobiontes" (Gordon et al., 2013) - sont nombreuses, à l'image de certaines formations coralliennes qui résultent de la symbiose entre un polype animal et des dinophytes unicellulaires, les zooxanthelles.

Lorsque de nombreuses espèces sont présentes au sein d'une communauté, plusieurs mécanismes peuvent mener à l'émergence de comportements collectifs entre espèces.

Dans le cas de l'utilisation d'une même ressource - *i.e* un bien commun - par différentes espèces, des comportements collectifs sont observés dans des milieux aux conditions environnementales contraignantes. En modifiant les conditions environnementales, ces espèces peuvent notamment faciliter leur accès collectif à une ressource et en maintenir l'approvisionnement. C'est notamment le cas de plantes vivant en milieu désertique (Kéfi et al., 2007) dans lesquels la disponibilité en eau est faible. Ce phénomène par lequel les espèces modifient leur environnement est qualifié de "construction de niche". Les conséquences évolutives de ce processus ont reçu beaucoup d'attention de la part des écologues depuis les années 1990 (Odling-Smee et al., 1996, 2003). En revanche, les conséquences écologiques de tels processus n'ont été explorées que plus récemment, notamment en écologie théorique (Kylafis and Loreau, 2008, 2011). Plusieurs exemples suggèrent que la construction de niche puisse augmenter le niveau d'intégration d'une communauté, notamment par une modification collective de l'environnement bénéfique pour de nombreuses espèces (De longe et al., 2008; Sternberg et al., 2007).

Plusieurs espèces de palétuviers sont notamment capables de modifier la salinité de l'eau (Sternberg et al., 2007) dans des écosystèmes côtiers. Ceci a pour conséquence l'exclusion d'autres espèces d'arbres peu tolérantes aux eaux saumâtres, ce qui peut être interprété comme un cas de compétition inter-communauté. Cependant, peu de recherches théoriques ont été réalisées afin d'identifier les conditions sous lesquelles de tels processus peuvent être observés (Bearup and Blasius, 2017; Jiang and DeAngelis, 2013), et quels sont leurs conséquences sur les patrons spatiaux.

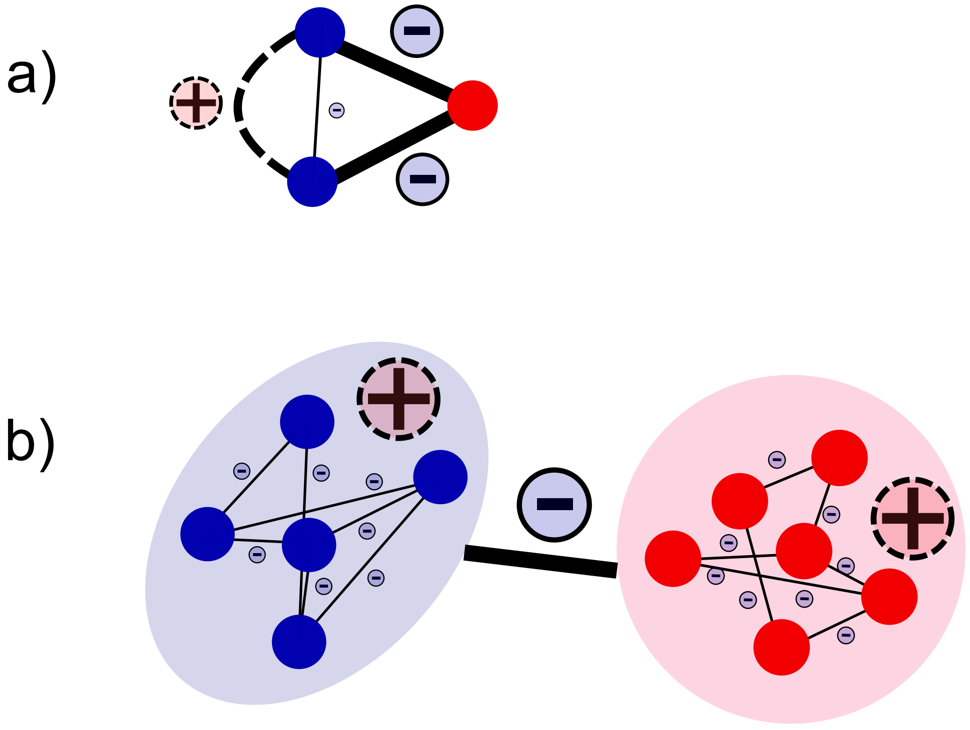

Figure 6: Emergence d'interactions indirectes positives (+) entre espèces en présence d'interactions négatives directes (-) : a) cas à trois espèces, b) Présence de nombreuses espèces. Les disques pleins représentes les espèces, l'épaisseur des liens d'interactions est liée à l'intensité de ceux-ci.

Un haut niveau d'intégration peut également émerger du fait d'interactions inter-spécifiques indirectes. C'est notamment le cas en présence de deux groupes d'espèces, dans lesquels les interactions compétitives sont faibles en intra-communauté, et fortes en inter-communauté. Dans ce cas, des interactions positives nettes peuvent alors émerger au sein d'une communauté, et dépasser la compétition directe en intensité. L'importance des interactions indirectes, notamment positives, avait déjà été mise en avant par divers travaux en écologie théorique (Lawlor, 1979; Wootton, 1994; Levine, 1976). En se focalisant sur l'exemple des communautés bactériennes, des études théoriques récentes ont notamment montré qu'une communauté pouvait être remplacée par une autre communauté dans un contexte purement compétitif, et en l'absence d'interactions positives directes (Tikhonov and Monasson, 2017; Tikhonov, 2016a). Observés expérimentalement (Rillig et al., 2015), ces phénomènes qualifiés de "coalescence" impliquent que la présence d'une espèce est davantage prédite par la communauté dans laquelle elle est incluse, plutôt que par ses performances individuelles. Ces conclusions s'opposent à l'hypothèse purement individualiste, qui impliquerait l'émergence d'une communauté tierce comprenant les espèces les plus performantes de deux communautés.

Le degré d'intégration des communautés est pressenti pour avoir une influence déterminante sur les changements dans la composition spécifique lorsque l'environnement change. L'hypothèse individualiste, avec un très faible degré d'intégration, prédit des changements graduels uniquement basés sur les préférences des espèces considérées individuellement. Au contraire, dans le cas de communautés hautement intégrées, on s'attend à des changements importants de composition spécifique dans le temps ou dans l'espace, avec le remplacement d'une communauté par une autre dans les cas les plus extrêmes.

Objectifs généraux

Malgré de nombreux travaux empiriques réalisés dans divers écosystèmes, les mécanismes impliquant des changements individuels ou collectifs sont mal connus. Le long de gradients environnementaux, des changements graduels tout comme des discontinuités dans la composition des communautés ont été observés dans l'espace comme dans le temps. L'objectif de cette thèse est de mettre en évidence les conditions sous lesquelles différents types de patrons de communautés peuvent émerger, dans le temps ou dans l'espace. Nous avons utilisé une approche de modélisation théorique dans l'ensemble de ce travail, en nous focalisant sur le rôle des interactions entre les espèces et avec leur environnement abiotique. Dans de nombreux cas, on s'attend à ce que la réaction des communautés aux changements de leur environnement se situe entre les deux types de patrons prédits par les visions individualiste et de la communauté-organisme. Ce travail, en plus d'identifier les conditions sous lesquelles ces différentes dynamiques peuvent émerger, s'intéresse également à quantifier l'intensité des changements spécifiques, et à les repositionner entre ces deux visions opposées.

Dans le premier chapitre, nous nous intéressons en particulier au rôle que peut jouer la compétition inter-spécifique dans l'émergence de différents types de patrons spatiaux. Dans quelles conditions des remplacements graduels ou au contraire abrupts et collectifs sont-ils attendus le long d'un gradient environnemental ?

Le second chapitre se focalise plus précisément sur des changements abrupts de composition spécifique, appelés écotones. Nous nous intéressons au rôle que peuvent jouer les interactions entre des espèces ingénieures et l'environnement dans l'émergence de discontinuités dans la composition spécifique.

Des changements abrupts (collapses) dans la composition des communautés peuvent advenir dans le temps ou dans l'espace, même lorsque l'environnement change graduellement. Dans le troisième chapitre de ce manuscrit, nous nous focalisons sur le rôle que peut jouer la biodiversité contre de telles transitions abruptes, dans le cas où les communautés sont soumises à différents types de perturbations environnementales dans le temps.

Résumé des chapitres

Chapitre 1

Les visions individualiste et de la communauté-organisme prédisent des patrons d'abondances spécifiques différents le long de gradients environnementaux.

La vision individualiste prédit des changements graduels dans la composition et l'abondance des espèces, quand la vision de la communauté-organisme prédit des changements abrupts.

L'objectif de cette étude est de déterminer dans quelles conditions des changements graduels ou discontinus dans la composition des communautés sont susceptibles d'être observés. Nous nous focalisons dans ce travail sur l'influence de la compétition inter-spécifique, et le rôle que peut jouer la dispersion dans l'émergence de patrons spatiaux. Une approche de modélisation théorique est développée, avec l'utilisation d'un modèle de compétition Lotka-Volterra couplé à un modèle de dispersion.

Nos résultats montrent que la compétition inter-spécifique influence fortement les patrons de communautés le long des gradients environnementaux. Les patrons discrets et continus ne constituent en réalité que deux cas extrêmes au sein d'un continuum de possibilités. Dans le cas où les interactions sont faibles, avec une faible variance, les changements d'abondances sont graduels le long du gradient. En revanche, lorsque des interactions faibles et fortes sont présentes au sein de la communauté, on observe l'émergence de patrons discrets, avec des zones séparant des communautés discrètes, au niveau desquelles un fort renouvellement d'espèces est observé. Ces transtitions abruptes d'une communauté à l'autre sont dues à la présence d'états stables alternatifs dans le système. Ces derniers résultent de la présence d'intéractions mutualistes indirectes entre espèces, alors même que toutes les espèces ont des interactions directes compétitives. Nos résultats montrent également le rôle de la dispersion dans l'émergence de patrons de communautés. Une augmentation de l'intensité de celle-ci contribue notamment à uniformiser la composition des communautés, et à masquer les effets de la compétition.

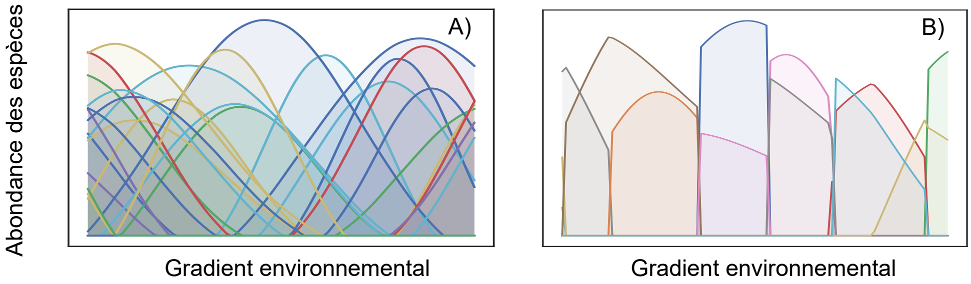

Figure 7: Patrons spatiaux de communautés : A) Faibles interactions compétitives, B) Forte intensité et forte variance des intéractions compétitives

Ces résultats montrent que la prise en compte des interactions compétitives est primordiale dans l'étude des patrons spatiaux de communautés. Lorsque de forts et de faibles compétiteurs sont présents au sein de la communauté, des interactions positives indirectes peuvent apparaître et mener à l'émergence de communautés discrètes dans l'espace.

Chapitre 2

Les changements rapides dans la composition des communautés, qualifiés d' "écotones", peuvent être la conséquence de changements rapides des conditions environnementales. C'est notamment le cas lors de variations des propriétés physico-chimiques d'un sol. Ces changements rapides de composition peuvent également advenir en présence d'un seuil physiologique, comme l'occurrence régulière d'événements de gel le long d'un gradient altitudinal. La possibilité que des écotones soient la résultante d'intéractions entre des espèces et leur environnement abiotique a cependant été peu étudiée. Des espèces capables de modifier leur environnement sont qualifiées d'ingénieures de l'écosystème. Lorsque la modification de l'environnement se fait au bénéfice de leur propre croissance, le phénomène est alors qualifié de "construction de niche écologique". Cette étude a pour objectif d'identifier dans quelles conditions la construction de niche peut conduire à l'émergence de discontinuités dans la composition spécifique des communautés, associées à des discontinuités dans les conditions abiotiques le long de gradients environnementaux.

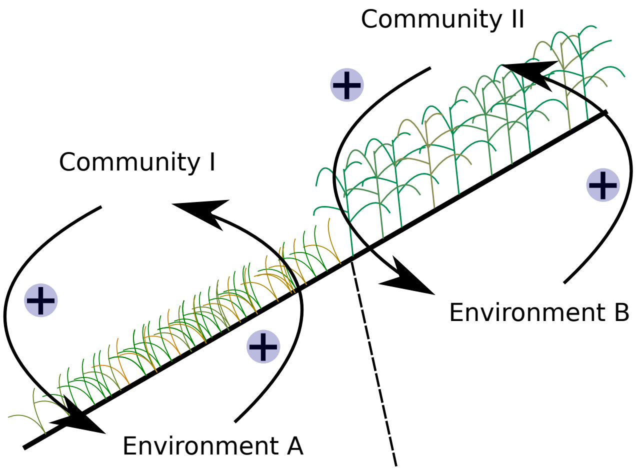

Figure 8: Illustration qualitative de l'effet d'interactions espèces-environnement sur l'émergence d'un écotone

Nous utilisons dans cette étude une approche de modélisation, avec l'utilisation d'un modèle de compétition Lotka-Volterra qui couple la dynamique des espèces à la dynamique d'une variable environnementale. Des simulations numériques ainsi que des techniques analytiques sont utilisées afin de déterminer les conditions dans lesquelles des écotones peuvent apparaître.

Les résultats montrent que la modification de l'environnement par divers ingénieurs de l'écosystème induit l'apparition d'intéractions indirectes entre espèces. Ces interactions indirectes, qui peuvent être positives ou négatives, peuvent conditionner l'apparition d'écotones, avec des changements abrupts dans la composition des communautés et des conditions environnementales. La biodiversité joue un rôle important dans l'apparition de ces écotones, au travers de deux effets distincts. Dans le cas où les ingénieurs modifient fortement les conditions environnementales, c'est la diversité fonctionnelle - c'est à dire les préférences environnementales de ces espèces - qui entre en compte et influence le nombre d'écotones et leurs localisations le long d'un gradient. En revanche, lorsque les ingénieurs sont faibles, le nombre d'espèces va jouer un rôle important dans l'apparition des écotones. Une espèce, seule, n'est pas capable de modifier l'environnement pour son propre bénéfice, et ainsi créer une discontinuité. En revanche, de nombreuses espèces ayant des exigences écologiques similaires vont être capables de modifier collectivement l'environnement pour leur bénéfice commun, et créer un écotone.

La prise en compte des interactions entre les espèces et leur environnement est donc primordiale dans l'étude des patrons spatiaux de communautés. La biodiversité jouant un rôle important dans l'apparition de ces patrons spatiaux, l'érosion actuelle de celle-ci pourrait impacter fortement la distribution spécifique des espèces à diverses échelles.

Chapitre 3

Dans ce chapitre, nous étudions le rôle que peut jouer la biodiversité dans la protection des communautés contre des collapses.

Les écosystèmes répondent de différentes façons à des changements des conditions environnementales. Dans certains cas, des changements abrupts dans la composition des communautés comme dans leur fonctionnement peuvent advenir. Parmi les différents effets induits par la biodiversité sur le fonctionnement des écosystèmes, il a été démontré que celle-ci augmentait la productivité, au travers d'effets de complémentarité entre espèces et de sélection des espèces les plus productives. Dans certains écosystèmes, le maintien d'un certain niveau de biomasse est crucial afin de maintenir le fonctionnement de ceux-ci. C'est notamment le cas de certains écosystèmes forestiers dans lequel le maintien d'un certain niveau de biomasse permet de limiter les dégâts liés à l'occurence de feux, susceptibles de menacer le maintien d'un stade forestier. Dans cette partie, nous illustrons les conséquences de la perte de biodiversité sur le risque de collapse, en utilisant un modèle de compétition Lotka-Volterra avec un effet d'Allee sur la biomasse totale de la communauté. Deux types de perturbations environnementales sont considérés : une pression excercée sur les espèces, et des fluctuations stochastiques de l'environnement. Nous montrons premièrement qu'une diminution du nombre d'espèces induit une baisse de l'intensité des pressions environnementales nécessaires à une transition brutale. Dans ce cas, la disparition d'espèces réduit la résistance de la communauté. Nous illustrons également le fait qu'une baisse de diversité fonctionnelle au sein de la communauté induit également une augmentation du risque de collapse en présence de stochasticité environnementale.

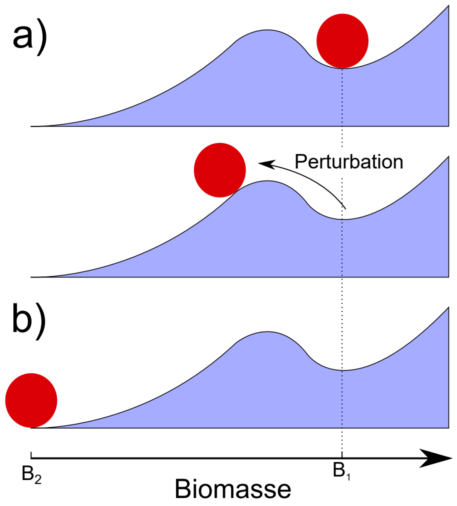

Figure 9: Illustration qualitative d'un collapse dû à une perturbation environnementale. La balle rouge représente l'écosystème, le paysage de stabilité montre les différents équilibres. En présence d'une perturbation, le système passe d'un état B_1 (a), à un état B_2 (b).

General Introduction

Historical context

Ecological communities are composed of different species that interact with each other and with their environment. The way in which communities respond to changes in abiotic conditions over time and space is an ancient research theme in ecology. In particular, the ways in which the specific composition changes when the environment gradually changes have always been a subject of debate. In the 19th century, the naturalist Alexandre de Humbolt was one of the first to describe vegetation changes along an altitudinal gradient in the equatorial Andes (Bonpland and von Humboldt, 1805). The founder of phytogeography, *i.e* field of science studying plant spatial distributions, described disctinct ”plant regions” with particular species composition that were easy to identify and distinguish. He notably described an ”alpine plant region”, followed by a ”lichen region” as the elevation increased along the gradient (Figure 1). The scientist, however, provided little information on the rate at which changes in species composition occur in space. The way in which species appear or disappear when the abiotic conditions - such as temperature, soil conditions or precipitations - change will then give rise to numerous debates within the ecologist community (Egerton, 2015). And once again, it is among the field of plant ecology that one of the most important controversy occurred at the beginning of the 19th century. Frederic Clements, an American plant ecologist, argued that changes in specific composition are discrete in space when the environment gradually changes : a community replaces another one. In contrast, Henry Gleason (1926) suggested that such changes are gradual, and that no discrete entities in community composition can be distinguished when the environment changes gradually (Fig. 2). This viewpoint of the gradualism in changes will subsequently be called "the continuum hypothesis".

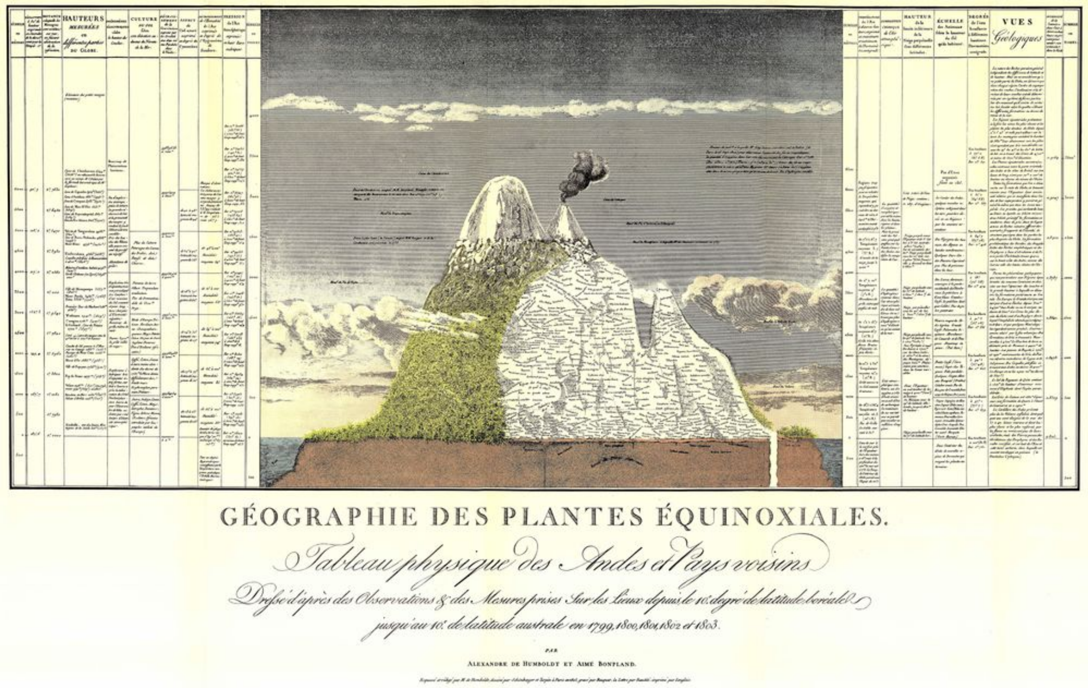

Figure 1: Map of plant distribution along an altitudinal gradient in the equatorial Andes, by Alexandre de Humbolt. (Bonpland and von Humboldt, 1805)

The study of species distribution in space is developing concurrently with the interest in species' temporal succession (Egerton, 2015). The first observations of successions are fairly old, as attested by the observations of William King in "Of the Bogs, and Loughs of Ireland" (King, 1685). In his essay "Oeconomia naturae", Carl Von Linnaeus described the succession from a practically bare rock state with lichens to a forest (Von Linne, 1972). At the beginning of the 20th century, Frederic Clements developed in "An analysis of the development of vegetation", the idea that succession dynamics are composed of several discrete "stages", culminating in a terminal plant association called "climax" (Clements, 1916). In contrast, Henri Gleason argued that it is generally not possible to discriminate distinct communities in time (Gleason, 1926) (Figure 2).

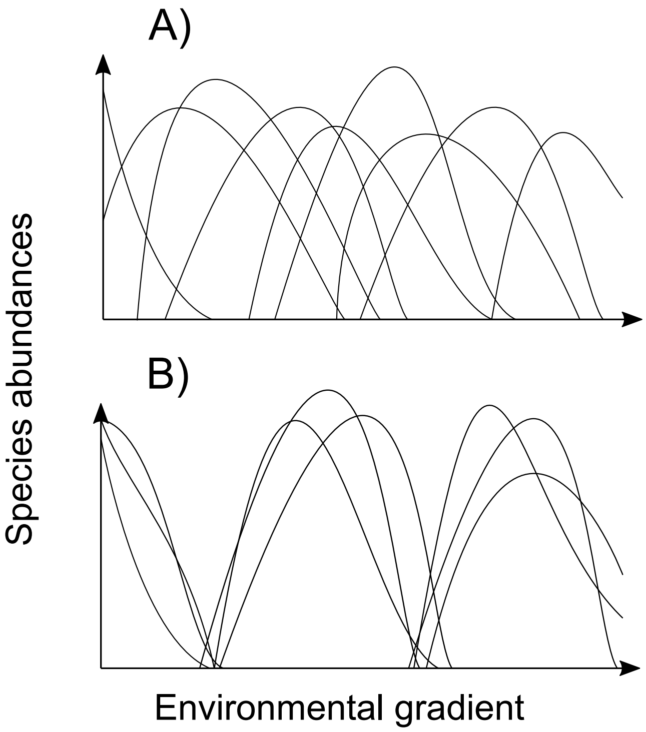

Figure 2: Community patterns along an environmental gradient (spatial or temporal gradient) : A) Under the continuum hypothesis, changes in composition and species abundance are gradual in space and in time. B) Under the Clementsian view of nature, communities are discrete entities separated by boundaries (space) or short period (time) in which a high species turnover is observed.

This debate, beyond an opposition regarding changes in specific composition in time or space, raised deeper questions about the nature of communities. Notably, Clements compared the succession dynamics leading to the climax to a complex organism's development : *"The developmental study of vegetation necessarily rests upon the assumption that the unit or climax formation is an organic entity. As an organism the formation arises, grows, matures, and dies."* (Clements, 1916). With this vision, he unified temporal succession and spatial changes in community composition within a single phenomenon of "development". When the environment gradually changes in space, Clements interpreted vegetation zones as distinct stages of a development dynamics : *In the case of water, for example, the bare area of excess is the starting-point for the series of zones, as it is for the series of stages. In short, zones are stages* (Fig. 3). This view of communities as super-organisms was rejected by Tansley (1935), even though he recognized the existence of high organization levels in some plant associations, naming them ”quasi-organism”. Henri Gleason brought a stronger opposition to the concepts related to ”community as organisms”. He rather considered that community dynamics are primarily based on the species’ dynamics, individually taken, that are present in the community : *every species of plant is a law unto itself, the distribution of which in space depends upon its individual peculiarities of migration and environmental requirements. Its disseminules migrate everywhere, and grow wherever they find favorable condition.* This is the individualistic hypothesis, in opposition to Clements’ organismic view of nature.

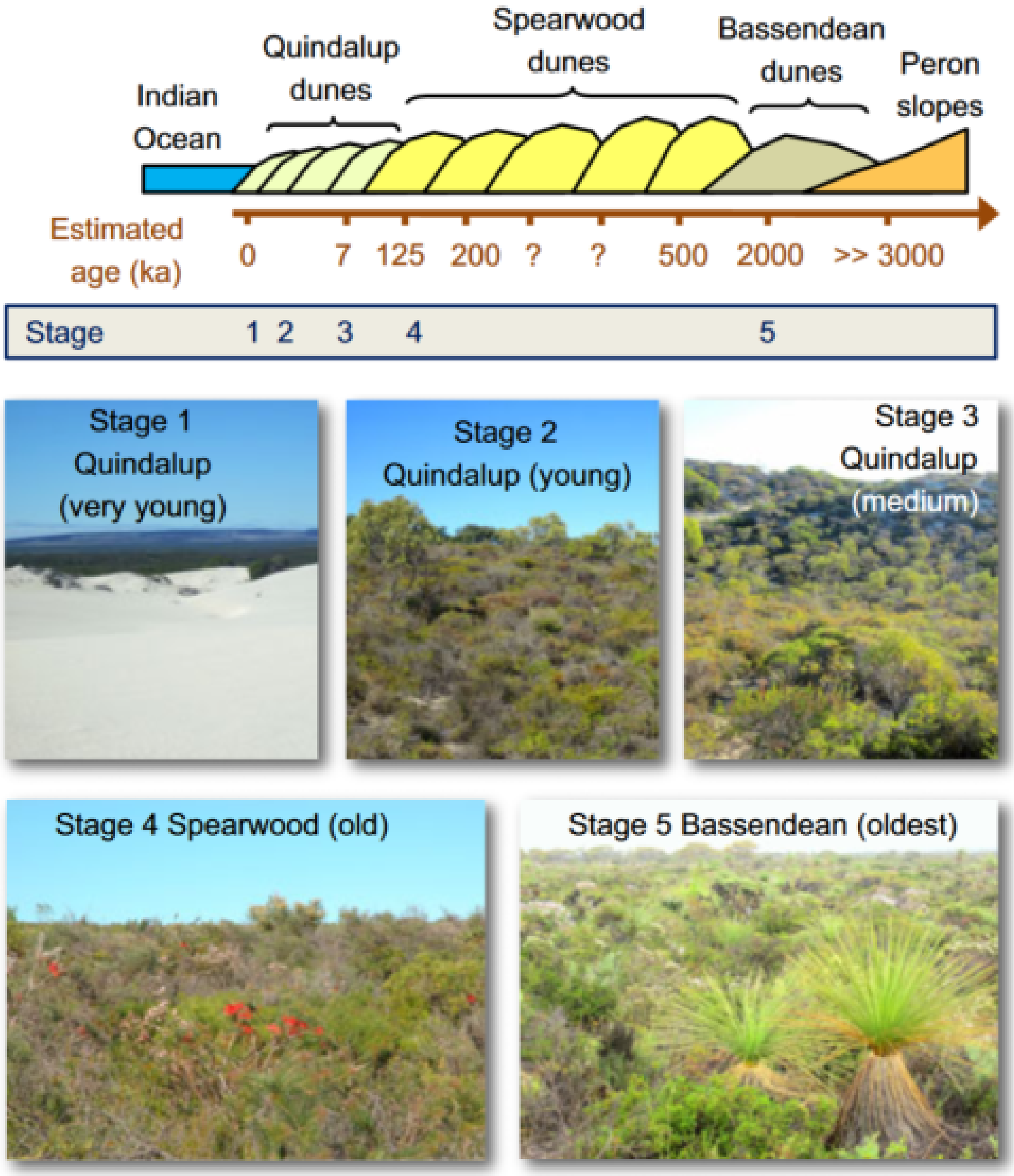

Figure 3: Vegetation chronosequence. In this example of a coastal ecosystem, we can observe different stages of a succession dynamics. The age of dune formation increases as the distance from the coastline increases. Next to the sea, dune formation is recent (0 - 125 000 years), and early stages of a plant succession are observed. As the distance to the coast increases, the age of dune formation increases (between 125 000 ans and 2 million years), and more advanced succession stages can be observed. Species composition as well as vegetation type (grass, bushes, etc.) changes along the chronosequence. Illustration : (Laliberté et al., 2012)

Interactions and spatial species' distribution

These 20th century controversies rely more on observed patterns, rather than on the intrinsic causes of these various patterns. The intensity and nature of specific interactions, or the relationships between species and their environment are among the various processes that might influence species distribution in time or in space. The recognition of interspecific interactions is fairly old in the field of plant ecology, in which the individualistic versus organismic controversy emerged. In 1820, swiss botanist De Candolle already noticed the existence of plant competition : *All the plants of a given country, [all those of a given place,] are at war one with another* (de Candolle, 1820). First foundations of the competition theory are based on the work of Vito Volterra (1926) and Alfred James Lotka (1926), who proposed the Lotka-Volterra equations to formalize competitive dynamics. These equations are themselves based on the Verhulst logistic equation (Verhulst, 1838), but they include interspecific competition coefficients that reduce species' growth rates. These equations are among the most widely used models in the study of population dynamics nowadays. New theoretical developments were then added to these pioneering works, describing more accurately competition for resources (Tilman, 1982; MacArthur, 1969), or interference competition between species (Case and Gilpin, 1974).

Interspecific competition was early designated as a potential factor influencing species distribution in space. In "Geographical ecology", Robert MacArthur (1972) made the assumption that the spatial distribution of Kingfisher *Megaceryle alcyon* is not constrained by resources at the south of its distribution, but rather by the competition with two other Kingfisher species : *Chloroceryle americana* and *Megaceryle torquata* (Fig.4). The question whether interspecific competition influences species' spatial distribution then led to several significant controversies. In 1975, Jared Dimaond made the assumption that community composition in space is mainly influenced by interspecific competition (Diamond, 1975). He argued that some species cannot coexist together, resulting in a checkerboard pattern as he observed in bird communities of several Oceanian islands. These results, based both on empirical observations and theoretical works were strongly contested. In particular, Connor and Simberloff considered that no null-hypothesis were included in Diamond's studies (Connor and Simberloff, 1979), and argued that differences in species' dispersal, among others, could be responsible for the observed patterns. At large spatial scales, the influence of competition on the species distribution is still debated nowadays.

At smaller geographical scales, however, the influence of competition on species distribution is more evident (Robertson, 1996; Tilman, 1982). For instance, Terborgh and Weske (1975) showed that competition can constrain bird distribution along an altitudinal gradient in the Peruvian Andes. These results are consistent with those of Choler et al. (2001), who showed that competition can constrain plant colonization along an altitudinal gradient.

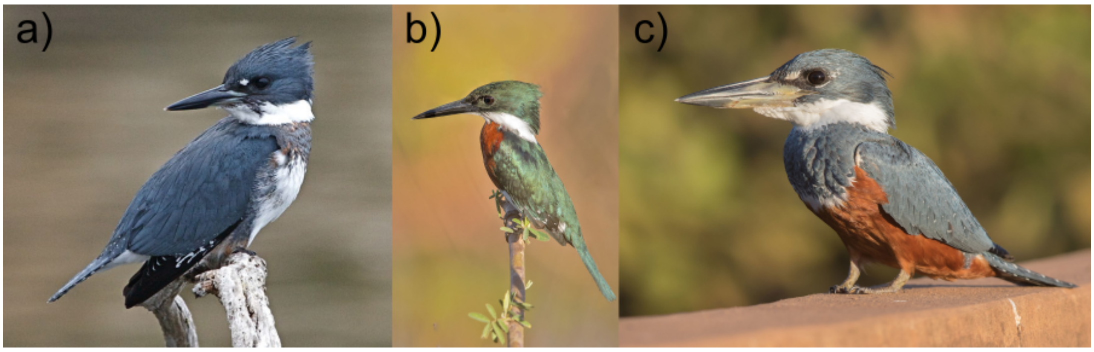

Figure 4: Robert MacArthur made the assumption that kingfisher *M.alcyon*'s southern distribution (a) is constrained by the presence of two other kingfisher species : *C. americana* (b) and *M.torquata* (c). Pictures : a) Teddy Llovet , b) & c) : Andreas Trepte.

Positive interactions are also likely to influence the spatial distribution of species. One of the first examples described in the literature is the Saguaro cactus *Carnegiea gigantea* whose survival is increased when growing close to a "nurse species", such as *Parkinsonia microphylla* (Niering et al., 1963). Similarly, it has been shown that positive interactions can allow an extension of plant distribution along an altitudinal gradient (Choler et al., 2001).

In harsh environments, interactions between plants and their environment is also likely to result in different spatial community patterns (Fig. 5). This is notably the case in the presence of species called ”ecosystem engineers”, that are able to substantially modify their abiotic environment. For instance, spotted or banded vegetation patterns can emerge from species-environment interactions in arid environments (Meron et al., 2004; Gilad et al., 2004; von Hardenberg et al., 2001). In this example, micro-climatic conditions are improved in the presence of a plant cover, as well as water and nutrient retention, which in turn promote plant survival and development (von Hardenberg et al., 2001; Kéfi et al., 2007). These improvements in environmental conditions are also likely to facilitate other species, as described above. In the presence of a bare soil, however, environmental conditions prevent plant development.

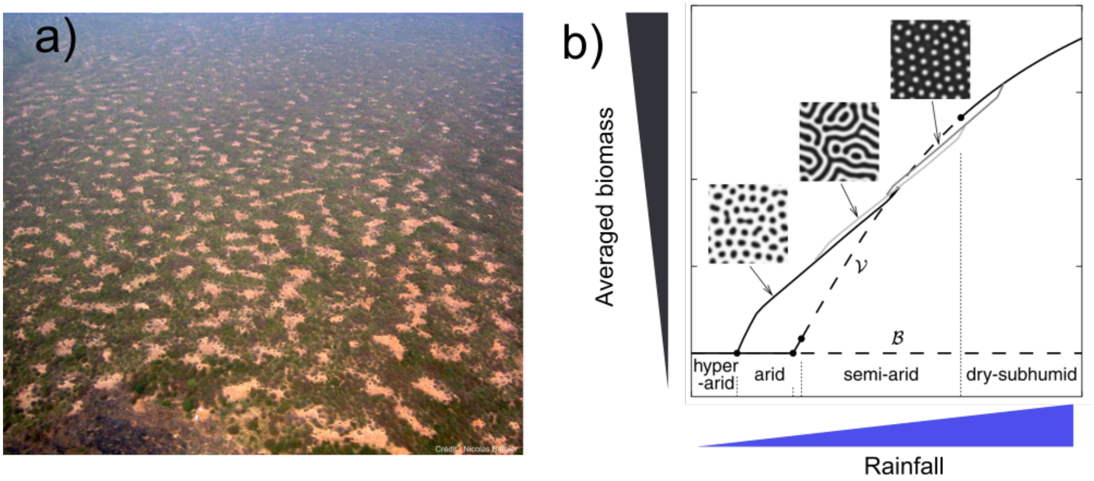

Figure 5: A) Vegetation patterns in an arid ecosystem, Niger. b) Theoretically predicted vegetation patterns depending on rainfall. Modified from von Hardenberg et al. (2001)

Degree in community integration : from individuals to the super-organism

The integration degree of a community corresponds to the level of inter-dependence among species. Integration degree is by definition weak, or zero, under the individualistic hypothesis. In this case, the community dynamics can be understood by considering all its compounds - *i.e* species - individually taken. There are no collective behaviours emerging from interspecific interactions. Under the organismic hypothesis, however, each species interacts with others, resulting in collective behaviours emerging at the community level. In this case, the community dynamics cannot be understood by considering each species separately. These two views of communities are still debated, either about their implications for evolution -such as group-selection (Wilson and Sober, 1989) - or for community patterns (McIntosh, 1998).

The existence of high integration degrees has been recognized for a long time in ecology, particularly in the presence of a few species. These highly integrated associations are based upon positive interactions between species, whether direct or indirect. In the case of direct positive interactions between two species, the presence of each member is beneficial, or even mandatory, for the other's survival. These associations, also termed ”holobionts”, are common (Gordon et al., 2013), such as the association between coral polyps and unicellular zooxanthellae (Dinophyta).

When there are numerous species, several processes are likely to lead to the emergence of collective behaviours among species.

When several species are using common resources - *i.e* common good - collective behaviours can be observed under harsh environmental conditions. By modifying the abiotic environment, species can facilitate their collective access to a resource, and maintain its supply. This is notably the case in arid environments (Kéfi et al., 2007), in which water availability is low. The process by which species modify their environment is called ”niche construction”. While the evolutionary consequences of niche construction have been widely studied since the 1990s (Odling-Smee et al., 1996, 2003), the ecological consequences were more recently addressed, notably in theoretical ecology (Kylafis and Loreau, 2008, 2011). Several examples suggest that niche construction is likely to increase the community's integration degree, by a collective modification of environmental conditions which benefits many species (De longe et al., 2008; Sternberg et al., 2007). For instance, several mangrove tree species are able to modify water salinity in coastal ecosystems (Sternberg et al., 2007). A consequence is the exclusion of other tree species that are not tolerant to high water salt concentrations. This can be interpreted as inter-community competition. Little is known, however, about the theoretical conditions in species interactions and environmental conditions under which such collective behaviours can emerge (Bearup and Blasius, 2017; Jiang and DeAngelis, 2013), and what are their consequences for spatial community patterns.

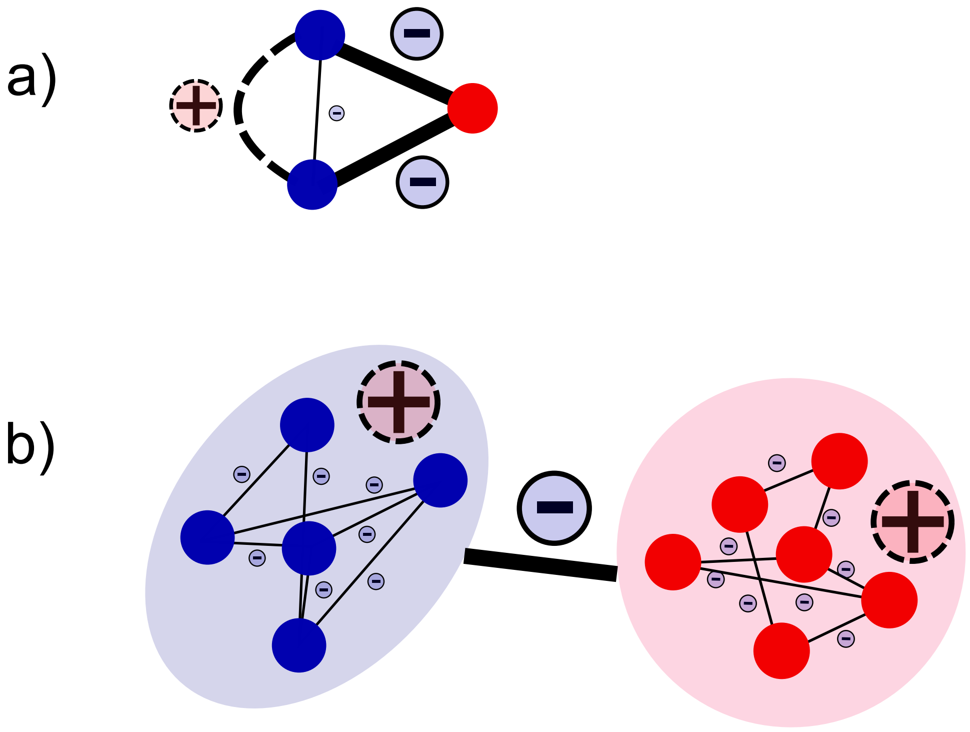

Figure 6: Emergence of indirect positive interactions between species (+) when species are in direct competition (-) : a) 3-species case, b) Numerous species. Solid disks represent species, and the width of solid lines represent the competition intensity.

A high integration degree within a community can also emerge from indirect species interactions. This is notably the case in the presence of two communities, for which competitive interactions are weak within a community, and strong among communities (Figure 6). In this case, net positive interactions can emerge within a community, with indirect positive interactions exceeding direct competition in intensity, as illustrated in Fig. 6. The emergence of such indirect interactions had already been the subject of studies in theoretical ecology (Lawlor, 1979; Wootton, 1994; Levine, 1976). Focusing on bacterial communities, recent theoretical findings showed that a community can be replaced by another one in a purely competitive context, and in absence of direct positive interactions among species (Tikhonov and Monasson, 2017; Tikhonov, 2016a). This phenomenon termed ”coalescence”, also observed in experiments (Rillig et al., 2015), implies that the presence of a species is best predicted by the community in which it is included, rather than on its own performances. These conclusions are in conflict with the purely individualistic hypothesis, under which a third community including the species with best performances of each group is expected to emerge.

The community integration degree is thus expected to have a critical influence on changes in species composition when environment changes. Under the individualistic hypothesis, gradual changes in species composition are expected. These changes are based on the species' environmental preferences, individually considered. In contrast, when the integration level is high, important and collective changes are expected, as predicted under the organismic hypothesis. In the most extreme case, a community can be replaced by another one.

Main objectives

Despite the large number of empirical studies conducted in different ecosystem types, the mechanisms leading to individual or collective behaviours are poorly understood. Along environmental gradients, gradual changes as well as discontinuities in community composition have been recorded in time and in space. The main objective of this thesis is to determine the conditions under which different community patterns can emerge in space or in time. Throughout this work, we have adopted a theoretical modelling approach, and we notably focused on the role played by the interactions between species, and between the species and their abiotic environment. In many cases, patterns in between those predicted by the individualistic and organismic extreme views are expected to occur. We thus focused on quantifying the rate at which changes occur - such as species turnover - with the aim to compare our results to those expected under the different hypothesis. In chapter one, we mostly focused on the role played by interspecific competition on the emergence of different types of community patterns. Under which conditions gradual, or rather discontinuous changes in community composition are expected along a spatial environmental gradient ? In chapter two, we focused specifically on abrupt changes in community composition, termed "ecotones". We studied the role played by ecosystem engineers - *i.e* species that modify their abiotic environment - in the emergence of discontinuities in species composition. Abrupt changes in community composition and functioning - *i.e* collapses - may occur in time, even though changes in environmental conditions are gradual. In the third chapter, we studied the role biodiversity might play in protecting ecosystems against collapse, in the presence of different environmental perturbations.

Summary of the chapters

Chapter 1

The aim of this study is to determine the conditions under which gradual or rather abrupt changes in species composition can be observed along a spatial environmental gradient. We specifically focus on the role played by interspecific competition and dispersal, by using a spatially explicit multispecies Lotka-Volterra competition model.

Our results show that organismic and individualistic forms of community organisation are two limiting cases along a continuum of outcomes. A high variance of competition strength leads to the emergence of organism-like communities. In this case, indirect positive interactions are observed, which result in the emergence of alternative stable states. By contrast, weak and uniform interactions induce gradual changes in species composition (Fig. 7). Dispersal plays a confounding role in these patterns. An increase in dispersal distance and intensity tends to homogenize species composition across space.

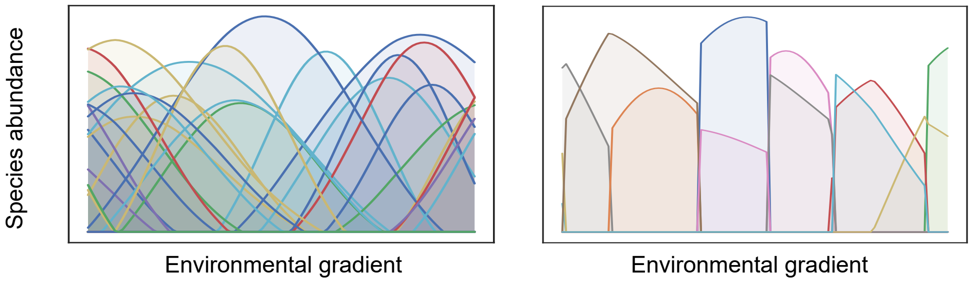

Figure 7: Spatial community patterns : A) Weak competition, B) Strong competition with a high variance

Our work highlights the critical importance of considering species interactions to understand and predict the responses of species and communities to environmental changes.

Chapter 2

Rapid changes in community composition, termed ”ecotones”, can result from the presence of rapid changes in environmental conditions, such as a change in soil physical or chemical properties. These abrupt changes can also be the result of physiological thresholds, such as the occurrence of frost events along an altitudinal gradient in an alpine ecosystem. The possibility that ecotones arise from interactions between species and their environment, however, has received little attention (Fig. 8).

Species that are able to modify their abiotic environment are called ”ecosystem engineers”. When the environment modification is profitable for the engineer, the process is called ”ecological niche construction”. In this study, we investigate how the diversity of ecosystem engineers, and their interactions, can give rise to ecotones. We build a spatially explicit dynamical model that couples a multispecies community and its abiotic environment. We use numerical simulations and analytical techniques to determine the biotic and abiotic conditions under which ecotone emergence is expected to occur, and the role of biodiversity therein. We show that the diversity of ecosystem engineers can lead to indirect interactions through the modification of their shared environment. These interactions, which can be either competitive or mutualistic, can lead to the emergence of discrete communities in space, separated by sharp ecotones where a high species turnover is observed.

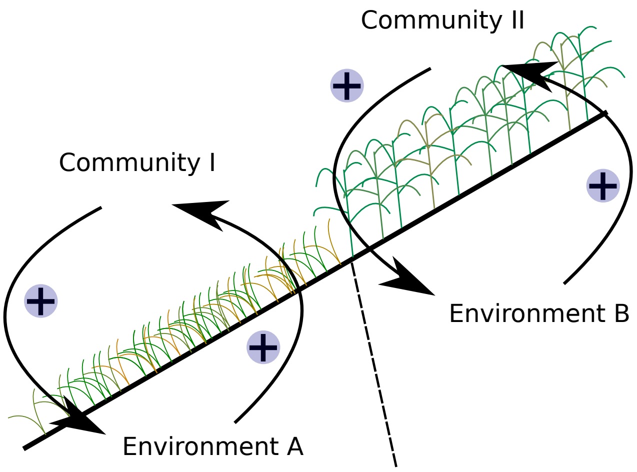

Figure 8: Qualitative scheme of the influence of species-environment interactions on ecotone emergence

Considering biodiversity is thus critical when studying the influence of species-environment interactions on the emergence of ecotones. This is especially true for the wide range of species that have small to moderate effects on their environment. Our work highlights new mechanisms by which biodiversity loss could cause significant changes in spatial community patterns in changing environments.

Chapter 3

In this chapter, we focus on the role biodiversity might play in protecting ecosystems against collapse. Ecosystems respond in different ways to environmental or anthropogenic perturbations. In some cases, abrupt shifts in community composition and ecosystem functioning can occur (Fig. 9). Among others, it has been shown that diversity could foster biomass productivity, notably through complementarity and selection effects. The maintenance of sufficient biomass levels can be critical for the maintenance of ecosystem functioning, as observed in various ecosystem types. This is particularly true when the ecosystem is facing environmental perturbations, as it is the case in tropical forest ecosystems, in which fire events can lead to a shift from a forest state to savannah. In this chapter, we illustrate the consequences of biodiversity loss on the risk of collapse. We use a competition Lotka-Volterra model with an Allee effect on total community biomass. Two perturbations types are studied : a press exerted on all species, and stochastic environmental perturbations (white noise). In the case of an environmental pressure, we first show that biodiversity loss results in a decrease of the critical press intensity leading to collapse. In this case, biodiversity loss decreases the community's resistance. We also show that a loss in functional diversity within a community increases the risk of collapse when the environment fluctuates stochastically.

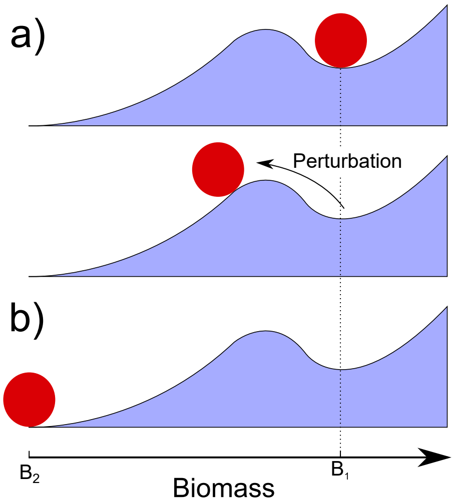

Figure 9: Qualitative illustration of a collapse due to an environmental perturbation. The ball represents the ecosystem, and the stability landscape shows the different equilibria. When the system is perturbed, it abruptly shifts from a state B_1 (a) to a state B_2 (b).

Chapter 1

Superorganisms or loose collections of species? A unifying theory of community patterns along environmental gradients

Title of the scientific article :

Superorganisms or loose collections of species? A unifying theory of community patterns along environmental gradients [1]

Keywords : Alternative stable states, community organisation, competition theory, critical transitions, environmental gradient, Lotka–Volterra model.

1.1 Abstract

The question whether communities should be viewed as superorganisms or loose collections of individual species has been the subject of a long-standing debate in ecology. Each view implies different spatiotemporal community patterns. Along spatial environmental gradients, the organismic view predicts that species turnover is discontinuous, with sharp boundaries between communities, while the individualistic view predicts gradual changes in species composition. Using a spatially explicit multispecies competition model, we show that organismic and individualistic forms of community organisation are two limiting cases along a continuum of outcomes. A high variance of competition strength leads to the emergence of organism-like communities due to the presence of alternative stable states, while weak and uniform interactions induce gradual changes in species composition. Dispersal can play a confounding role in these patterns. Our work highlights the critical importance of considering species interactions to understand and predict the responses of species and communities to environmental changes.

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[1] This work represents a collaboration with Egbert van Nes, Matthieu Barbier, Marten Scheffer and Michel Loreau. It is published in *Ecology Letters* : **Liautaud, K.**, van Nes, E.H., Barbier, M., Scheffer, M. and Loreau, M. (2019), Superorganisms or loose collections of species? A unifying theory of community patterns along environmental gradients. Ecol Lett, 22: 1243-1252. doi:10.1111/ele.13289

1.2 Introduction

A question that has long puzzled ecologists is the degree to which ecological communities should be regarded as integrated entities rather than loose collections of species or individuals. Clements (1916, 1936) and Gleason (1926) were the first to debate over this question, the former considering plant communities as complex superorganisms, whereas Gleason considered them as mere statistical collections of individuals.

This centennial debate lasts to this day, in no small part because the superorganism concept faces major definition issues (Wilson and Sober, 1989). Recent theoretical advances however, have provided a context in which this question can be addressed meaningfully: we can identify ecological dynamics that share enough important features with the concept of superorganism to support the use of this metaphor. A central ingredient is the existence of positive feedbacks in complex communities, whether there is direct facilitation between species or not. Positive feedbacks create integration: species benefit from each other, and appear or disappear together. As a consequence, we expect to see distinctive associations rather than arbitrary collections of species. In addition, these dynamics can show directionality in space (structuration and spread) and time (succession). Bunin (2018) showed that all these properties can occur together in widely-used models of ecological assembly dynamics, and therefore, that ecological communities can in principle exist in a recognizably organismic state.

We propose that the dichotomy between organismic and individualistic communities may now be reframed within a unified theoretical framework, with clearly identified ecological consequences. We choose to focus here on spatial patterns that can distinguish between Clementsian and Gleasonian communities, but a similar analysis applies to temporal patterns. In space, these two views of nature lead to very different predictions regarding species distributions and community patterns along environmental gradients. If the environment changes gradually, an individualistic community organization predicts the gradual replacement of species by new species as the environment changes (Gleason, 1926). In contrast, an organismic community organization implies the presence of discrete communities separated by sharp boundaries (Clements, 1916). Small changes in environmental conditions can thus be responsible for major shifts from one community to another. While the Clementsian organismic view of communities was widely accepted during the first part of the twentieth century (see Whittaker (1962) for an historical review), the individualistic view became dominant after the influential work of Whittaker (1951, 1956, 1967), who showed gradual changes in plant species composition and abundance along spatial environmental gradients.

Numerous empirical studies have studied species abundances and distributions along spatial environmental gradients, with widely divergent conclusions. For instance, Lieberman et al. (1996) and Vazquez G. and Givnish (1998) failed to find discrete plant communities along altitudinal gradients, in agreement with Whittaker's (1956) earlier results. (Smale, 2008) also observed continuous benthic community changes along a depth gradient in a marine ecosystem. In contrast, other studies (Kitayama and Mueller-Dombois, 1992; Dech and Maun, 2005; Hemp, 2006) highlighted the presence of clear discontinuities in species composition along environmental gradients. It seems that both continuous and discontinuous changes are possible but few of these studies identified the ecological and environmental conditions leading to the observed patterns. Even discontinuous changes have been interpreted from an individualistic viewpoint, as the result of physiological thresholds or abrupt changes in the environment (Kent et al., 1997; Schils and Wilson, 2006; Peppler-Lisbach and Kleyer, 2009). There is need to understand how abrupt changes in species composition can emerge from species interactions, even when the environment changes gradually. Therefore, a theory is still missing to unify these different types of community organization. Communities that show abrupt changes in space might also be expected to show abrupt changes in time as environmental conditions change gradually. Such abrupt changes can have important implications for the maintenance of ecosystem services in a changing world, and thus for human well-being

(Schroter, 2005; Worm et al., 2006). In a context of rapid global change (Vitousek, 1997; Halpern et al., 2008; Nagelkerken and Connell, 2015) , identifying the ecological conditions leading to abrupt changes in space might thus help us identify communities prone to show abrupt changes in the next decades.

The possibility of organism-like communities hinges on interdependences between species: in the absence of species interactions, we expect a fully individualistic pattern where a species' distribution along the gradient is determined mainly by its fundamental niche and dispersal. In previous studies, organismic patterns have mostly been discussed in the context of facilitative interactions (Wilson and Sober, 1989; Callaway, 1997) as the concept of organism suggests a mutual dependence and synergy between components. In an ecological community, a high degree of species interdependence can arise from positive feedback loops, such as those created by facilitation (Kéfi et al., 2016, 2007).

Whether non-facilitative interactions can also lead to synergy between species is less intuitive. Competition has been shown to be an important ecological driver of species abundance and distribution in space, both theoretically (MacArthur, 1972; Tilman, 1982) and empirically (Terborgh and Weske, 1975; Case and Bolger, 1991; Robertson, 1996) . Along spatial environmental gradients, interspecific competition is expected to greatly influence the presence and abundance of species, as supported by several empirical studies (Terborgh and Weske, 1975; Choler et al., 2001). But these studies did not explicitly discuss the individualistic or synergistic nature of patterns created by competition. The aim of the present work is to assess whether competition theory can encompass these two opposite views of nature. We study the influence of competition on the emergence of different community patterns using a spatially explicit multi-species Lotka-Volterra model, where species competitive abilities vary smoothly along a 1-D spatial gradient of environmental conditions. How strong competition is, and how unevenly it is distributed can both influence community structure and properties (Kokkoris et al., 1999, 2002; Bunin, 2017a). Therefore, we focus on the influence of the mean and variance of competitive interaction strength on the emergence of different community patterns, with and without dispersal among neighbouring sites.

1.3 Model and Methods

1.3.1 Competition

We model the dynamics of a community of 50 species using a multi-species Lotka-Volterra competition model along a gradient of an arbitrary environmental factor:

$$\frac{dN_{i,k}}{dt} = r_i N_{i,k} (1 - \frac{\sum_j \alpha_{ij} N_{j,k}}{K_{i,k}}) \tag{1.1}$$

where $N_{i,k}$ and $K_{i,k}$ are the abundance and carrying capacity, respectively, of species i at location k; r is the intrinsic rate of increase, assumed for simplicity to be equal for all species; and α_{ij} is the competition coefficient of species j on species i.

The competitive ability and dominance of each species is determined by both its carrying capacity and its interactions. If either depends on the environmental factor, different species will dominate in different locations along the gradient. In the main text, we assume that changes in dominance arise from varying carrying capacities and constant interaction coefficients, but we show similar results in the Supporting Information when interaction coefficients vary instead (see **Appendix S3.2**). Furthermore, we only consider symmetrical competitive interactions in the main text, i.e. :

$\alpha_{ij} = \alpha_{ji} \quad \text{with} \quad 0 \leq \alpha_{ji} \leq 2,$

but we relax this assumption in **Appendix S3.1**. Note that intraspecific competition coefficients (α_{ii}) are by definition equal to 1 in this model formulation. The environmental factor is represented by the variable p, which varies smoothly from 100 to 200 arbitrary units along the gradient. The fundamental niche of each species is defined by its carrying capacity, which is assumed to follow a Gaussian distribution along the gradient. It is characterized by a centre

C_i, the value of the environmental factor for which the carrying capacity reaches its maximum value O_i, and a tolerance range T_i. The centres of the fundamental niches of the various species are randomly assigned following a uniform distribution between 0 and 300, to model the dynamics of species that have their niche centres in the studied zone and others that have their niche centres outside this zone. Species tolerances are assigned following a uniform distribution between 15 and 30. Given the gradient size and the number of species, these tolerance values allow the coexistence of many species at each point of the gradient in the absence of competition, with a substantial overlap between fundamental niches. Maximum carrying capacities are randomly assigned following a uniform distribution between 80 and 120, which prevents strong differences in maximum abundances.

The carrying capacity of each species i at each environmental factor value p_k is described as follows:

$$K_{i,k} = O_i \, e^{-\dfrac{1}{2}\dfrac{(p_k - C_i)^2}{T_i^2}} \tag{1.2}$$

This unimodal, continuous distribution along the environmental gradient ensures a gradual response of each species to changes in the environment in the absence of competition. We also studied the case in which interspecific competition, instead of carrying capacities, smoothly changes along the gradient (see **Appendix S3.2**).

1.3.2 Dispersal

To test the influence of dispersal on spatial community patterns, we added dispersal among neighbouring sites to the above Lotka-Volterra model.

Dispersal was described by a unimodal kernel (Cousens et al., 2008; Clobert et al., 2012). The dynamics of the system then becomes :

$$\frac{dN_{i,k}}{dt} = r_i N_{i,k}(1 - \frac{\sum_j \alpha_{ij} N_{j,k}}{K_{i,k}}) + d \left(\sum_{s \neq k} (N_{i,s} - N_{i,k})\, e^{-\frac{(s-k)^2}{2\sigma_d^2}} \right) \tag{1.3}$$

Two key parameters control dispersal: d is the dispersal rate, and σ_d is the kernel size in unit of inter-site distance.

1.3.3 Species turnover and changes in species abundances

We analysed spatial community patterns by studying the intensity and spatial distribution of species turnover and abundance changes along the environmental gradient. We measured the inequality of changes in species abundances along the gradient using the Gini coefficient of Euclidean distances between species abundances $G(\Delta N)$. For each pair of adjacent sites, we first computed the Euclidean distance between species abundances. A large Euclidean distance between two sites implies large changes in species abundances, whereas a small Euclidean distance indicates similar species abundances. The Gini coefficient of these distances along the gradient allows assessing whether changes in species abundances are equally distributed along the gradient, or whether a few zones of the gradient concentrate the major part of the changes in species abundances. We also used Jaccard distance J_δ (Jaccard, 1912) as an estimator of species turnover between adjacent sites. This estimator is widely used empirically to quantify species beta-diversity in the field (Condit et al., 2002; Qian and Ricklefs, 2007). For two adjacent sites A and B,

$$J_\delta = 1 - \frac{A \cap B}{A \cup B}$$

where $(A \cap B)$ is the number of species that are present in both sites A and B, and $(A \cup B)$ is the total number of species in the two sites A and B combined. Species turnover is complete when $J_\delta = 1$, whereas $J_\delta = 0$ when communities are identical in composition. Species abundances were considered to be zero below a threshold abundance of 10^{-6}.

1.3.4 Effects of competition on community properties and community attractors

We also linked the patterns exhibited by communities along the gradient to changes in the system's equilibria as the environment changes in space. To do so, we defined a Community State Index (CSI) that characterizes the equilibrium state of the system at each site by a single number. This number must take different values for alternative equilibria, and vary continuously as they change smoothly along the gradient. It can be computed as a projection of the vector B_p of abundances at site p for a given equilibrium. Since two distinct vectors are highly unlikely to have the same projection along a random direction (Candes and Tao, 2006), we defined CSI_p as the scalar product of B_p and a vector v of numbers between 0 and 1, which was chosen at random and kept constant in all calculations.

$CSI_k = \sum_{i=1}^{n} v_i B_{i,k}$ with $B_{i,k}$ the abundance of species i at site k

We also computed an index that describes the stability properties of the system. The Observed Multistability Index (OMI) represents the fraction of simulation runs for which multistability was observed, that is, for which different equilibria were reached from different initial conditions. The classic view of communities as complex organisms is associated with the existence of positive interactions between species. Here, direct interactions are competitive, but indirect feedbacks between pairs of species may be positive. We thus developed a Positive Feedback Index (PFI) to quantify the prevalence of positive indirect interactions.

For all $i \neq j$, we computed:

$$P_{ij} = \frac{dN_i}{dK_j}$$

with P_{ij} corresponding to the response of species i to a press in the abundance of species j at equilibrium. A positive value of P_{ij} indicates the presence of positive indirect interactions between the two species. PFI is then measured as the fraction of positive values of P_{ij} in the community at equilibrium. More details are provided in SI **(Appendix S1.2)**. We also developed an Absolute Turnover Index (ATI). For a given combination of ($\mu(A)$, $\sigma(A)$), it is expressed as:

$$ATI = G(\Delta N). \textstyle\sum_{k=1}^{n} \frac{S_k^*}{n}$$

where $G(\Delta N)$ is the Gini coefficient of abundance changes along the gradient, and S_k^* the number of species on site k of the gradient at equilibrium. This metric not only captures how unequal changes are along the gradient, but also the absolute magnitude of those changes, represented by how many species appear or disappear. This encapsulates the qualitative notion of abrupt transitions between diverse communities, whereas $G(\Delta N)$ does not account for diversity.

1.3.5 Numerical simulations

We first studied competition without dispersal ($d = 0$). We explored a wide range of competition matrices A that differ in both the mean, $\mu(A)$, and standard deviation, $\sigma(A)$, of the non-diagonal competition coefficients they contain, as these two parameters are known to greatly influence community structure and properties (Kokkoris et al., 1999, 2002; Bunin, 2017a). We built different competition matrices A by drawing their elements from a uniform distribution: $A \sim U(m - w, m + w)$, with m in $[0, 1]$ and w in $[0, m]$, in steps of 0.02. Under these conditions, we do not observe facilitation ($\alpha_{ij} < 0$). The initial conditions of species abundances were set equal for all species at all sites. We ran the dynamics until $t = 20000$, and verified that the equilibrium was reached.

We studied the influence of dispersal on community patterns by exploring 900 combinations of d and σ_d, with σ_d ranging from 1 to 15, and d ranging from 0.001 to 100 on a log_{10} scale. To study the influence of the mean and standard deviation of competition coefficients on species turnover and inequality in abundance changes along the gradient, we simulated the dynamics of 9 different species pools with identical values of $\mu(A)$ and $\sigma(A)$. For a given combination of $\mu(A)$ and $\sigma(A)$, we calculated the Gini coefficient of abundance changes along the gradient for each of the 9 simulations. For each of the 9 simulations, we also computed the different indices (Positive Feedback Index, Absolute Turnover Index) for all combinations of $\mu(A)$ and $\sigma(A)$, and then took the average value of each index. The Observed Multistability Index (OMI) was computed on the same simulations. We plotted histograms of turnover intensity (Jaccard's distance) by merging the results of 100 different competitive pools for 4 different points in parameter space. Lastly, for each species pool, we calculated CSI at each site for 50 simulations with different initial conditions, yielding bifurcation diagrams of CSI along the gradient.

1.4 Results

1.4.1 Effects of competition on spatial community patterns without dispersal

In the absence of dispersal, if the average competition strength is moderate to high and the variability of competition coefficients is high, there are abrupt shifts in community composition along the gradient, leading to a few discrete communities separated by narrow transition zones (Fig. 1, B, II & III). The Gini coefficient $G(\Delta N)$ takes high values, meaning that changes in species abundances are unequally distributed along the gradient, with a few adjacent site pairs accounting for most of these changes. We observe numerous adjacent sites in which no turnover is observed and narrow zones with high species turnover rates (Fig. 1, C, II & III). In contrast, if competition between species is uniformly weak, gradual changes in species abundances and composition along the gradient are observed (Fig. 1, B, I). In this case, the Gini coefficient is low, meaning that changes in species abundances are equally distributed along the gradient (Fig. 1, A, I). Jaccard's distance shows a unimodal distribution of turnover, with the predominance of zero or very low species turnover values, and no high species turnover values (Fig. 1, C, I). In the special case of very high mean competition

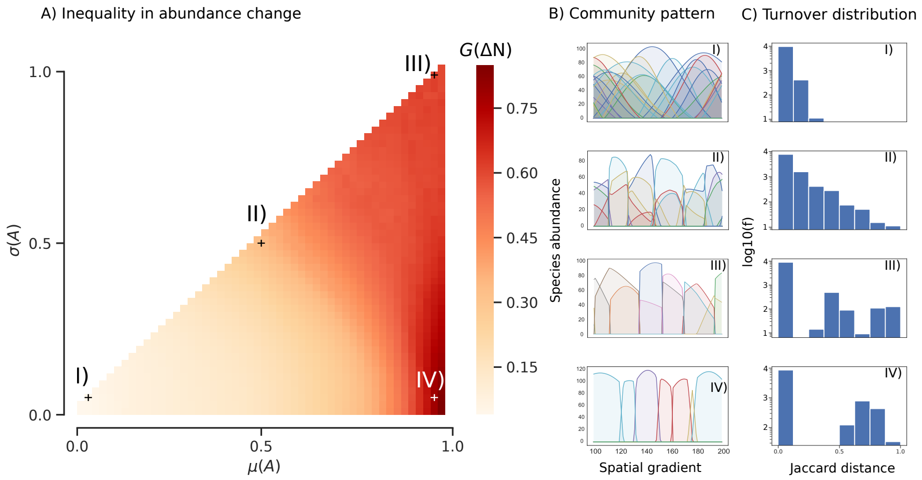


Figure 1.1: Effects of the mean, $\mu(A)$, and standard deviation, $\sigma(A)$, of competition strength on the inequality of abundance change along the gradient, $G(\Delta N)$. B) Spatial community patterns associated with cases I, II, III and IV in A. C) Histograms of Jaccard's distance, representing species turnover, associated with cases I, II, III and IV in A. X-axis: Intensity of turnover, Y-axis: Number of turnover events on a log scale.

strength and low variability in competition strength, only the most competitive species is present at equilibrium in each site, and is abruptly replaced by another species when the environment changes (Fig. 1, B, IV). Here we observe discrete species-poor communities, with narrow to medium-sized zones of transition where several species coexist. The Gini coefficient is high (Fig. 1, A, IV), and the histogram of Jaccard's distances shows the predominance of zero turnover zones, with several medium to high turnover zones (Fig. 1, C, IV). All these results are robust to the introduction of asymmetry in the competition coefficients (see **Appendix S3.1**), with an increase in $G(\Delta N)$ when both the mean and variance of competition strength increase.

The bifurcation diagrams associated with gradual community patterns (Fig. 1, B, I) show gradual changes in the Community State Index (CSI) along the environmental gradient (Fig. 2, A, I). Whatever the initial conditions, only one

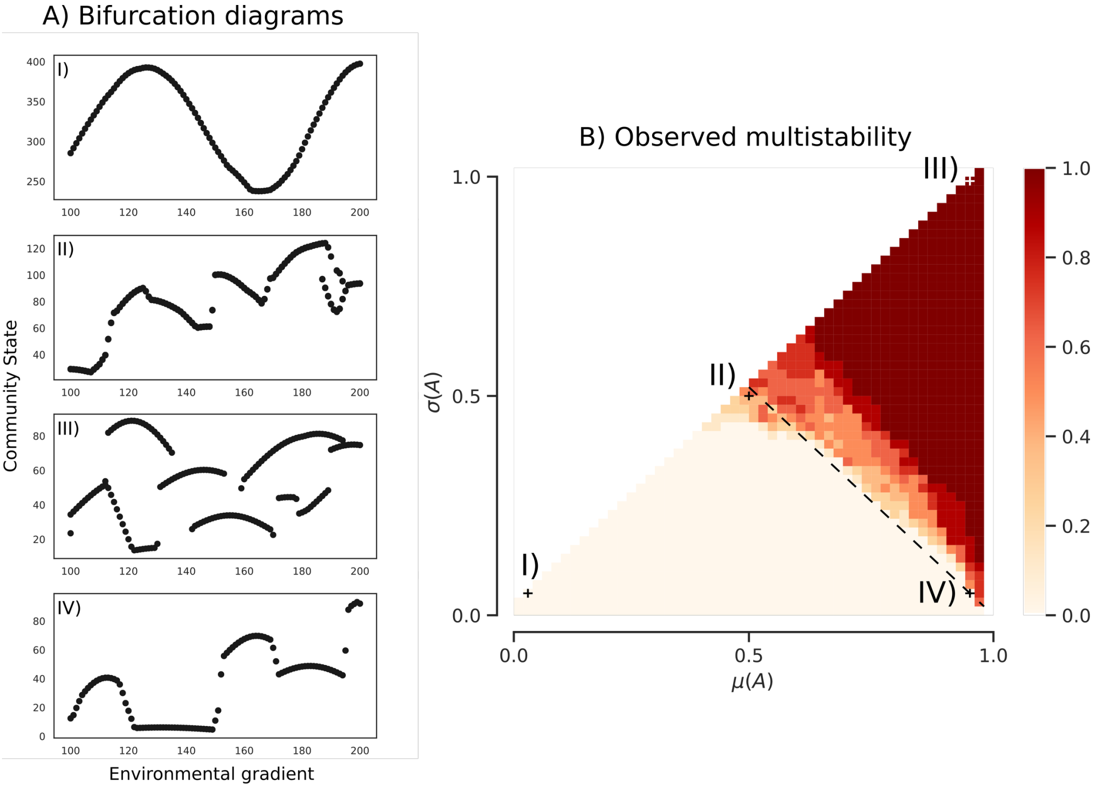


Figure 1.2: A) Bifurcation diagrams obtained by the superimposition of the various community state indices (CSI) obtained from 100 simulations with different initial conditions. Each point on the bifurcation diagram represents a stable equilibrium. B) Observed Multistability Index. This index represents the fraction of 9 simulation runs for which mulstistability is observed. Theoretically, multistability is predicted to occur above the dashed line (Bunin, 2018)

equilibrium can be reached by the local community. In contrast, bifurcation diagrams of systems with stronger competition (Fig. 1, B, II & III) show abrupt shifts in both community composition and CSI (Fig. 2, A, II & III). In these cases, an equilibrium can suddenly appear or disappear after a small environmental change. In these cases, we do observe different alternative stable states on the bifurcation diagram (multiple CSI values at some points along the gradient, Fig. 2, A, II & III). Multistability is predicted to occur only when some coefficients α_{ij} are above 1 (Bunin, 2018), which is consistent with observations (Fig. 2, B). In these cases, initial conditions do matter, and can lead to different communities at equilibrium. In the case of discrete single-species communities (Fig. 1, B, IV), bifurcation diagrams show abrupt changes in CSI, but no alternative stable

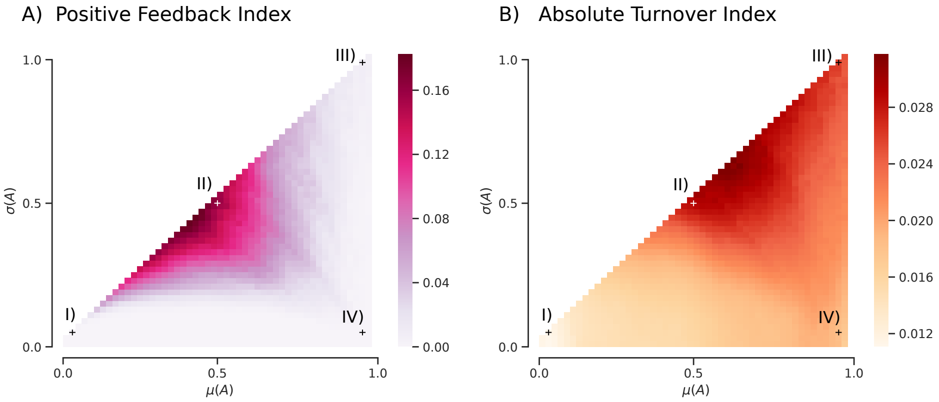


Figure 1.3: A) Positive Feedback Index, which measures the fraction of indirect interactions that are positive. B) Absolute Turnover Index, which combines two effects: (1) how many species appear or disappear in compositional shifts, and (2) how unequally these shifts are distributed along the gradient. For both indices, results are averaged over 9 simulations.

states (Fig. 2, A, IV).

When both the mean and variance of competition strength are intermediate, we observe high values of the Positive Feedback Index (Fig. 3, A). In this case, competition leads to the emergence of indirect positive interactions. In some cases, PFI values reach 0.15, meaning that 15% of all indirect interactions are positive. The Absolute Turnover Index takes high values under the same conditions. Changes in species abundances are then very unequally distributed along the gradient, and they affect many species.

1.4.2 Effects of dispersal on spatial community patterns

When spatial community patterns are gradual in the absence of dispersal, dispersal has relatively small effects on these patterns. Therefore, we focus here on the effects of dispersal in the case where there are abrupt shifts in community composition in the absence of dispersal (Fig. 1, B, III). Increases in both the dispersal rate d and kernel size σ_d tend to reduce the inequality in abundance

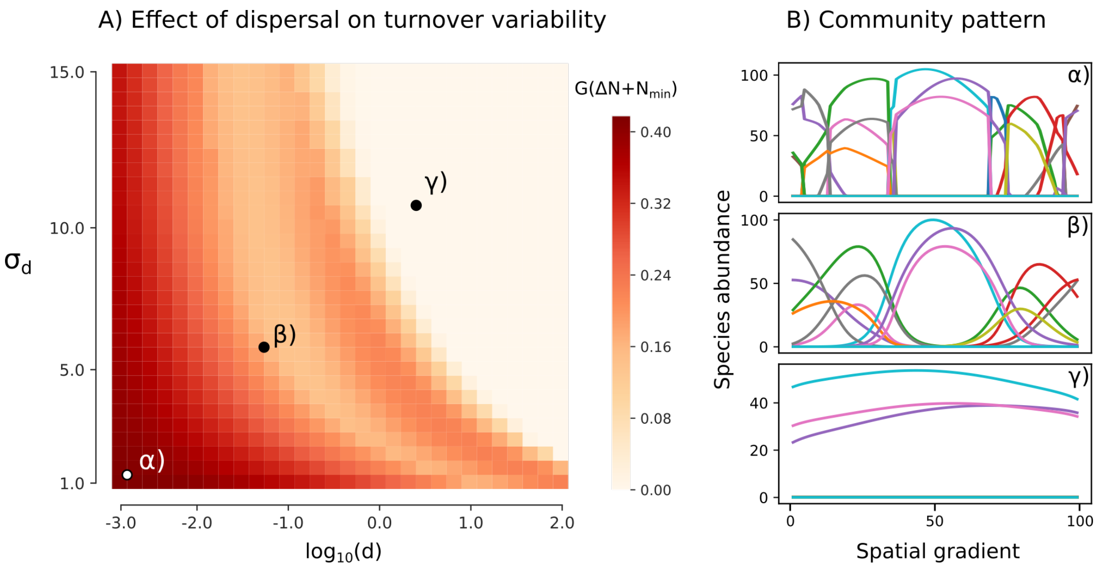


Figure 1.4: Effects of dispersal on spatial community patterns. A) Effects of dispersal rate (d) and kernel size (σ_d) on inequality in abundance changes $G(\Delta N)$ along the gradient. B) Spatial community patterns associated with cases 1, 2, and 3 in A. At high dispersal, changes in species abundances along the gradient are very small and their inequality (as measured by the Gini coefficient) does not reflect any perceptible abruptness. To overcome this issue, we computed $G(\Delta N N_{min})$ with a threshold $N_{min} = 1$.

changes along the environmental gradient (Fig. 4, A). Thus, there are discrete communities along the gradient when both the dispersal distance and dispersal rate are low (Fig. 4, B, α). But as these dispersal parameters increase, changes in community composition and species abundances become more gradual (Fig. 4, β), and eventually yield a monotonic pattern with very small variations (Fig. 4, B, γ).

1.5 Discussion

For decades, the organismic and individualistic views of nature have been considered irreconcilable (McIntosh, 1967). In particular, the debate over whether species respond gradually to environmental changes in space or show discrete communities with sharp transitions is still alive because of the lack of strong empirical evidence and appropriate theory. A complicating factor is that sharp transitions in species composition can also be due to sharp transitions in either species' physiological responses or the environment (McIntosh, 1967), and the latter can itself be modified by species' exploitation of resources (Lampert and Hastings, 2014) or ecological niche construction (Bearup and Blasius, 2017). We have shown here that, even if the environment changes gradually in space, both organismic and individualistic patterns can be expected, depending on the characteristics of competition and dispersal. At one extreme of the spectrum of possibilities, competition can generate discrete communities along a smooth environmental gradient in space, supporting Clements' view. Under other conditions, gradual changes in community composition and species abundances occur, supporting Gleason's view. Competition theory can thus encompass these different views of nature and place them in a broader context, where they appear as two limiting cases along a continuum of community patterns.

Gradual changes in species abundance and species replacement along environmental gradients occur when both the mean and variance of competition strength between species are small. In the absence of dispersal limitation, the probability that a species will be present across its range of favourable environmental conditions at equilibrium is high. Species distributions are thus close to their spatial fundamental niches, a situation that we define as an individualistic pattern. It is noteworthy that this individualistic view of communities is still widely adopted in predictive biodiversity science, for example when using niche models to forecast future species distributions (Huntley et al., 1995; Bakkenes et al., 2002). In these models, species interactions such as competition are considered negligible, and species' responses to environmental changes are assumed to be gradual and independent of each other (but see (Austin, 2007; Zimmermann et al., 2010). Our theoretical results suggest that these assumptions should be carefully analysed and justified, as gradual changes in species abundances are only one possibility along a continuum of possible outcomes. In contrast, when competition between all species is uniformly high, the community is very sensitive to the competitive advantage of one of its members. As a consequence, only the best competitor can be present at equilibrium at any site, in accordance with the competitive exclusion principle (Hardin, 1960). This species, however, quickly loses its supremacy when the environment changes, leading to a pattern in which discrete single-species communities are separated by narrow transition zones where a few species can coexist.

Perhaps the most interesting situation arises when competitive interactions are more complex and include a mix of strong and weak interactions (Bunin, 2018). In this case, organismic patterns are observed at equilibrium, i.e. there are discrete communities across space, separated by sharp boundaries where a nearly complete species turnover occurs. Small changes in the environment can thus lead to abrupt shifts from one community to another, with considerable changes in species composition. In this case, direct competition is responsible for the emergence of indirect positive interactions that generate alternative stable states. These alternative stable states cause abrupt shifts in community composition, and induce a dependence on initial conditions (priority or founder effect). Different initial conditions can thus drive the system to different attractors, and the presence of a species at a site depends strongly on the initial species pool. The spatial distribution of a species along an environmental gradient can then be best understood by considering the community in which the species is integrated, rather than by its fundamental niche only, which supports an organismic view of communities. More generally, shifts that are not abrupt but still rapid and nonlinear can be a signal of proximity to the domain of alternative stable states.

Previous studies have emphasised the importance of positive interactions in the emergence of alternative stable states (Kéfi et al., 2007, 2016). Direct positive interactions between species or groups of species, such as facilitation and mutualism, are then at the origin of the positive feedback loops that generate abrupt shifts in a changing environment. Our model, however, shows that alternative stable states can also emerge from interspecific competition. In this case, the positive feedback loops required to generate alternative stable states arise from the suppression of competitors, as described by GILPIN and CASE (1976) and van Nes and Scheffer (2004). However, these positive feedbacks might not be apparent within the community at equilibrium. If we only consider surviving species, positive feedbacks between them can be observed when the mean and variance of competition strength are intermediate. But this situation is not, in general, conducive to stable alternative states (Kessler and Shnerb, 2015; Biroli et al., 2018). By contrast, when the mean and variance of competition strength are high, we do observe multistability in the system, and no positive indirect interactions at equilibrium. In this case, positive feedbacks did come into play during the assembly process, but they are no longer present between surviving species. These assembled communities can be seen as cliques, with weak competition within the cliques and very high competition with species outside them (Fried et al., 2016). This situation is an instance of the 'ghost of competition present' (Miller et al., 2009), which provides a general mechanism for complex interactions to lead to the emergence of organismic community behaviour (Bunin, 2018).

Species dispersal also plays a major role in shaping spatial community patterns. Our model shows that an increase in either the dispersal rate or kernel size relative to the size of the gradient can smooth out the organismic patterns that emerge from competition, and lead to more gradual patterns. Dispersal thus tends to erase the spatial boundaries between zones, and to homogenize species composition. This recovers results from metacommunity theory showing that dispersal decreases beta-diversity among communities (Mouquet and Loreau, 2003; Leibold et al., 2004), a theoretical prediction that is supported by empirical studies (Forbes and Chase, 2002; Kneitel and Miller, 2003; Simonis and Ellis, 2014; Wandrag et al., 2017). In nature, the absence of clear discontinuities in species composition along spatial environmental gradients, as observed in plant species along altitudinal gradients (Lieberman et al., 1996; Vazquez G. and Givnish, 1998) or in marine benthic organisms along depth gradients (Smale, 2008), might thus reflects either a truly individualistic organization or the effects of dispersal blurring the boundaries of discrete communities. While our indices still distinguish these two regimes in simulations for low to moderate dispersal, we hope that our theory will prompt and facilitate the development of more robust empirical metrics of spatial turnover in species composition driven by species interactions. Our work reframes the perennial debate between individualistic and organismic views of ecological communities, by showing that both can emerge as different modalities within the same theoretical framework. We identify organismic behaviour as a valid possibility, even in the absence of widespread facilitative interactions. A robust mechanism is provided by a high variance in competition strength. This variance allows the emergence of alternative stable states, which correspond to different cliques of species that persist through weak within-clique competition but strong between-clique competition. This simple mechanism creates discrete and directional spatio-temporal patterns, which were explored theoretically by (Bunin, 2018). We argue that these patterns represent an organismic regime in the spectrum of possible community organizations.

Communities that we identify as organismic, including a mix of strong and weak competitive interactions, are more prone to abrupt transitions and should thus receive more attention from ecologists and environmental managers. A wide range of experiments hint at the prevalence of strong (e.g. Fort (2018)) and heterogeneous (e.g. Xiao et al. (2017)) competitive interactions. In such communities, strong feedbacks are hidden at equilibrium, and only revealed during the dynamics, a situation termed the “ghost of competition present” (Miller et al., 2009). A small change in the environment across space can then lead to abrupt shifts from one community to another; similarly, a gradual environmental change in time may induce abrupt shifts in community composition and ecosystem functioning. In the current context of increasing alteration of ecosystems by human activities (Hoegh-Guldberg et al., 2007; Vitousek, 1997; Dodds et al., 2013), abrupt responses can lead to potentially dramatic consequences for social-ecological systems in the next decades (Steele, 1996; Carpenter et al., 1999; Gunderson and Holling, 2002). Including interspecific interactions has been recognised as a major challenge in predictive ecology (Mouquet et al., 2015), in particular to improve species distribution models (Guisan and Thuiller, 2005; Araújo and Guisan, 2006; Gilman et al., 2010). Our theoretical study strongly supports this claim, and shows concretely when, how and why organismic or individualistic views on community organization should prevail and be taken into account to predict the responses of species and communities to environmental changes.

1.6 Appendix

Indices of dynamical regimes

Empirical indices of abrupt shifts

Definitions

To detect abrupt community changes along a gradient, we must first evaluate the amount of change between neighboring points. A large number of indices have been proposed to estimate beta diversity, i.e. the difference in composition across different sites (Anderson et al., 2011). Similarly, many techniques have been suggested to detect zonation in empirical data such as altitudinal transects (Bach and Robbert Gradstein, 2011).

We have considered three measures of composition difference between two sites, whose meaning is discussed below:

- the Jaccard index $J_\delta = 1 - B \cap B'/B \cup B'$ where B and B' are the sets of species that persist on the two sites,
- the Euclidean distance $E_\delta = ||N - N'||$ where $\vec{N}$ and $\vec{N}'$ are the vectors of abundances on the two sites.
- the rescaled Euclidean distance $e_\delta = ||n - n'||$ where $\vec{n} = \vec{N}/\max(N)$ and $\vec{N}'/\max(N)$ are the vectors of abundances on the two sites normalized by the maximal abundance of each species. The rationale for using it is that the Euclidean distance is biased toward abundant species, and may ignore abrupt compositional changes reflected mostly in rare species. In our study, this distinction was not qualitatively essential as we did not have coexisting species differing by orders of magnitude in their abundance, as may happen in empirical data.

We show in Fig. A1 the distribution of these two indices aggregated over 100 replicate simulation runs, for different values of the parameters $\mu(A)$ and $\sigma(A)$ (mean and standard deviation of the interaction matrix, as defined in the main text).

In the main text, we show some of these distributions, but also use an aggregate metric of abruptness: the Gini coefficient, defined for an arbitrary vector $\vec{x} = \{x_i\}$ of length M as

$$G(x) = \frac{\sum_{i,j}^{M} |x_i - x_j|}{2M \sum_j x_j}. \tag{1.1}$$

This coefficient is commonly used as a measure of inequality, e.g. in economic systems. Here, it measures how “inequal” compositional changes are along the gradient. It will be high (close to 1) when we see regions of smooth change alternating with fast and abrupt shifts.

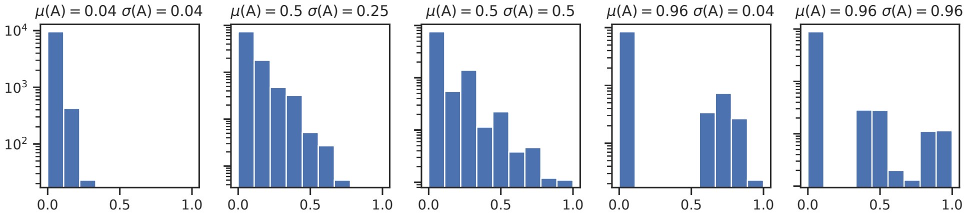
Discussion

The Jaccard index is widely used as a qualitative indicator of compositional change, but it may be sensitive to the choice of extinction threshold and the number of sites sampled along the gradient (in our model, the spatial resolution). As we show in Fig. A2, our aggregate metrics of abruptness using the Jaccard index, whether the standard deviation $\sigma(J_\delta)$ or the Gini coefficient $G(J_\delta)$, both correlate strongly with the inverse of the number of species alive at any given point along the gradient. Thus, they are more successful as a measure of total turnover, or paucity, than as a measure of abruptness. On the other hand, subsampling does not affect their usefulness as much as could be expected: a strong correlation is found between $\sigma(J_\delta)$ computed on the full gradient and the same computed on 1/10th of the points.

The Euclidean distance provides a more quantitative indicator of change. The main visual difference between its distribution and that of the Jaccard index, as seen in Fig. A1, is that the latter displays a bimodal shape in the case of strong but homogeneous interactions $\mu(A) \approx 1$, $\sigma(A) \approx 0$. By contrast, the distribution of either Euclidean distances (here relative) only exhibits bimodality in the highly abrupt regime $\mu(A), \sigma(A) \approx 1$.

The ability of these metrics to detect the different regimes even when subsampled also suggests their robustness to the blurring action of dispersal: weak to intermediate levels of dispersal will cause less sharp boundaries between communities at the local scale, but will not affect low-resolution metrics computed using differences between sites that are far apart (further than the typical spatial scale of dispersal).

a) Jaccard index



b) Euclidean distance

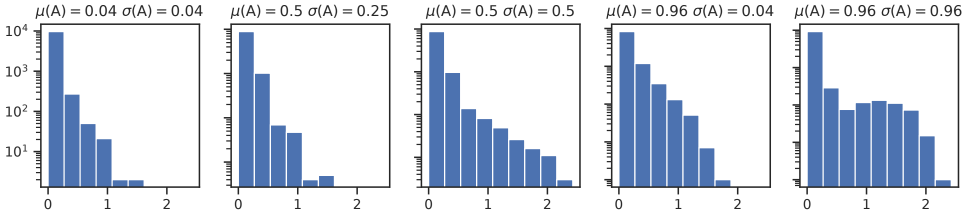


Figure A1: Empirical indices of abrupt shifts. **a)** Histogram of Jaccard indices between successive sites along the gradient. **b)** Histogram of Euclidean distance between successive sites.

Positive Feedback Index

An organism is generally seen as comprised of interdependent parts that benefit from (or even require) each others' presence. Hence, it may seem counter-

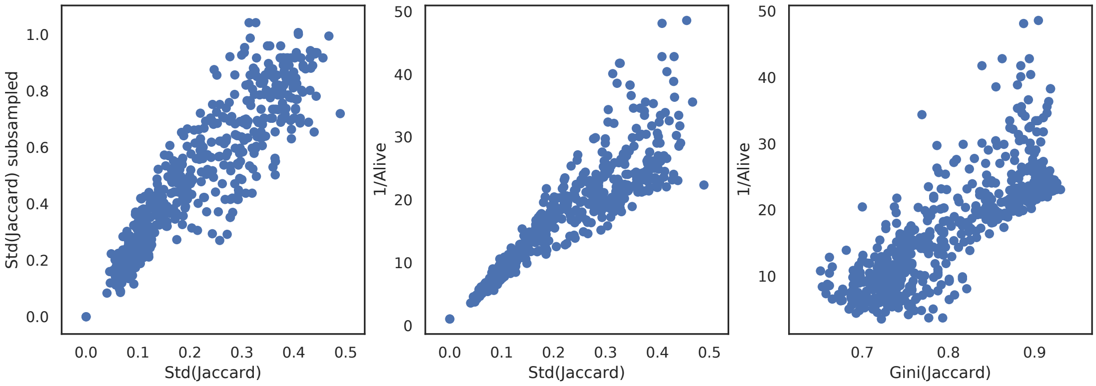


Figure A2: Properties of metrics based on the Jaccard index. **Left:** The standard deviation $\sigma(J_\delta)$ is quite robust to subsampling, with a strong correlation between its value computed over the full gradient (x-axis), and its value computed over one in ten points only (y-axis), $R = 0.9$. **Center and right:** Given S^* the average number of species alive at any point in the gradient, we find a strong correlation between $1/S^*$ and $\sigma(J_\delta)$ ($R = 0.9$, center) and the Gini coefficient $G(J_\delta)$ ($R = 0.8$, right).

intuitive to study whether super-organismic behavior may arise in communities of competitors.

To resolve this paradox, it is crucial to notice that, even when all direct interactions are competitive, long-term feedbacks between some species may in fact be positive. Indeed, the benefits of keeping away shared enemies may greatly outweigh the cost of coexisting with a competitor, as seen for example in the microbiome (Pillai et al., 2014).

We can formalize the notion of long-term effects of a species on another. A good way to probe it is to ask: if conditions become more favorable for a species, does this benefit or harm another?

Consider the Lotka-Volterra equation for species i (among S species) at a single site:

$$\frac{dN_i}{dt} = \frac{r_i}{K_i} N_i \left(K_i - N_i - \sum_j^S A_{ij} N_j \right) . \tag{1.2}$$

If we restrict it to the $S^* \leq S$ surviving species, i.e. those with $N_i > 0$, we find at equilibrium that

$$N_i + \sum_j^{S^*} A_{ij} N_j = K_i \qquad \text{for } i \leq S^* \tag{1.3}$$

which can be written in matrix notation as:

$$N^* = (1 + A^*)^{-1} K^* . \tag{1.4}$$

From this expression, it is apparent how the equilibrium abundance of one surviving species i responds, in the long term, to a change of carrying capacity of another surviving species j

$$\frac{dN_i^*}{dK_j^*} = (\mathbb{I} + A^*)^{-1}_{ij} = P_{ij} \tag{1.5}$$

where $\mathbb{I}$ is the identity matrix. This matrix is thus the matrix of response to *press perturbations*, i.e. permanent changes, of any species' carrying capacity. In any stable equilibrium, we can expand the expression above, as is often done in Loop Analysis (Levins, 1974). In matrix notation:

$$P = (\mathbb{I} + A^*)^{-1} = \mathbb{I} - A^* + (A^*)^2 - (A^*)^3 + \dots \tag{1.6}$$

or element-wise (if $i \neq j$):

$$P_{ij} = -A_{ij} + \sum_k A_{ik}A_{kj} - \sum_{kl} A_{ik}A_{kl}A_{lj} \dots \tag{1.7}$$

where it is apparent that P_{ij} involves all the possible effects starting from species j and reaching species i through any path in the community (via interactions with and between species k, $l \dots$). The alternating sign explains how it is possible to have $P_{ij} > 0$ even when the first term (direct interactions) is negative.

Thus, we define the Positive Feedback Index as the fraction of elements of the matrix P_{ij} that are positive in a given equilibrium.

But these positive feedbacks between coexisting species are also destabilizing, just as positive interactions themselves are destabilizing (Costello et al., 2012). With many species, with external noise, and if nothing prevents abundances to fluctuate (e.g. no extinction threshold), this region of positive feedbacks thus corresponds in our model to the *chaotic* regime described below. This is reflected here by the fact that we see the largest absolute amount of turnover in that region (for a given total number of species across the gradient), as shown in Fig. A3 and in the main text. Therefore, we argue in the main text that the region of strong positive feedbacks at equilibrium (where the PFI is high) is an intermediate region between Gleasonian and Clementsian patterns. In that region, Clementsian patterns might be possible

Robust Clementsian behavior instead occurs for even larger interaction strength and variance, where species can form cliques: some species, competing weakly with each other, can ally against others that strongly compete with them. In that case, coexisting species have very strong positive feedbacks *out of equilibrium* (during assembly or invasions) to repel third parties, but the Positive Feedback Index lower at equilibrium, meaning that these species form a more stable state together. This is thus a region of *hidden* positive feedbacks, following the notion of the "ghost of competition present" (Miller et al., 2009).

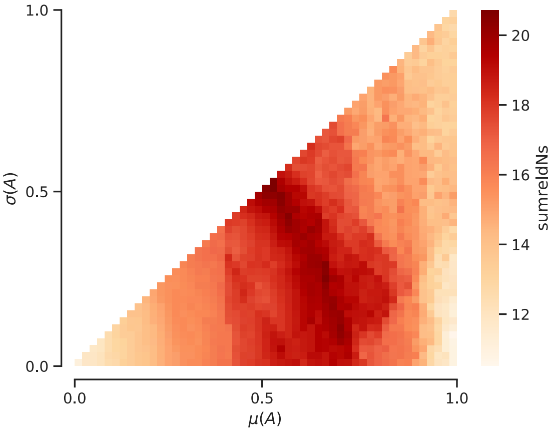


Figure A3: Total amount of turnover along the gradient, measured using the rescaled euclidean distance (see S1.1) $\sum_k |e_\delta(k, k+1)|$. We see that it is maximal in an intermediate region corresponding roughly to the onset of multistability. Beyond this point, fewer species survive, with sharper transitions (as measured by our previous indices) but less total compositional change. An alternative metric conveying the same qualitative intuition is proposed in main text as $S^* G(e_\delta)$ with S^* the mean number of surviving species and and G the Gini coefficient.

Different regimes of community dynamics

To discuss the emergence of abrupt shifts and collective behavior, we have chosen to use the Random Lotka-Volterra Competition model, where species at a given site follow the usual Lotka-Volterra dynamics

$$\frac{dN_i}{dt} = \frac{r_i}{K_i} N_i \left(K_i - N_i - \sum_j^S A_{ij} N_j \right) \tag{1.8}$$

and K_i and A_{ij} are both drawn at random, with $A_{ij} \geq 0$ (only competitive interactions). We later discuss how our qualitative results hold in a few variations on that model.

This model, and closely related ones, have been studied extensively from a theoretical point of view. Its most important feature for us is the existence of distinct regimes where dynamical properties change dramatically. For very large communities ($S \to \infty$), these regimes are well separated in the space of parameters $\mu(A)$, $\sigma(A)$, as shown by Kessler and Shnerb in extensive numerical simulations (Kessler and Shnerb, 2015).

Their work distinguishes four successive phases as one increases both $\mu(A)$ and $\sigma(A)$:

Phase 1 All species coexist

Phase 2 Some species go extinct but a single global equilibrium exists (both stable and uninvadable)

Phase 3 The global equilibrium disappears and one sees instead a multiplicity of possible fixed points, but none of them are stable in the limit of many species (for few species they are stable but weakly so). This typically results in chaotic fluctuations (unless some extinction threshold is imposed and chaos "kills itself" by driving some species extinct until the system is stabilized)

Phase 4 True multistability, with multiple well-separated and stable equilibria.

A more analytical understanding of these phases and their transitions is provided by a large body of work:

- The transition from Phase 1 to Phase 2 happens when the full-coexistence equilibrium is either not stable or not feasible, and it has been widely explored under the guise of the feasibility problem (Rohr et al., 2014) and the limits on stability of a large random matrix (May, 1972)
- In Phase 2, as some species are eliminated, the interaction matrix is not fully random anymore; hence, the classical results for Phase 1 are not exactly applicable as such (Bunin, 2016). The transition from Phase 2 to Phase 3 has been described by Galla (Galla, 2006) and recently by Bunin (Bunin, 2017b). These studies state that, for many species, the transition occurs precisely when

  $$\left(\sigma(A)\sum_i P_{ii}\right)^2 = S^* \tag{1.9}$$

  with P_{ij} the matrix of response to press defined in the previous section, and S^* the number of surviving species.
- The behavior in Phase 3 has been investigated in detail by Biroli et al (Biroli et al., 2018).
- The behavior deep into Phase 4 is the subject of recent work by Bunin (Bunin, 2018) and Fried et al (Fried et al., 2017). Bunin demonstrates that, in addition to spatial patterns that can be understood as organismic, this phase also displays a number of features that present similarity to Clements' viewpoint, including emergent directionality in succession, spread of different communities, and more (Bunin, 2018).

The phase of interest to us is therefore Phase 4 to describe the organismic pole in the spectrum of possible behaviors.

For *random* interaction matrices, Bunin (Bunin, 2018) suggests that the transition to Phase 4 requires, at the very least, the existence of one pair (i, j) of species in mutual competitive exclusion, $\alpha_{ij}\alpha_{ji} > 1$. This leads us to locate the theoretical transition to Phase 4 as the line where $\max_{ij} \alpha_{ij} > 1$ (dashed line in Fig. 2, main text).

For *nonrandom* interaction matrices, Phase 4 can be reached even when individual interactions are weaker, for instance by having two groups of species that achieve mutual exclusion at the group level, although species cannot achieve it at the pair level (Barbier et al., 2018). Arnoldi and Barbier (unpublished) are developping an analytical criterion that will allow to understand the role of interaction structures in precipitating or delaying the transition to multistability.

Model extensions

Asymmetrical interactions

Mechanisms such as resource competition or niche overlap generally induce symmetrical interactions $A_{ij} = A_{ji}$. However, interactions may also be asymmetrical ($corr(A_{ij}, A_{ji}) = 0$) or antisymmetrical ($corr(A_{ij}, A_{ji}) = -1$). As we now show in Fig. A4, this delays the onset of multistability, but does not otherwise change our qualitative results.

To control the symmetry $\gamma \in [-1, 1]$ of the matrix without changing its distribution (at the cost of losing half the degrees of freedom), we draw $S(S-1)/2$ random numbers a_i sorted in increasing order. The index $i = x_i$ of each number is the ith element of a vector of positions $\vec{x} = \{1, 2, 3, 4 \dots\}$.

Next, we draw another vector $\vec{y}$ corresponding to a random permutation of the same positions, e.g. $\vec{y} = \{4, 1, 7 \dots\}$. We compute a vector with a parameter Γ

$$\vec{z} = (1 - |\Gamma|)\vec{y} + \Gamma\vec{x} \tag{1.10}$$

so that elements of $\vec{z}$ are maximally correlated with those of $\vec{x}$ if $\Gamma = 1$, independent if $\Gamma = 0$ and maximally anticorrelated if $\Gamma = -1$.

Hence, we can define a new sequence b_i such that $b_i = a_j$ with $j = \text{rank}(z_i)$ the rank of the ith term of $\vec{z}$ among the set $\{z_j\}$. We finally use the two sequences a and its Γ-correlated permutation b to populate the interaction matrix:

$$A_{ij} = a_{(i-1)S+j}, \qquad A_{ji} = b_{(i-1)S+j}, \qquad i < j. \tag{1.11}$$

We note that the actual correlation γ is monotonic in, but not equal to, our control parameter Γ.

Gradient-dependent interactions

An important consideration for the robustness of our conclusions is whether they are specific to the setting of a fixed interaction matrix A and changing carrying capacities K across the gradient. This setting is intuitive if one considers that carrying capacities express environmental filtering, while interactions express biotic filtering. Yet it is plausible for interactions to change with environmental conditions as well, if they are mediated by resources and other external factors that may be affected by the environment.

One should note that resource-mediated interactions are often modelled as being a function of the distance between species' *preferences* (Mac Arthur, 1969), which are fixed properties of a species and do *not* vary along the gradient. In that case, the interaction matrix A is again constant throughout the gradient. The

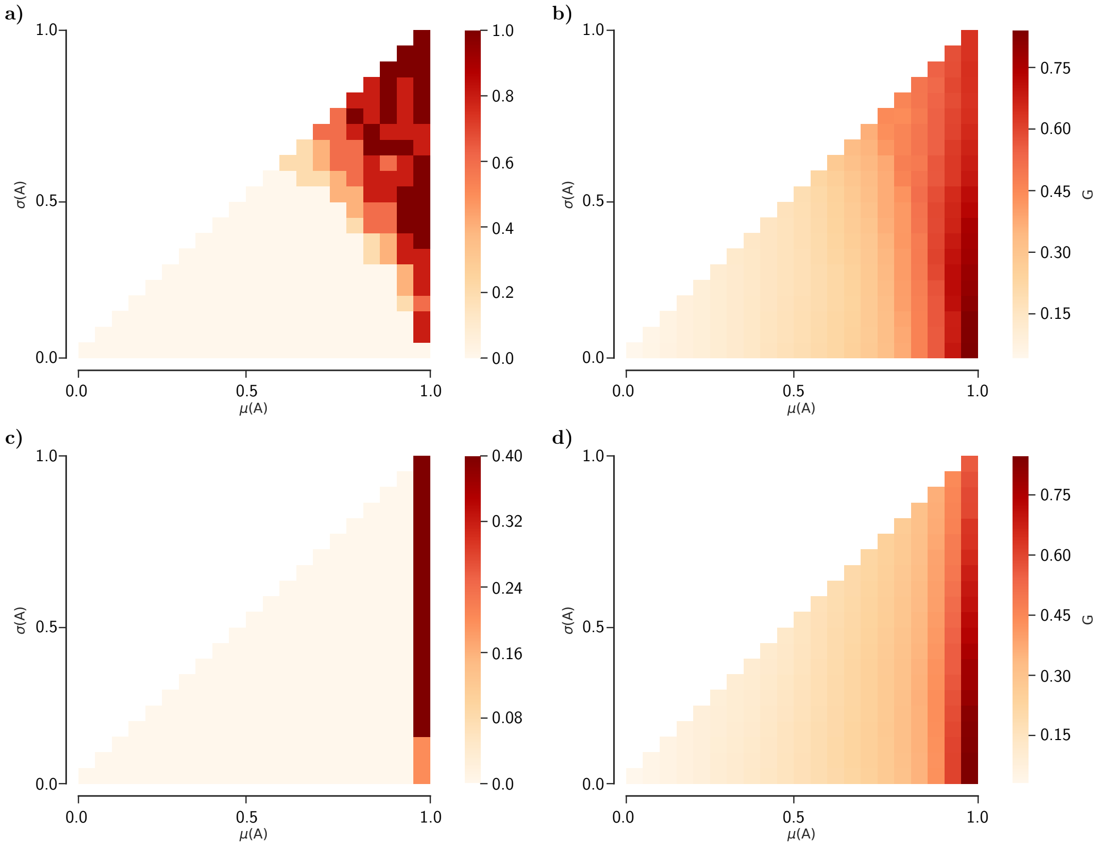


Figure A4: Observed Multistability Index (a,c) and Gini index (b,d) as a function of interaction symmetry. **Top row (a,b):** Asymmetrical interactions $\gamma = 0$. The transition to multistability is driven further away. **Bottom row (c,d):** Antisymmetrical interactions $\gamma = -1$. In the limit of perfect antisymmetry, there is no multistability for $\langle A_{ij} \rangle < 1$, as predicted by Bunin (Bunin, 2017b).

only differences of that setting with our results might arise from the particular features of an interaction matrix based purely on resource competition (Gatto, 1990; Barabás et al., 2012), such as the impossibility of multistability. These features are not robust to the inclusion of direct (e.g. interference) competition (Yoshino et al., 2007).

Instead, we propose here a situation where species interactions involve different (implicitly modelled) factors that change along the environmental gradient. This may represent consumers competing through depletion of other prey species that appear or disappear at different points in the gradient.

Realistic ecological settings may have both K and A depend on the environmental variable p. Since the main text demonstrates the case of K only varying, we now present the effect of changing only A. The dynamical equation for the abundance of species i at site k along the gradient is then

$$\frac{dN_{i,k}}{dt} = \frac{r_i}{K_i} N_{i,k} \left(K_i - N_{i,k} - \sum_j A_{ij}(p_k) N_{j,k} \right) . \tag{1.12}$$

where p_k represents the value of the environmental factor at site k on the gradient. Rather than each species, it is now each interaction that is given a "niche" with center C_{ij} and width T_{ij} along the gradient:

$$A_{ij}(p) = c_1 + c_2 \exp \left[-\frac{1}{2} \left(\frac{p - C_{ij}}{T_{ij}} \right)^2 \right] . \tag{1.13}$$

Here, c_1 and c_2 are parameters that control $\mu(A)$ and $\sigma(A)$ the mean and standard deviation of elements A_{ij}.

The main difference with the setting studied in the main text is that, if $\sigma(A) = 0$, species retain the same abundance across the entire environmental gradient, since their carrying capacities K_i are independent of the environment. Hence, the different qualitative behaviors that we studied are not expected to occupy the same locations in this new parameter space.

But the same set of behaviors exists, as shown in Fig. A5, and we demonstrate again the role of interaction variance in giving rise to collective organization.

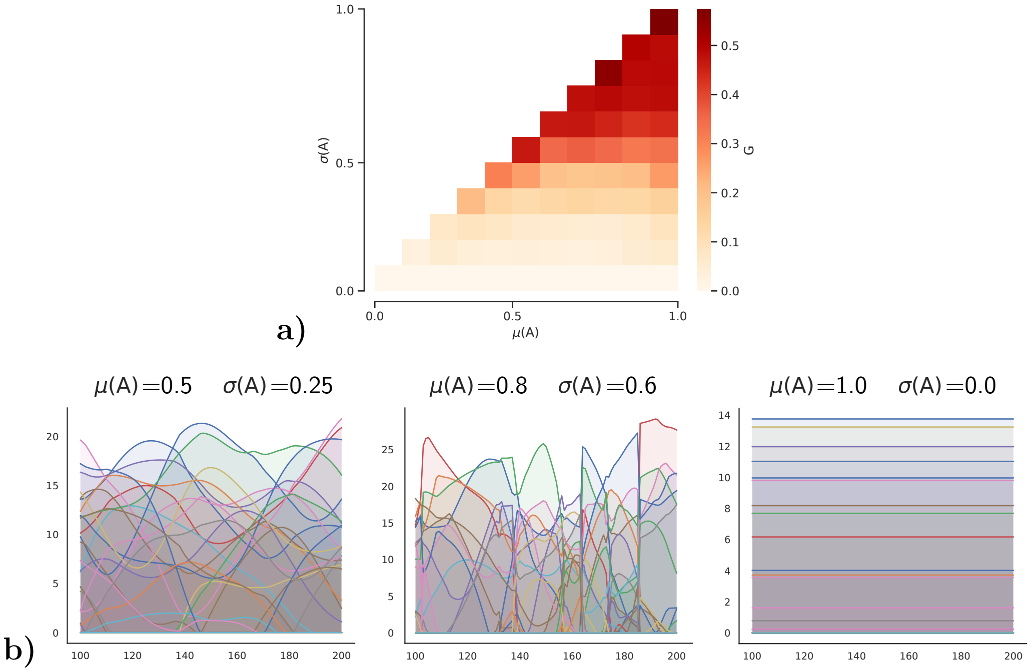


Figure A5: Gradient-dependent interactions. a) Gini coefficient of composition changes (see above). b) Species abundance profiles at different locations in parameter space, showing the same qualitative features as the figures in main text, with a difference in the bottom-right corner: surviving species now persist along the entire gradient if $\sigma(A) = 0$.

Chapter 2

Ecotone formation through ecological niche construction: the role of biodiversity and species interactions

Title of the scientific article :

Ecotone formation through ecological niche construction: the role of biodiversity and species interactions[1]

Keywords : Biodiversity, Community patterns, Ecological niche construction, Ecosystem engineers, Ecotones, Species interactions

2.1 Abstract

Rapid changes in species composition, also known as ecotones, can result from various causes including rapid changes in environmental conditions, or physiological thresholds. The possibility that ecotones arise from ecological niche construction by ecosystem engineers has received little attention. In this study, we investigate how the diversity of ecosystem engineers, and their interactions, can give rise to ecotones. We build a spatially explicit dynamical model that couples a multispecies community and its abiotic environment. We use numerical simulations and analytical techniques to determine the biotic and abiotic conditions under which ecotone emergence is expected to occur, and the role of biodiversity therein. We show that the diversity of ecosystem engineers can lead to indirect interactions through the modification of their shared environment. These interactions, which can be either competitive or mutualistic, can lead to the emergence of discrete communities in space, separated by sharp ecotones where a high species turnover is observed. Considering biodiversity is thus critical when studying the influence of species-environment interactions on the emergence of ecotones. This is especially true for the wide range of species that have small to moderate effects on their environment. Our work highlights new mechanisms by which biodiversity loss could cause significant changes in spatial community patterns in changing environments.

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[1] This work represents a collaboration with Matthieu Barbier and Michel Loreau. It is published in *Ecography* : **Liautaud, K.**, Barbier, M., and Loreau, M. (2020), Ecotone formation through ecological niche construction: the role of biodiversity and species interactions. Ecography, Volume 43, Issue 5 : 714-723. doi:10.1111/ecog.04902

2.2 Introduction

Whether species composition changes gradually, or forms discrete zones along environmental gradients has been the subject of a long-standing debate in ecology (Clements, 1916; Gleason, 1926; Braun-Blanquet, 1928; Hedberg, 1955; McIntosh, 1967). Observational studies have found both gradual (Whittaker, 1956; Vazquez G. and Givnish, 1998; Ellison et al., 2010; Lieberman et al., 1996) and discrete patterns (Kitayama, 1992; Hemp, 2006; Tuomisto and Ruokolainen, 1994; Kessler, 2000). Rapid changes in community composition along gradients, also termed ecotones (Kent et al., 1997), have been observed in a wide range of ecosystems, such as alpine treelines (Germino et al., 2002), tropical mountain forests (Martin et al., 2007) and coastal environments (Sternberg et al., 2007; Walker et al., 2003). Hereafter, a transition will be termed ”rapid” when its scale is much smaller than the spatial scale of the landscape, even though the transitional area may show mixing of species.

While rapid changes can be blurred by species dispersal (Liautaud et al., 2019b) or stochasticity in nature, it is important to understand the theoretical conditions under which rapid community changes can emerge. These rapid changes in species composition can coincide with rapid changes in environmental conditions, such as the frost line (Kitayama and Mueller-Dombois, 1992) or discontinuities in edaphic conditions (Tuomisto and Ruokolainen, 1994; Kessler, 2000). In these cases, it is often assumed that changes in abiotic conditions are responsible for the change in species composition (McIntosh, 1967; Kent et al., 1997). This assumption is supported in many cases, but it may obscure the possibility that, in other settings, the two boundaries emerge together from the influence of species on their abiotic environment. The mechanisms that can lead to such transitions are poorly known, and in particular the respective contributions of species-environment feedbacks and interspecific interactions.

Species that are able to modify their abiotic environment are often called ”ecosystem engineers” (Jones et al., 2010). Classical examples range from beavers that impact water flow and habitat heterogeneity (Wright et al., 2002), to cushion alpine plants that buffer extreme temperatures and increase soil moisture (Badano et al., 2006). Ecological niche construction is a particular case in which engineers modify the environment to their own benefits (Kylafis and Loreau, 2008, 2011), creating a feedback with the environment (an example in which engineers can instead create succession is presented in the Appendix). This ecological process should be distinguished from the related concept of niche construction in evolutionary theory in which we would also expect species traits to evolve over time (Odling-Smee et al., 2003, 1996). Examples of ecological niche construction range from plant-water feedbacks in arid environment (Dekker et al., 2007) to increases in nutrient inputs by trees in tropical ecosystems (De longe et al., 2008). Such feedbacks can govern species distributions (Wilson and Agnew, 1992), particularly under harsh environmental conditions (Kéfi et al., 2007; Gilad et al., 2004; Meron et al., 2004; von Hardenberg et al., 2001), and lead to the emergence of ecotones (Bearup and Blasius, 2017; Jiang and DeAngelis, 2013). Classical studies on ecosystem engineers, however, have generally focused on the effects of a particular species having strong effects on the abiotic environment (Jones et al., 2010; Bouma et al., 2010; Prugh and Brashares, 2012). But many more species have small or moderate impacts on their environment. Such species, which are often neglected individually, might substantially affect their environment when aggregated. Furthermore, previous studies have scarcely explored what types of interactions can arise between multiple species that engineer their shared environment. We thus propose to focus on the role of diversity and species interactions in the emergence of ecotones through ecological niche construction.

Biodiversity can have two main effects on the emergence of species-environment feedbacks : a cumulative effect of species number, and a heterogeneity effect due to variations in species' preferences and engineering ability. Cumulative effects are similar to complementarity in biodiversity-ecosystem functioning relationships (Loreau and Hector, 2001; Hooper et al.). The fact that species coexist with weak or no competition implies the existence of different niches, i.e. other factors beyond the environmental preference modelled here. This cumulative effect arises when there is no single identifiable engineer, but where community acts collectively to create an ecotone. A potential example is the occurrence of ecotones between mangroves and hardwood forests, where several mangrove tree species can modify water salinity in synergy (Sternberg et al., 2007). In contrast, the heterogeneity effect of biodiversity arises when there are differences in species' preferred environmental states. We investigate the effect of these differences on emergent competition or facilitation between ecosystem engineers, and how this could play a role in ecotone emergence.

In this study, we build a theoretical model that couples the dynamics of a community and of its abiotic environment to assess the role of ecosystem engineers and of their diversity in the emergence of ecotones in space. In our model, ecotones are represented by abrupt changes, including discontinuities. In the presence of multiple interacting species, we show that ecological niche construction can lead to the emergence of indirect interspecific interactions -which can be either positive or negative - through environmental modifications. Similarly, we show that even species with different preferences can act synergistically as a single community. We then assess the consequences of these different interaction types for community patterns in space, and identify the conditions under which ecotone formation is predicted to occur.

2.3 Model and methods

2.3.1 Species growth and niche construction

We model the dynamics of a community of n species, each of which obeys a logistic growth along a gradient of an arbitrary environmental factor E. We consider independent locations along this environmental gradient, assuming no fluxes between the locations [2] . For a given location k, the population dynamics

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[2] But see Liautaud et al. (2019b) for the role of dispersal in smoothing abrupt transitions.

of species i is given by:

$$\frac{dN_{i,k}}{dt} = r_i N_{i,k} \left(1 - \frac{N_{i,k}}{K_i(E_k)}\right) \tag{2.1}$$

where E_k represents the value of the environmental factor at location k, N_{i_k} is the abundance of species i at that location, and r_i is its intrinsic growth rate, assumed to be equal for all species, $r_i = r$. The fundamental niche of each species is defined by its carrying capacity $K_i(E)$, which is assumed to depend on the environmental value E according to a Gaussian function:

$$K_i(E) = K_i^{\max} \exp\left[-\frac{(E - C_i)^2}{2{T_i}^2}\right] \tag{2.2}$$

The classical Hutchinsonian niche (Hutchinson, 1957) would instead be defined in terms of growth rate, but these two assumptions are equivalent in the case of logistic growth as considered here. The above function is characterized by the species' fundamental niche centre C_i, i.e. the value of the environmental factor for which its carrying capacity reaches its maximum value $K_i^{\max}$, and its tolerance range T_i. This unimodal, continuous distribution ensures a gradual response of each species to changes in the environment.

At each location k on the gradient, the environmental factor has a distinct physical baseline value B_k representing its state in the absence of environment modification. Species, however, can affect the environmental value E_k by pushing it toward their preferred value C_i at a maximum rate m_i, which we call the niche construction rate. These species will be called "ecosystem engineers". The environment tends to return spontaneously to its baseline value B_k at a rate μ. The dynamics of the environmental factor at location k is therefore:

$$\frac{dE_k}{dt} = \mu(B_k - E_k) + \sum_i m_i \frac{N_{i,k}}{K_i^{\max}}(C_i - E_k) \tag{2.3}$$

where abundance $N_{i,k}$ is rescaled by its maximum $K_i^{\max}$ so that m_i is the maximum rate at which species i can affect the environment. In this study, we assume that species' carrying capacities are only influenced by a single factor E, although we recognize that many abiotic factors can also affect K in nature. The presence of direct competition between species can also have an influence on species distributions in space (Liautaud et al., 2019b), we describe this case in Appendix A3. In this simplified model, the only role played by growth rates is to determine how fast species reach their carrying capacities, and which equilibrium is reached from given initial conditions when there are multiple equilibria. The identification of alternative equilibria in described in the next section.

2.3.2 Potential landscape and alternative equilibria

To predict the long-term spatial patterns created by dynamics (2.1) and (3.7), we propose a simple method for finding their equilibria at each location k along the gradient. This method is based on the notion of potential landscape, whose role in ecology was pioneered by Holling (1973).

Let us consider a local community at a given location k with baseline environmental state B_k. If species population dynamics are much faster than that of the environment ($r \gg \max(m_i, \mu)$) we expect that species quickly reach their carrying capacity for a given environment value, $N_{i,k} = K_i(E_k)$, while E_k changes over longer time scales according to :

$$\frac{dE_k}{dt} = \mu(B_k - E_k) + \sum_i m_i \frac{K_i(E_k)}{K_i^{\max}}(C_i - E_k) \tag{2.4}$$

We show in the Appendix A2.1 that this can be expressed as a gradient descent dynamics,

$$\frac{dE_k}{dt} = -\frac{d}{dE_k}U(E_k) \tag{2.5}$$

where $U(E_k)$ is a potential function. This equation imposes that, from any initial condition, the variable $E_k(t)$ always moves over time toward the closest minimum of $U(E)$, and then stays there at equilibrium. This potential takes the form:

$$U(E_k) = U_E(E_k) + U_{sp}(E_k) \tag{2.6}$$

where $U_E(E_k)$ represents the contribution of abiotic processes returning the environment to its baseline state, with

$$U_E(E_k) = \frac{\mu}{2}(E_k - B_k)^2 \tag{2.7}$$

and $U_{sp}(E_k)$ represents the species' contribution

$$U_{sp}(E_k) = -\sum_i m_i T_i^2 \exp\left[-\frac{(E_k - C_i)^2}{2{T_i}^2}\right] \tag{2.8}$$

which we illustrate in Fig.1 for a single species. The relative effect of abiotic and biotic factors in encapsulated in the ratio :

$$\gamma_i = \frac{m_i}{\mu} \tag{2.9}$$

such that niche construction is weak for $\gamma \ll 1$ and strong for $\gamma \gg 1$. This parameter will be termed "niche construction strength".

This potential landscape provides an intuitive interpretation of the action of engineer species. In the absence of niche construction ($m_i = 0$), the only minimum of $U(E_k)$ is at the physical baseline $E_k = B_k$. When present, ecosystem engineers "dig" in that landscape, creating wells of width T_i centered on their preferred value C_i. As we see in Fig.1, weak engineering only slightly displaces the equilibrium, while strong engineering can create an alternative equilibrium, or even overcome abiotic dynamics entirely.

We also show in the Appendix A2.1 that, for arbitrary values of the rates r, m_i and μ, the dynamics of $E_k(t)$ become more complex than a gradient descent (i.e.

the function $U(E_k)$ can increase for part of the time), but all possible equilibria are still given by the minima of the potential $U(E_k)$ defined in (6).

2.3.3 Numerical simulations

In the presence of a single ecosystem engineer, the niche construction strength (γ) is expected to be the main driver of the dynamics. We thus study the influence of this parameter on the shape of potential landscape, and the consequences for species' distribution in space.

In diverse communities, the similarity of species in their ressource use or environmental requirements has been shown to influence species interactions (Abrams, 1983; MacArthur and Levins, 1967; Levin, 1970), and species distribution in space (MacArthur, 1972). Therefore, we study how the difference in the environment optimum of the various species (ΔC) and the niche construction strength (γ), can influence the nature and intensity of species interactions (I) in a two-species system. To do this, we compute the abundance of a species 1 when alone (N_{1a}), or in the presence of a second species 2 (N_{1b}), for different values of (γ, ΔC). We use the relative change in the abundance of species 1 as a measure of the net effect of species 2 on species 1 :

$$I_{12} = \frac{N_{1b} - N_{1a}}{N_{1a}} \tag{2.10}$$

In our study, the two species have equal niche construction abilities, but distinct environment optima. In the case where bistability is observed, we only study the equilibrium for which species 1 predominates ($C_1 = 40$, $C_2 = C_1 + \Delta C$, $E_{t=0} = B = 50$). We then extend these results to a larger number (S) of engineer species.

To address the role of these different factors - (γ,ΔC, S) - on community pattern in diverse communities, we study an environmental gradient of 101 cells ranging from $k = 100$ to $k = 200$ in arbitrary units, with a step size of 1.

The baseline value of the environment gradually increases along the gradient, as $B_k = k$. The centres of the fundamental niches of the various species, C_i, are randomly assigned following a uniform distribution between 0 and 300, so that species may have their niche centre in or outside the studied zone initially.

The model is run independently on each cell. The initial value of the environment at each location equals its baseline value($E_k(t = 0) = B_k$). For all simulation results in the main text, species were given equal maximal carrying capacity $K^{\max} = 1$ and tolerance range $T \leq 10$. Environmental return rate is set to $\mu = 1$, and species intrinsic growth rate is set to $r = 10$. Under these conditions, with $r \gg \mu$, species quickly reach their carrying capacity, with $N_{i,k} = K_{i,k}(E)$ (see 2.2). Initial species abundances are set equal for all species in all locations. We run the model with different values of the different parameters of interest (γ, ΔC, S) until $t = 1000$, and verify that the equilibrium is reached.

2.4 Results

2.4.1 Effects of niche construction strength on local equilibria

In the case where niche construction is weak ($\gamma = 0.1$, Fig. 1), the dynamics goes towards the environmental baseline value B. However, when the niche construction strength of a species increases ($\gamma = 5$), it becomes able to influence the environment. With increasing niche construction, the species becomes able to create an alternative stable equilibrium, which corresponds to an environment value close to its optimum ($\gamma = 10$). For a very high niche construction ability ($\gamma = 100$), the species environment optimum becomes the single stable equilibrium in the system.

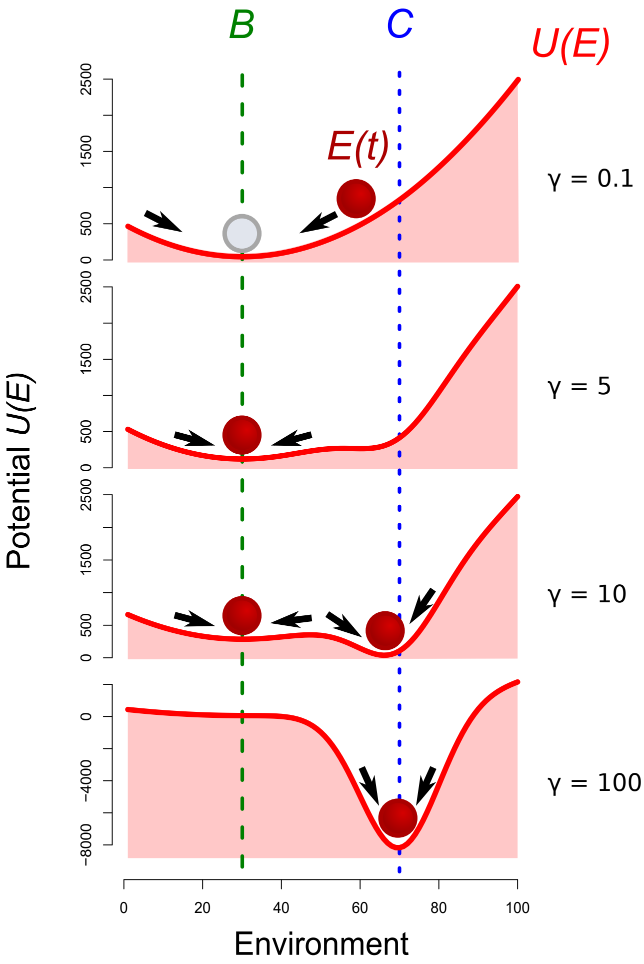

Figure 2.1: Representation of the environment as a potential under the action of physical processes and an ecosystem engineer. The ball representing the environmental state $E(t)$ follows the arrows down the slope until it reaches an equilibrium value, corresponding to a minimum of the potential function $U(E)$ (denoted by the solid curve). B is the baseline environment value, and C is the species' environmental optimum. Four parameter conditions are depicted, from weak engineering ($\gamma = 0.1$) to strong engineering ($\gamma = 100$).

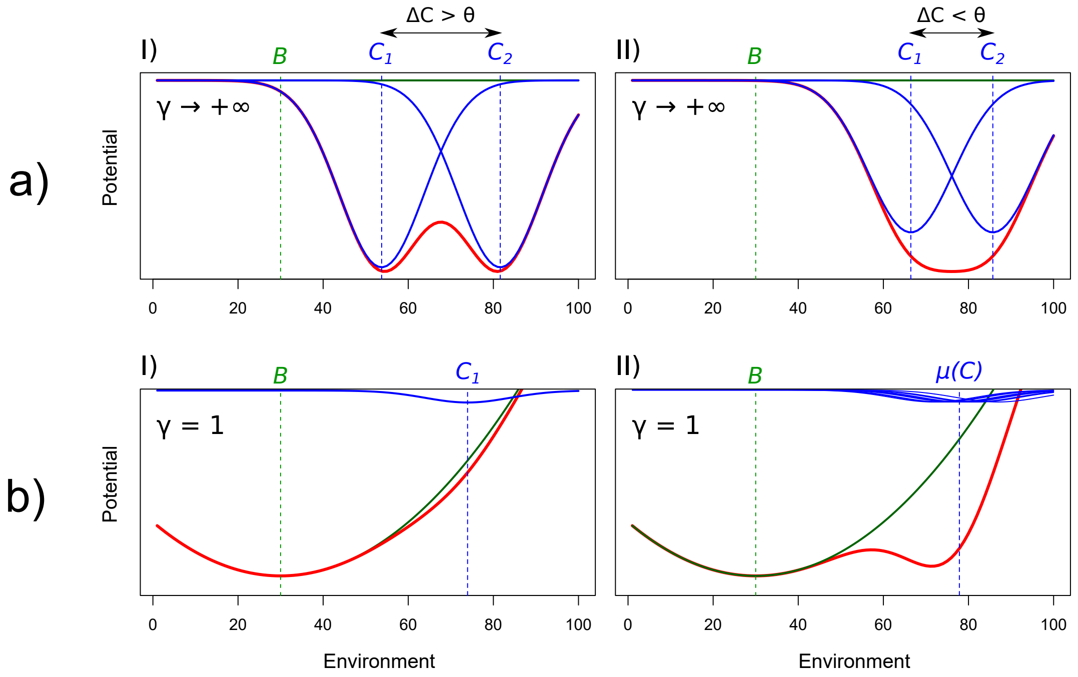

Figure 2.2: Influence of the similarity in species' environmental optima (ΔC) and diversity (S) on the potential landscape. Blue and green curves show the contributions of species ($U_{sp}(E)$) and environment ($U_E(E)$), respectively, to the potential $U(E)$ (red curve). a) : Influence of strong ecosystem engineers ($\gamma = +\infty$) on the potential landscape for two values of optimum similarity ΔC. θ represents the threshold in ΔC that separates cases in which species' contribution to the potential ($U_{sp}(E)$) show one or two minima. b) : Influence of diversity in engineering species on the potential landscape for two levels of diversity : $S = 1$ (I) and $S = 10$ (II), for low niche construction strength ($\gamma = 1$).

2.4.2 Engineer similarity, attractors and species interactions

Here we study the influence of the difference in engineers' environment optima (ΔC) on the potential landscape. For 2 species with a high niche construction rate ($\gamma \to +\infty$, Fig. 2, a) ΔC determines the number of attractors in the system. We can calculate a threshold θ of ΔC that separates cases in which species' contributions to the potential (U_{sp}, Eq 6) create a single attractor, from cases where two attractors are observed. When $\Delta C > \theta$, there are two minima in U_{sp} . As we have assumed that the abiotic contribution $U_E(E)$ is negligible, the species create distinct minima in the potential $U(E)$ (red curve) that correspond to distinct attractors (i.e alternative stable states), in which the environment is optimal for either of the two species (Fig. 2, a, I). By contrast, when $\Delta C < \theta$, there is a single minimum in U_{sp}. In this case, the two species create a common well in the potential landscape, which corresponds to a single equilibrium in between the two species' optima (Fig. 2, a, II). We show in the Appendix A2.2 that $\theta = 2T$ for species with equal tolerance ranges T and maximal carrying capacities K_{max}.

The similarity (ΔC) of engineers therefore influences the nature and intensity of species net interactions. When niche construction is weak and the similarity in environmental optima is high, the abundance of species 1 is increased when associated with species 2 (Fig. 3, red). The relative increase in species 1's abundance in association with species 2 can reach 8% when compared with its abundance when alone, indicating a positive net interaction between the two species ($I > 0$). By contrast, when niche construction is high and dissimilarity in environment optima is high, species 1 has a lower abundance in the presence of species 2 (Fig. 3, blue, indicating a negative net interaction ($I < 0$)). The relative decrease in the abundance of species 1 in the presence of species 2 can reach more than 30%, and is maximal for $\Delta C \approx \theta$. For a given niche construction rate γ, indirect interactions can thus be alternatively positive or negative, depending on the species' similarity ΔC.

The diversity of ecosystem engineers also has an influence on system properties. In the case where species have weak niche construction abilities ($\gamma = 1$, Fig. 2, b), a single species is unable to create a well in the potential. Instead, the environment controls the dynamics and the only equilibrium corresponds to the environment baseline B. By contrast, when several weak engineer species with close optima are present, they are able to dig a common well in the potential landscape (Fig. 2, b, II). This leads to the emergence of an alternative stable equilibrium, in which the environment lies between the various species' optima.

2.4.3 Influence of engineer similarity on species distribution and environmental changes in space

As described in section 3.2, the similarity of species environment optima (ΔC) influences the number of stable equilibria. When two ecosytem engineers are present along an environmental gradient, different community patterns can emerge, depending on ΔC. In the case where $\Delta C > \theta$ (Fig. 4, I), each species pushes the environment to its own optimum. Along an environmental gradient, this leads to the emergence of distinct zones where the environment is driven close to the respective species optima. These zones are separated by abrupt changes in both the environment (Fig. 4,I,b) and species abundances (Fig. 4,I,c). Within these zones, each species is dominant in the spatial extent over which it controls the environment (Fig. 4,II). A distinct pattern emerges in the case where $\Delta C < \theta$, with the two species pushing the environment between their respective optima. This leads to the emergence of a single spatial zone where the environment is modified, and allows species coexistence at high abundances (Fig. 4, II, b-c). The transition between zones where the species can or cannot modify the environment is abrupt, with a discontinuity in both the environment and species abundances.

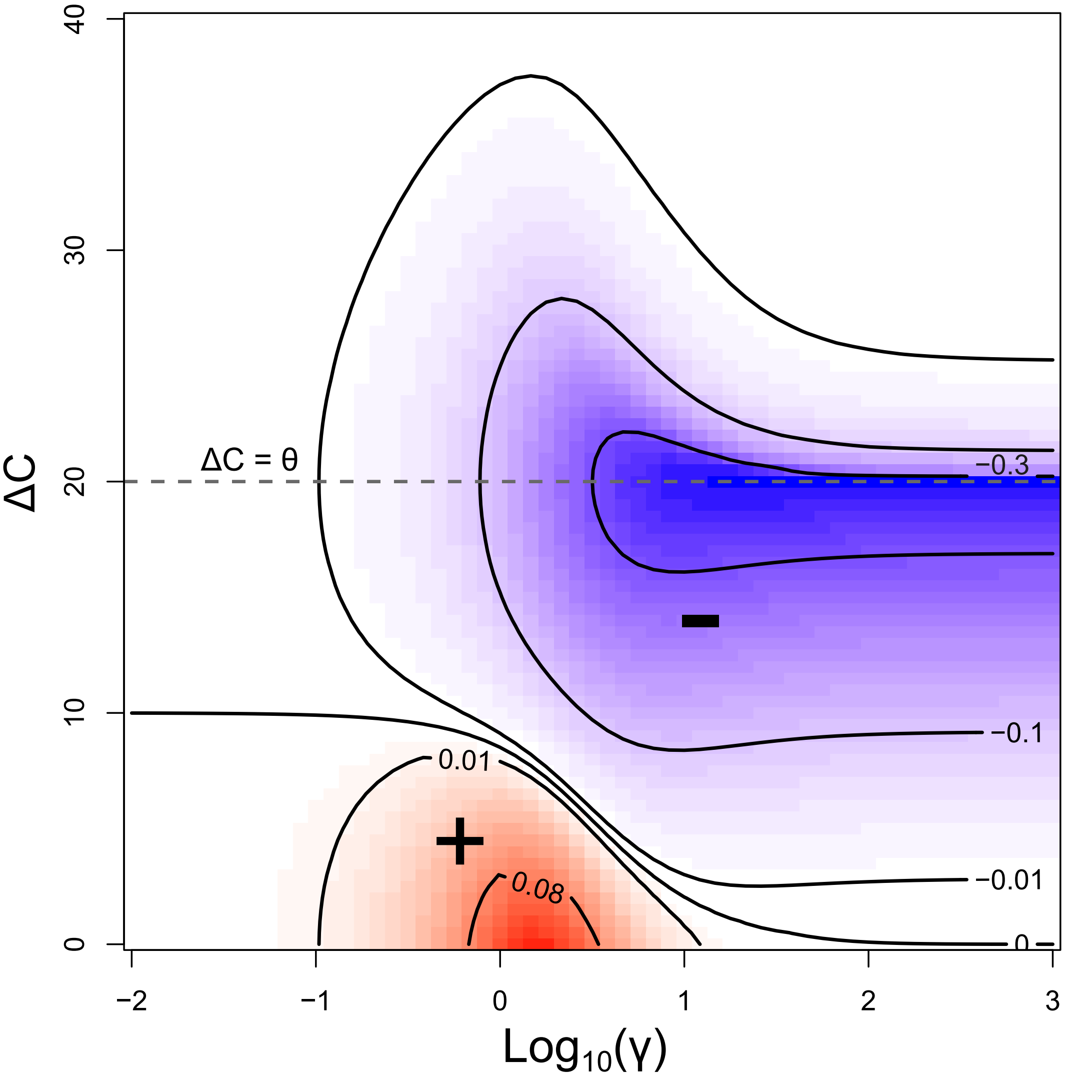

Figure 2.3: Emerging net species interactions as a function of the similarity of species' environment optima (ΔC), and niche construction strength (γ). Parameter values for which net competitive interactions (-) are observed are depicted in blue, whereas net mutualistic interactions (+) are depicted in red. Interaction strength is measured by the relative change in the abundance of species 1 when associated with species 2, compared with its abundance when alone (Eq. 10). **Dashed line** $\Delta C = \theta$ represents the threshold in environment optimum similarity that separates cases in which species' contribution to the potential shows one or two minima. In the case where bistability is observed, we only study the equilibrium for which species 1 predominates ($C_1 = 40$, $C_2 = C_1 + \Delta C$, $E_{t=0} = B = 50$).

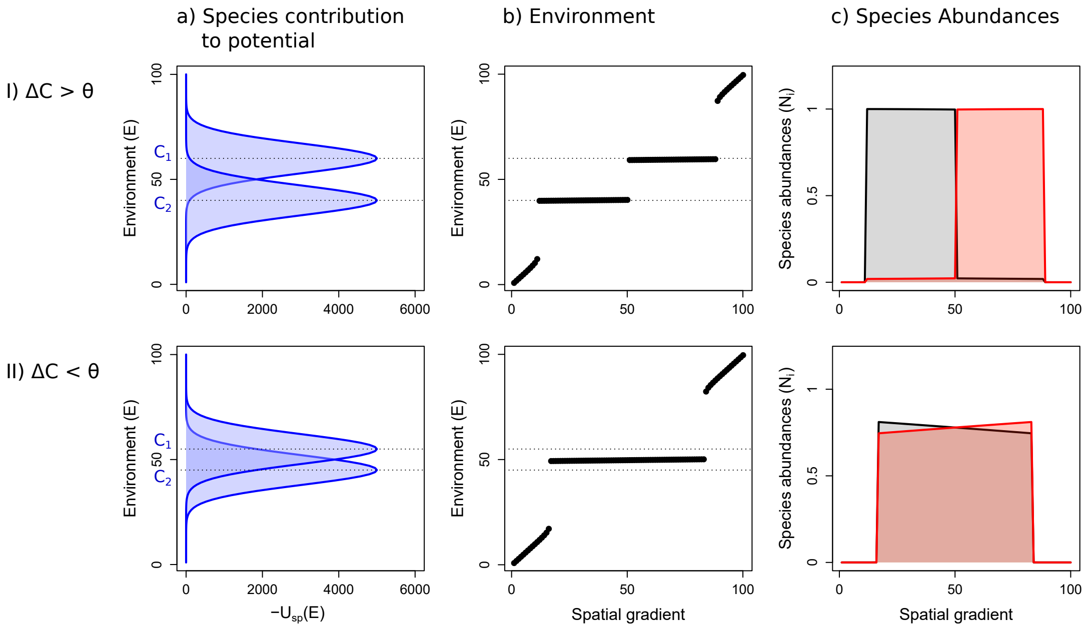

Figure 2.4: Influence of the similarity in ecosystem engineers on species distributions and the environment along a spatial gradient. We show results for : I) a difference in species' environmental optima ΔC larger than the threshold θ, II) a difference in species' environmental optima ΔC smaller than the threshold θ. (a) : Species contribution - $U_{sp}(E)$ - to the potential $U(E)$. (b) : Value of the environment along the spatial gradient . (c) : Species abundances along the spatial gradient at equilibrium. In the two depicted cases, species are strong ecosystem engineers ($\gamma = 10$).

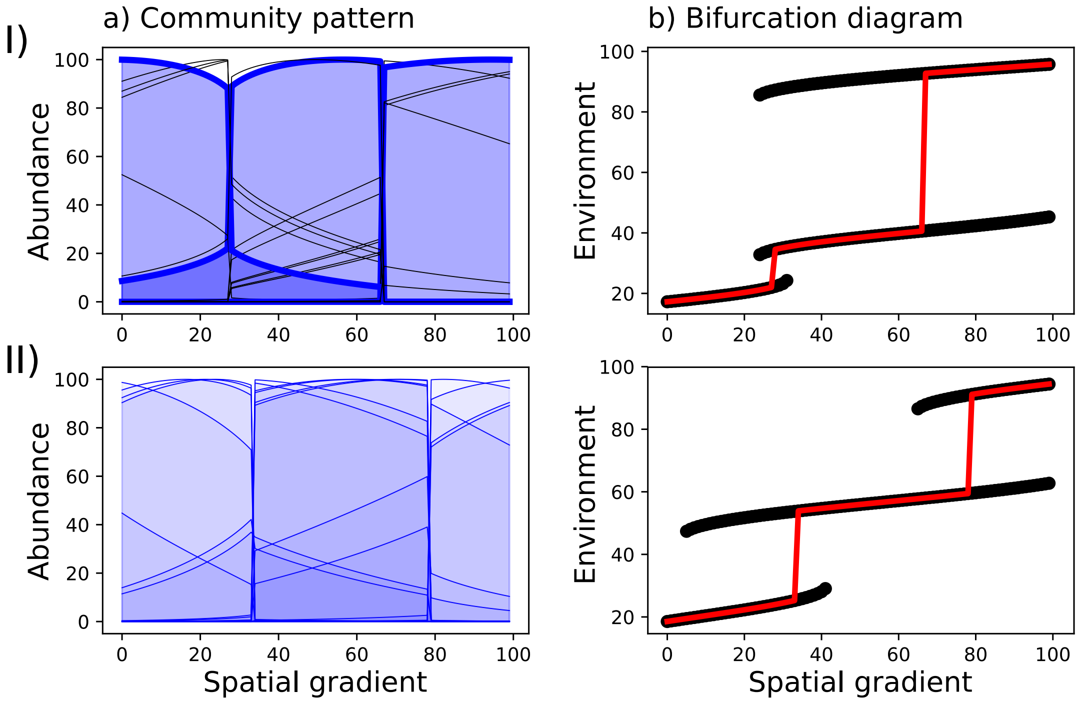

Figure 2.5: Species abundances along a spatial gradient (a) and bifurcation diagrams (b) in the case where: I) both strong ecosystem engineers ($\gamma = 10$, bold blue curves) and non-engineers ($\gamma = 0$, black curves) are present, II) numerous weak ecosystem engineers ($\gamma = 2$, blue curves) are present. In bifurcation diagrams (b), black curves represent all potential stable equilibria, and red lines represent equilibria observed in depicted cases in (a). Many weak engineers create fewer zones than there are engineers, and a pattern similar to the case where there are a few strong engineers.

2.4.4 Spatial community patterns in diverse communities

We now extend these results to many-species communities. In the case where several strong ecosystem engineers are present ($\gamma_i = 10$), we observe discrete communities in space, separated by sharp boundaries where important changes in both the abundance of ecosystem engineers (blue curves, Fig. 5, I) and in the environment (Fig. 5, I, b) occur. Non-engineers species ($\gamma_i = 0$, black curves) follow this pattern, with abrupt changes in their abundances. The bifurcation diagram shows the existence of alternative stable states, with different environment equilibria for a given location in space (Fig. 5, I, b). Similar patterns are observed when there are numerous weak ecosystem engineers ($\gamma = 2$), with the coincidence of abrupt changes in both the environment and species abundances in space. We observe much fewer discrete zones than there are engineers, because of the fusion of their potential wells (see section 3.2).

2.5 Discussion

In this work, we investigated the role of biodiversity and species interactions in the emergence of ecotones through ecological niche construction. In particular, we studied the respective contributions of niche construction strength (γ), similarity in the environment optimum of the species (ΔC) and diversity (S). Our results show that, depending on the engineering strength γ, the contribution of biodiversity to ecotone emergence will be either through the similarity of species' environmental optima ΔC, or through the diversity of engineering species S.

In the case of a single ecosystem engineer acting on the environment, discontinuities occur when a high niche construction rate (γ) allows the engineer to control its environment. These abrupt shifts are explained by the presence of two alternative stable states in the system that correspond to: 1) a modified state, with the environment close to the engineer's optimum, and 2) a non-modified state, corresponding to the baseline value of the environment. A small change in the environmental conditions can thus lead to an abrupt shift from one attractor to the other.

In the case where species are strong ecosystem engineers, the difference in environmental optima (ΔC) is the main contribution of biodiversity to the emergence of ecotones. The presence of various engineers with distinct environment optima leads to the emergence of indirect interactions that influence the community patterns. We showed in a two-species system that these indirect interactions can be competitive or mutualistic, depending on the value of the difference ΔC.

When engineers have distant environmental optima and strong engineering abilities, their net interaction is competitive. At a given location, a species has a lower abundance when associated to a second engineer, as compared with its abundance when alone. Indirect competition through the environment can be observed in cases where there is multistability in the system, but also when a single equilibrium exists. In the extreme case where the modified environmental conditions are outside the other species' fundamental niche, the latter can be excluded. By contrast, when the species' environmental optima are close, with weak engineering abilities, we observe the emergence of net mutualistic interactions. In these cases, the two species are able to improve their carrying capacities, by modifying the environment to their mutual benefit. The abundance of a species is thus higher when associated with another engineer. In our study, the more species differ in their environmental optima, the stronger the negative effect they have on each other. This differs from classical limiting similarity theory (Abrams, 1983; MacArthur and Levins, 1967). Considering limiting resources such as water or light, limiting similarity theory predicts an increase in competition strength as the similarity in the resource requirements of the various species increases. By contrast, when species modify the abiotic environment to their own benefit, we showed that competition decreases, and then can turn into a net mutualistic interaction as the similarity of species' environmental optima increases.

With more than two strong engineers along the gradient, engineers with close optima will tend to modify the environment to their collective benefit. When the ability of a community to modify the environment becomes higher than the ability of another one, the former will replace the latter along environmental gradients. This can be interpreted as a situation where there is competition between communities. In this case, the community shows a high level of integration (Clements, 1916; Wilson and Sober, 1989). This type of community organization tends to create particular species abundance patterns in space, with discrete communities separated by sharp boundaries.

In the case where the species are weak ecosystem engineers, the main contribution of biodiversity to community organization is through the number of engineering species. In this case, a weak ecosystem engineer alone is not able to substantially modify the environment and create a species-environment feedback. But when numerous weak engineers with similar optima are present, we do observe the emergence of species-environment feedbacks. In these cases, species jointly modify the environment to their collective benefit, as described above. In our model, an increase in species diversity can lead to an increase in each species' biomass, through facilitation. The collective action of a large number of different ecosystem engineers can thus lead to the emergence of discrete communities along an environmental gradient, associated with sharp changes in the environment. In this study, the effect of several weak ecosystem engineers on the environment is not qualitatively different from the effect of a single strong engineer, but the spatial extent of the environmental change may be larger. The existence of several species may indeed broaden the spectrum of abiotic conditions under which the environment is modified, as seen in the case of positive interactions between two engineers. Biodiversity is potentially a key factor influencing the emergence of species-environment feedbacks in nature, and thus the emergence of sharp ecotones separating discrete communities. This might be the case in mangrove ecosystems, where several species can have similar effect on water salinity (Sternberg et al., 2007). As shown in this study, a certain level of biodiversity in ecosystem engineers might be necessary to maintain species-environment feedbacks. Likewise, Gonzalez et al. (2008) showed that the accumulation of small environmental changes by weak engineers can ultimately lead to a substantial change in the abiotic environment, and thus allow an ecosystem engineer to invade. A decrease in biodiversity, as currently observed worldwide (Pimm et al., 2014; Ceballos et al., 2015), might thus have important consequences, not only for community composition and organization, but also for the abiotic environment and for ecosystem functioning.

Species that do not modify their environment can also be influenced by ecological niche construction. By changing the environment, ecosystem engineers can promote species that benefit more from the modified state than the baseline conditions. In this case, ecosystem engineers indirectly facilitate other species through environmental modification. Facilitation has been shown to occur, particularly under harsh environmental conditions, such as in arid ecosystems (Soliveres and Maestre, 2014; Vega-Álvarez et al., 2018; Armas and Pugnaire, 2005) or in cold environments (Choler et al., 2001; Callaway et al., 2002). When an engineer facilitates another species, it can be considered as a "nurse species" (Niering et al., 1963) that modifies the environment and allows the growth of species that would not have the ability to grow otherwise. Nevertheless, ecosystem engineering can also have negative effects on other species. For example, van Breemen (1995) showed how *Sphagnum* species can depress the growth of vascular plants by changing the environmental conditions in peat bogs ecosystems. A sharp ecotone can thus be explained by the appearance or disappearance of an engineer along the gradient, facilitating or preventing the growth of other species. In the case where species do not modify the environment to their own optimum, succession in time can be observed. In this case, the engineer can foster the growth of its successors, thus having a negative impact on its own performances (Appendix A4).

Species interactions - such as competition or mutualism - have been identified as drivers of species abundance along environmental gradients (Terborgh and Weske, 1975; Choler et al., 2001). We have shown in this paper that interactions between species and the abiotic environment can have unexpected consequences on species interactions themselves. These interactions can lead to the emergence of discontinuities in the environment, associated with sharp ecotones where important species turnover are observed . Explicit consideration of species-environment feedbacks is thus likely to increase our understanding of species distributions along environmental gradients. It may similarly be essential when studying the responses of species or communities to temporal changes in their environment. Finally, we have also shown that biodiversity can influence community organization along an environmental gradient. Current biodiversity loss can have major consequences for species distributions, abiotic environmental conditions, and ecosystem functioning.

2.6 Appendix

Overview

Setting

When can we unambiguously identify the state of an ecosystem, demarcate its boundaries and follow its change over time? This is most easily done if its many component species, each with their individual goals and needs, behave and respond as a collective. Multiple mechanisms can plausibly lead to such large-scale self-organization in ecological communities.

A first possibility is a community of purpose, when all species have shared goals. This brings to mind the picture of a superorganism (Clements, 1916), a network of interactions carefully arranged toward self-perpetuation. But this picture has long been contested in ecology (Gleason, 1926).

A second possibility is a community of means – a public good or marketplace tying together many individuals with different interests. When we can identify a large-scale ecosystem function, it is often tied to some shared resource – water, energy, basic elements. The existence of such a “common currency”, through which a species can affect all others in a coherent fashion, is a widespread source of collective behavior.

This second possibility has already been largely explored in ecological theory, where resource competition plays a central role (Mac Arthur, 1969), and can indeed lead to collective organization (Tikhonov, 2016b). Public goods models often assume that all agents benefit from accumulating some common resource; these works thus focus on setting up a tension between individual and collective means to achieve that profit.

Yet, the environment is no mere stockpile of resources: it is not only used, but also constructed and transformed. The environmental state – say, the concentration of various nutrients – differentially advantages some species over others, and the changes induced by a species need not be beneficial to itself. This can prompt many complex dynamics, such as a succession of different community stages, each benefitting from the outputs of the previous one.

Model

We have S species, each with abundance N_i, growth rate r_i and interference competition α_{ij}

$$\frac{dN_i}{dt} = r_i N_i \left(1 - \frac{N_i + \sum_j \alpha_{ij} N_j}{K_i(E)}\right) \tag{2.1}$$

Their carrying capacities are given by their environmental niche

$$K_i(E) = k_i^{\max} e^{-(E-C_i)^2/2T_i^2} \tag{2.2}$$

with a maximum of $k_i^{\max}$ when the environmental variable equals the species' optimum $E = C_i$, and a tolerance (niche width) of T_i. For numerical stability and clarity of interpretation, we can decide of an extinction threshold θ (e.g. a single individual) such that we treat smaller carrying capacities as being zero

$$K_i(E) < \theta \qquad \sim \qquad K_i(E) = 0. \tag{2.3}$$

Finally, each species affects the environment at a rate m_i (the species' "engineering ability"), pushing it toward some value ε_i, while the environment tends to return to its baseline value B with rate μ,

$$\frac{dE}{dt} = \mu(B - E) + \sum_i m_i N_i (\varepsilon_i - E) \tag{2.4}$$

Perfect engineer species will have $\varepsilon_i = C_i$ and always draw the environment toward their own optimum. By contrast, imperfect engineers may create an environment which is suboptimal for themselves, $\varepsilon_i \neq C_i$, for instance by depleting resources that they need, or accumulating harmful byproducts.

To understand the long-term consequences of these dynamics, we will first study the equilibrium conditions

$$\begin{aligned} 0 &= N_i \left(K_i(E) - N_i - \sum_j \alpha_{ij} N_j \right) \\ E &= \frac{\mu B + \sum_i m_i N_i \varepsilon_i}{\mu + \sum_i m_i N_i} \end{aligned} \tag{2.5}$$

Perfect coexisting engineers

Throughout this section, we assume perfect engineer species ($\varepsilon_i = C_i$) without interference competition, $\alpha_{ij} = 0$. Then, all species (with nonzero carrying capacity) can coexist, and at equilibrium

$$N_i = K_i(E). \tag{2.6}$$

Potential landscape and equilibria

Slow environment

If the dynamics of species abundances is much faster than that of the environment $r_i \gg m_i, \mu$, we expect that species quickly reach their carrying capacity for a given environment value, $N_i = K_i(E)$, and hence the dynamics of the system is given by

$$\frac{dE}{dt} = \mu(B - E) + \sum_i m_i K_i(E)(C_i - E) \tag{2.7}$$

We now show that is in fact a *gradient descent* dynamics, similar to

$$\frac{dx}{dt} = -\frac{dU(x)}{dx} \tag{2.8}$$

where $U(x)$ is a potential function, with the dynamics always going toward the closest minimum of $U(x)$.

Indeed, notice that

$$K_i(E)(C_i - E) = T_i^2 \frac{d}{dE} K_i(E) \tag{2.9}$$

Thus,

$$\frac{dE}{dt} = -\frac{d}{dE} U(E) \tag{2.10}$$

where the potential takes the form:

$$\begin{aligned} U(E) &= \frac{\mu}{2}(E-B)^2 - \sum_i m_i T_i^2 K_i(E) & (2.11) \\ &= \frac{\mu}{2}(E-B)^2 - \sum_i m_i k_i^{\max} T_i^2 e^{-(E-C_i)^2/2T_i^2} & (2.12) \end{aligned}$$

We see it has two components: a parabolic well $(E - B)^2$ which has a single minimum at B, and a sum of Gaussian wells created by each of the engineer species. If m_i are large enough, $U(E)$ can have local minima corresponding to these engineered wells, and if $m_i \gg \mu$, these wells are deeper than the parabola, so engineered states are more stable than the natural state.

The effective strength of a species' long term action on the environment is thus

$$\lambda_i = m_i k_i^{\max} T_i^2 \tag{2.13}$$

meaning that a species can be an important ecosystem engineer either through large engineering ability m_i, large maximum abundance $k_i^{\max}$, or wide niche T_i.

At a given patch, as $E(t)$ changes over time, $U(E(t))$ will decrease until it reaches the bottom of the local basin:

$$\frac{dU}{dt} = \frac{dU}{dE}\frac{dE}{dt} = -\left(\frac{dE}{dt}\right)^2 \leq 0 \tag{2.14}$$

See Fig. A4 for a map of the potential in a simulation and how it can be used to predict the final environmental state.

Fast environment

We now consider the opposite limit, when the dynamics of the environment variable E are faster than the species'. Crucially, equilibria are independent from the relative timescale of environment and species dynamics. Therefore, equilibria must always be minima of the potential $U(E)$, even for fast environment dynamics. However, in that case, there is no guarantee that these dynamics can be approximated by gradient descent, meaning that $E(t)$ will not necessarily remain within the initial basin of attraction.

To move out of the initial basin, there must be some time during which the dynamics are climbing up the potential landscape, i.e. $dU/dt > 0$. Notice that

$$\frac{dU}{dt} = \frac{dU}{dE}\frac{dE}{dt} = \frac{dU}{dE}\left(-\frac{dU}{dE} + \sum_i m_i(N_i - K_i(E))(C_i - E)\right) \tag{2.15}$$

hence $dU/dt > 0$ requires the second term in parentheses to be larger than the slope dU/dE of the potential. Given a potential barrier, the dynamics may climb it if:

- there exist basins beyond the barrier (in the same direction as the slope, i.e. same sign of dU/dE and $C_i - E$) that are created by species with $N_i > K_i(E)$
- there exist basins in the other direction (opposite sign of dU/dE and $C_i - E$) created by species with $N_i < K_i(E)$

In other words, faster environmental dynamics will be able to climb out of shallow wells provided that there are overabundant species attracting them, or, more likely for barren initial conditions, if the species creating these wells remain at low abundance $N_i < K_i(E)$ for sufficiently long. Thus, the dynamics are most likely to settle in a deep (and not necessarily wide) basin. By contrast, slow environment dynamics might favor the widest basin, which is more likely to contain the initial condition $E(0)$ (see Discussion).

Effective species interactions for fast environment

Let us set $\mu = 1$ for simplicity (i.e. m_i is measured in units of μ). Then the equilibrium environment value is

$$E = \frac{B + \sum_i m_i N_i C_i}{1 + \sum_i m_i N_i}$$

If the environment quickly reaches this value for any species abundance N_i, the dynamical equation for species becomes

$$\frac{1}{r_i N_i}\frac{dN_i}{dt} = 1 - \frac{N_i}{k_i^{\max}} \exp\left[\frac{1}{2T_i^2}\left(\frac{(B - C_i) + \sum_j m_j N_j (E_j - C_i)}{1 + \sum_j m_j N_j}\right)^2\right] \tag{2.16}$$

For $m_i \ll 1$, we can do a series expansion

$$\frac{(B - C_i) + \sum_j m_j N_j (E_j - C_i)}{1 + \sum_j m_j N_j} \approx (B - C_i) + \sum_j m_j N_j (E_j - B) \tag{2.17}$$

and thus

$$\frac{1}{r_i N_i}\frac{dN_i}{dt} \approx 1 - \frac{N_i}{K_i(B)}\left(1 + \frac{1}{T_i^2}\sum_j m_j N_j (B - C_i)(E_j - B)\right). \tag{2.18}$$

At equilibrium

$$N_i = \frac{K_i(B)}{1 + \frac{1}{T_i^2} \sum_j m_j N_j (B - C_i)(E_j - B)} \tag{2.19}$$

Once again, we do a Taylor expansion to get

$$N_i = K_i(B) \left(1 - \frac{1}{T_i^2} \sum_j m_j N_j (B - C_i)(E_j - B) \right) \tag{2.20}$$

which is equivalent to the equilibirum of a Lotka-Volterra model

$$N_i = K_i(B) \left(1 - \sum_j A_{ij} N_j \right), \qquad A_{ij} = \frac{d \log K_i}{d N_j}(B) = \frac{m_j}{T_i^2}(B - C_i)(E_j - B). \tag{2.21}$$

Effective facilitation and competition

When does an engineer species create an equilibrium?

Let us consider a single engineer species and ask when it can create an equilibrium with a value of E distinct from B. The equilibrium criterion is $dU/dE = 0$, i.e.

$$\mu(E - B) = m_1 k_1 (C_1 - E) e^{-(E - C_1)^2 / 2T_1^2} \tag{2.22}$$

For simplicity, let us consider the case $C_1 - B > T_1$. Then, we can approximate our question by asking whether the maximum of the right-hand term at some particular value E_m is larger in absolute value than the left-hand term $\mu(E_m - B)$ at that point. The maximum of the right-hand term is given by a zero of its derivative

$$m_1 k_1 \left(\frac{(E_m - C_1)^2}{T_1^2} - 1 \right) e^{-(E_m - C_1)^2 / 2T_1^2} = 0 \tag{2.23}$$

hence $E_m = C_1 - T_1$, and a sufficient condition for species 1 to create a new equilibrium is

$$\mu(C_1 - B - T_1) \lesssim m_1 k_1 T_1 e^{-1/2}. \tag{2.24}$$

We see that it is harder to create a new equilibrium far away from the baseline environment value, i.e. when $C_1 - B$ is large.

Two species

To understand the long-term interactions between two species through their engineering capabilities, we can study the environmental variable's potential landscape $U(E)$ and ask: does each species create a potential well (are there as many alternative stable states as there are species)?

The contribution of engineers to $U(E)$ is a sum of Gaussian terms,

$$U(E) = \frac{\mu}{2}(E - B)^2 - \sum_i \lambda_i e^{-(E - C_i)^2 / 2T_i^2} \tag{2.25}$$

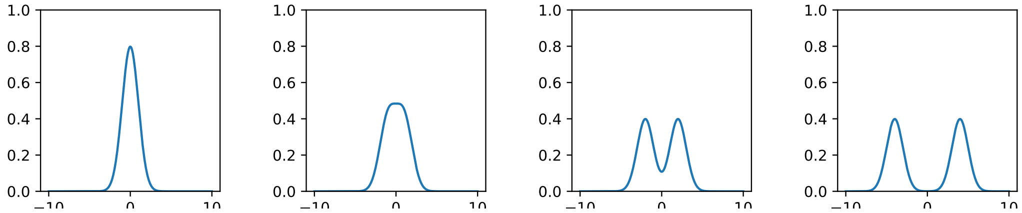

Figure A1: Joint effect of two species on the potential landscape: sum of two Gaussian functions of equal standard deviation T, separated by $\Delta C \in \{0, 2, 4, 8\}$ (left to right). Up to $\Delta C = 2T$, the sum of Gaussians is unimodal, indicating that the two species can create a single equilibrium together. Afterward, species are effectively in competition, as each one prevails in a different equilibrium state. Still, until $\Delta C \approx 8T$, the overlap increases the height of each peak, while beyond, there is little to no positive effect of one species on the other.

where λ_i is defined in (2.13). If we assume for now $\mu = 0$, our question becomes: when is the sum of two Gaussians unimodal?

Consider two species that are equal in every respect, save their optimum

$$\lambda_1 = \lambda_2, \quad T_1 = T_2 = T, \quad C_2 - C_1 = \Delta C \tag{2.26}$$

We find three cases (see Fig. A1)

- Pure competition: if $\Delta C \gg 2T$, the two Gaussians are well separated and each species forbids the other from existing

- Mixed facilitation and competition: if $\Delta C \gtrsim 2T$ (e.g. $\Delta \in [2T, 8T]$), the two species allow each other to exist, and even facilitate each other to some extent (making the other's potential well deeper, and thus more likely to overcome environment inertia or other competitors). Still, the sum of Gaussians remains bimodal: there are two possible equilibria, each favoring one of the species. This is a form of moderate competition between facilitators.

- Coalescence: if $\Delta C < 2T$, the sum of Gaussians becomes unimodal, with a peak halfway between the species optima. Now, the two species act together as a single, more influential species.

If species differ in other parameters, the same qualitative picture holds, although the weaker species (smaller λ) will need a larger ΔC to maintain its own distinct peak, rather than be absorbed in the stronger species'. There exists a general quantitative criterion for bimodality in a mixture of two arbitrarily different Gaussians (Robertson and Fryer, 1969), which we report in the next section, but it does not easily generalize to more species.

Criterion for bimodality of a Gaussian mixture

According to (Robertson and Fryer, 1969), a weighted sum of two gaussians

$$pG(x, 0, 1) + (1 - p)G(x, \mu, \sigma) \tag{2.27}$$

is bimodal if $\mu > \mu_0$ with

$$\mu_0 = \frac{1}{\sigma}\sqrt{2(\sigma^4 - \sigma^2 + 1)^{3/2} - (2\sigma^6 - 3\sigma^4 - 3\sigma^2 + 2)} \tag{2.28}$$

and $p \in [p_1, p_2]$ where

$$\frac{1}{p_i} = 1 + \frac{\sigma^3 y_i}{\mu - y_i} e^{-\frac{1}{2}y_i^2 + (y_i - \mu)^2/(2\sigma^2)} \tag{2.29}$$

with y_1 and y_2 the roots of the equation

$$(\sigma^2 - 1)y^3 - \mu(\sigma^2 - 2)y^2 - \mu^2 y - \mu\sigma^2 = 0 \tag{2.30}$$

with $0 < y_1 < y_2 < \mu$. Otherwise, the sum is unimodal.

Many species

For many species, no exact results exist but we can provide a scaling estimate of the average number of alternative states. Given S the number of species, with their optima distributed over interval $[0, L]$, the average distance between their optima is

$$\langle \Delta C \rangle = L/S. \tag{2.31}$$

If the optima are uniformly distributed, the number of optima within a certain interval follows a Poisson distribution, and thus, the probability that $\Delta C > 2T$ (avoiding coalescence) is the probability of having no optima within a span of $2T$, i.e.

$$P(\Delta C > 2T) \approx e^{-2\langle T \rangle / \langle \Delta C \rangle} \tag{2.32}$$

Hence, the typical number of clusters of coalesced species scales like

$$S_0 \sim S e^{-2\langle T \rangle S/L}. \tag{2.33}$$

This approximation will only hold up to $\langle \Delta C \rangle \sim T$, i.e. $S \sim L/2\langle T \rangle$, after which adding more species will typically not contribute more equilbria.

Now recall that species i on its own can create an alternative equilibrium despite the natural environmental dynamics only if

$$\mu(C_i - B) \lesssim m_i k_i^{\max} T_i \tag{2.34}$$

meaning that the potential well created by the species is deep enough to compensate the recovery of the environment, which gets faster as E moves away from B.

This means that species can only contribute to an equilibrium if their opti-

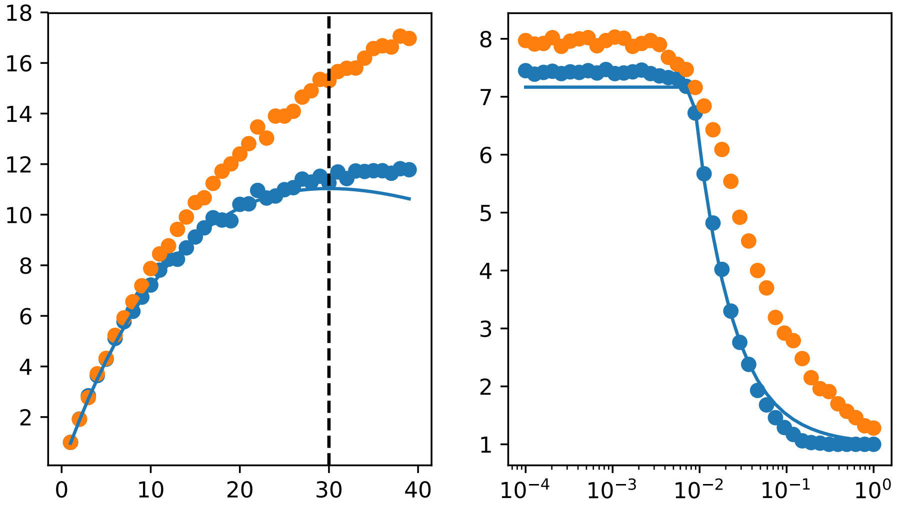

Figure A2: Number of alternate stable states N_{eq} as a function of number of species S (left panel) and environment recovery μ (right panel). Species have identical niches (blue dots) or heterogeneous niche widths T_i drawn from a Gamma distribution with variance 0.3 (orange dots). The solid lines represent the analytical prediction (2.36). The dashed line indicates $S = L/2\langle T\rangle$, the threshold above which N_{eq} saturates.

mum falls within a range

$$L' \leq \min\left(L, \frac{2\langle mkT\rangle}{\mu}\right). \tag{2.35}$$

Only the fraction L'/L of species clusters with optima within that range can create new equilibria.

Therefore, the expected number of equilibria (including the natural equilibrium at B) is

$$\begin{aligned} N_{eq} &\sim 1 + S_0\frac{L'}{L} \\ &\lesssim 1 + Se^{-2\langle T\rangle S/L}\min\left(1, \frac{\langle mkT\rangle}{\mu L}\right). \end{aligned} \tag{2.36}$$

This simple formula reproduces the qualitative behaviors within a wide range of parameters, see Fig. A2. Deviations happen if species are heterogeneous in their properties $k_i^{\max}$, m_i or T_i, and as mentioned above, our calculation does not account for the saturation beyond a threshold $S > L/2\langle T\rangle$ shown by the dashed line in Fig. A2.

Interference competition and imperfect engineers

Let us now consider the case of direct interference competition $\alpha_{ij} \neq 0$ and imperfect engineers $\varepsilon_i \neq C_i$. Now, some species can go extinct even while their carrying capacity is nonzero. Recall the equilibrium condition

$$0 = N_i \left(K_i(E) - N_i - \sum_j \alpha_{ij} N_j \right)$$

The abundance of surviving species $N_i^* \neq 0$ is given by

$$N_i^* + \sum_j \alpha_{ij} N_j^* = K_i(E) \tag{2.37}$$

or in vector form,

$$N^* = (\mathbb{I} + \alpha^*)^{-1} K^*(E) \tag{2.38}$$

where $\mathbb{I}$ is the identity matrix, α^* is the matrix of interactions restricted to the S^* surviving species, and $K^*(E)$ the vector of carrying capacities of surviving species. For convenience, define the matrix

$$V_{ij} = (\mathbb{I} + \alpha^*)^{-1}_{ij} \tag{2.39}$$

so that

$$N^* = V K^*(E). \tag{2.40}$$

Equivalence

Taking once again the limit of fast species dynamics, we now have

$$\begin{aligned} \frac{dE}{dt} &= \mu(B - E) + \sum_{ij} m_i(\varepsilon_i - E) N_i^* \\ &= \mu(B - E) + \sum_{ij} m_i(\varepsilon_i - E) V_{ij} K_j(E) \end{aligned} \tag{2.41}$$

which we can rewrite as

$$\frac{dE}{dt} = \mu(B - E) + \sum_i^{S^*} \hat{m}_i(\hat{\varepsilon}_i - E) K_i(E) \tag{2.42}$$

with

$$\hat{m}_i = \sum_j^{S^*} V_{ji} m_j, \qquad \hat{\varepsilon}_i = \frac{\sum_j^{S^*} V_{ji} m_j \varepsilon_j}{\sum_j^{S^*} V_{ji} m_j} \tag{2.43}$$

Thus, we see that direct competition appears equivalent, in terms of its equilibrium effect, to imperfect engineering with effective values of species engineering capability m_i and target environment value ε_i. An important consequence is that even perfect engineers ($\varepsilon_i = C_i$) will behave like imperfect ones if they also interact directly.

It is, however, crucial to note that the calculation above involves summing only on the S^* species that survive the direct competitive interaction. While the matrix V_{ij} depends only on interactions α_{ij} and not on the environment, it does depend on who survives, which is controlled by the carrying capacities as well. Thus, direct competition cannot simply be replaced by imperfect engineering, except in the regime where all species coexist (i.e. for weak direct interactions). In particular, if direct competition allows for alternate equilibria (mutual exclusion), each will correspond to a different equation (2.42).

Perhaps counter-intuitively, it is the action of species i on others that appears in the effective parameters above. For instance, if direct interactions are weak,

$$V = (\mathbb{I} + \alpha^*)^{-1} \approx \mathbb{I} - \alpha^* \tag{2.44}$$

$$\hat{m}_i \approx m_i - \sum_j^{S^*} \alpha_{ji} m_j, \qquad \hat{\varepsilon}_i \approx \varepsilon_i - \sum_j^{S^*} m_j \alpha_{ji} (\varepsilon_j - \varepsilon_i) \tag{2.45}$$

and we see that a species' effective engineering ability $\hat{m}_i$ decreases due to its competitive effect on others, α_{ji}, while its effective target environmental value $\hat{\varepsilon}_i$ moves away from the optima ε_j of the species it affects.

Skewed potential

From equation (2.42), we can construct the corresponding potential by noticing that

$$\frac{dE}{dt} = -\frac{dU(E)}{dE} = \mu(B - E) + \sum_i^{S^*} \hat{m}_i (C_i - E) K_i(E) + \sum_i^{S^*} \hat{m}_i (\hat{\varepsilon}_i - C_i) K_i(E) \tag{2.46}$$

The last term is the only one that differs significantly from the equation in the case of perfect engineers, (2.7). Thus, we can separate the resulting potential into two contributions: first, the usual potential for perfect engineers, obtained here with the S^* surviving species and effective engineering rates $\hat{m}_i$, and second, a correction $\Delta U(E)$ coming from the last term above. We write

$$U(E) = U_{pe}(E) + \Delta U(E) \tag{2.47}$$

where

$$U_{pe}(E) = \frac{\mu}{2}(E - B)^2 - \sum_i^{S^*} \hat{m}_i T_i^2 K_i(E) \tag{2.48}$$

is the contribution that is similar to the perfect engineer case. Since $K_i(E)$ is Gaussian, its integral is an error function, and the correction to the potential takes the form

$$\Delta U(E) = \sum_i^{S^*} \hat{m}_i T_i^2 (\hat{\varepsilon}_i - C_i)\, \mathrm{erf}\left(\frac{E - C_i}{\sqrt{2} T_i}\right) \tag{2.49}$$

Error functions are sigmoidal and comprised between 0 and 1, so $\Delta U(E)$ will have the general shape of a "staircase", i.e. a sum of step-like functions going up or down, with a step height of $\hat{m}_i T_i^2(\hat{\varepsilon}_i - C_i)$.

This could create new potential wells, if two (or more) species push E in the direction of each other's optimum, giving rise to a new type of interaction: obligate facilitation (or mutual stabilization), where each species degrades its environment from its own perspective, but improves it from the perspective of the other.

If $\hat{\varepsilon}_i - C_i$ has the same sign for many species (e.g. all species tend to degrade complex sugars into simpler ones, pushing the environment variable E in a constant direction), the effect will be to create a general slope in that direction, and thus, dynamics akin to succession.

Ecotones and succession

Ecotones on an environmental gradient

Let us assume an environmental (e.g. latitudinal or altitudinal) gradient, reflected in the fact that the baseline value of the environmental variable $B = B(x)$ now depends on position x along the gradient.

If we choose a solution of (2.5) and follow it along the gradient, as we progressively change parameters such as $B(x)$, we do not expect sharp ecotones (transition zones between communities with different species compositions and abundances). The only option for a singular transition is to have alternative stable states, with the transition occurring when one of the states loses its stability.

Whenever two or more attractors exist for the same patch x, see black lines on Fig. A4 top-right, there is potential for hysteresis.

Succession trajectories

In this model, including direct competition and imperfect engineering, one can imagine three different succession scenarios.

The reference scenario is the usual competition-colonization tradeoff setting (Tilman, 1994). In that case, species at later stages are expected to have slower growth but stronger competitive ability, either through direct competition, engineering ability, or a combination of both. As a consequence, later stages will be longer, but transitions between stages will also be slower.

Another scenario is succession driven by the environmental variable slowly descending down the potential landscape created by the engineer species. In that case, there is no implication that later stages will be longer. If the landscape is shaped by perfect engineers, we can expect a rather smooth change of the environmental variable. If it is shaped by imperfect engineers, it is possible to have

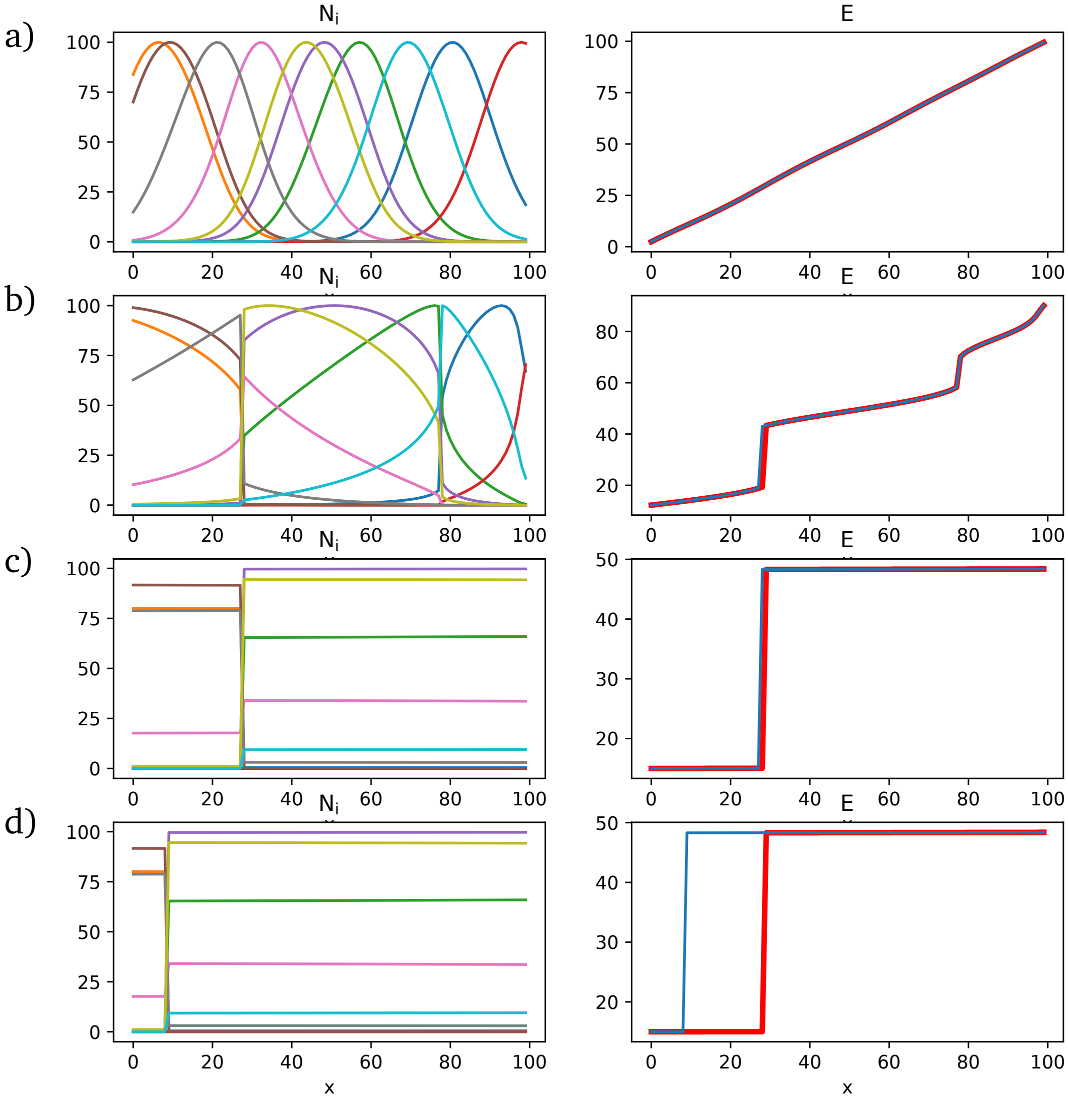

Figure A3: Realized abundance for species in the community (left) and values of the environmental variable (right) along a spatial gradient defining the baseline environmental variable $B(x) = x$ which is also the initial state at each point. Increasing $\bar{m}/\mu$ from 0.1 (a) to 10 (b) to 100 (c), we go from an environment that closely follows B, and thus a continuous turnover of species, to the existence of alternate stable states engineered by these species, and separated by sharp transitions. Finally, reducing the rate of species dynamics from $r = 10$ (c) to $r = 0.1$ (d) increases the difference between the pure gradient descent prediction (red line, right panels) and the observed environment value E at each position x. Possible equilibria are independent of r, but which equilibrium is reached does depend on it: as we explain in Fig. A4, high r entails gradient descent toward the closest equilibrium, while low r allows the dynamics to climb a potential wall, and tends to favor the deeper basins rather than the ones closest to the initial condition.

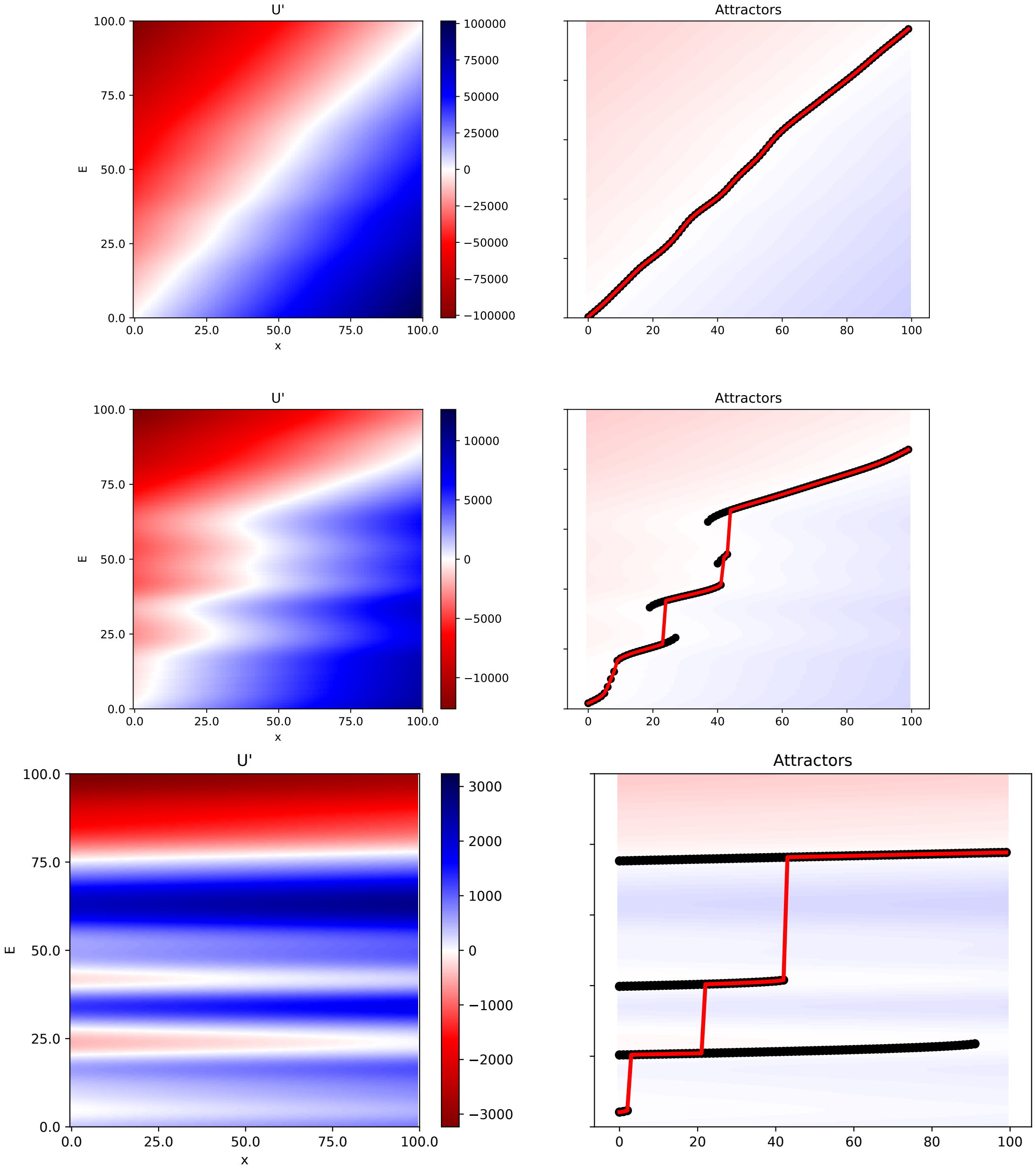

Figure A4: Using the potential landscape $U(E)$ to predict the equilibrium state, for $\mu = 1000, 100, 1$ (top to bottom). Left column: dU/dE as a function of the environment variable E (y-axis) and the position x on the gradient (x-axis) which controls the natural environment value $B(x) = x$. Equilibria correspond to white lines $dU/dE = 0$ (stable if red is above and blue below, or unstable the other way around). Right column. Following the stable equilibria (black dots) and predicting where gradient descent should go if $E(x, t = 0) = B(x)$ (red line).

long transition periods where all species have low abundance, separating shorter periods where a set of imperfect engineers dominates. There may be stabilization at low abundances if two sets of engineers are pushing the environment toward each other.

The third scenario is perturbation-driven succession: jumps between equilibria, either due to random noise, or to directed perturbations (e.g. a gradual increase in the baseline environmental value B). It is only in this scenario that succession will generically exhibit discrete stages separated by sudden transitions. Under random perturbations, succession will proceed on average toward deeper wells, and thus later stages will be longer on average (deeper wells resist perturbations longer), but there may be reversions to earlier stages.

Supplementary Discussion

Slow and fast environment

An intuitive aspect of the speed of environment change is its inertia upon removal of some engineer species. In one limit, the environmental state may remain the same for long times (for instance, peat created by Sphagnum mosses can remain for thousands of years (van Breemen, 1995)), long enough that the species could potentially recolonize at the same abundance before any significant change occurred. In the other limit, the environmental state may revert suddenly, even instantaneously when the engineering results from physical properties of the species themselves (e.g. shielding of light by the canopy).

As noted in Sec. 2.6, when the environment dynamics are slow, the environmental variable effectively follows a gradient descent. This means that the species (or group of species) creating the widest basin of attraction control the dynamics for a broad range of initial conditions. By contrast, when the environment dynamics are fast, they are drawn toward the optimum of the species with the largest carrying capacity and best engineering abilities, even if its niche is narrow. We thus predict a prevalence of generalists in slow environments, and specialists in fast environments.

Multiple environmental variables

A single environmental variable E may not suffice to accurately represent the ways in which species interact through modifications of their surroundings. On the other hand, our modelling approach for ecosystem engineers is most relevant if the number of environmental variables is limited, and small compared to the number of species – otherwise, it may be simpler to directly model pairwise species interactions.

There is one important qualitative feature that distinguishes the outcomes of this model, and those of a model with multiple environmental "dimensions": with only one dimension E, there can be at most as many equilibria as there are engineer species. This stops being the case with more environmental variables. A corresponding mathematical result states that a mixture of Gaussian components can have more maxima than components in dimension $d > 1$ (Ray and Ren, 2012; Wallace, 2013). This means that some equilibria could not be assigned to, nor expected from, the action of any given species on its own.

Chapter 3

The role of biodiversity in protecting ecosystems against collapse

Title of the scientific article :

The role of biodiversity in protecting ecosystems against collapse.[1]

3.1 Introduction

Ecosytems are currently facing major biodiversity loss due to anthropogenic activities (Díaz et al., 2019), with unprecedented species extinction rates in human history (Pimm and Raven, 2000; Pimm et al., 2014; Pereira et al., 2010). Biodiversity has been shown to play a key role in ecosystem functioning, notably by increasing community stability (Loreau and de Mazancourt, 2013) and productivity (Tilman, 2001; Hooper et al.). Biodiversity can increase the resistance and resilience of communities facing environmental and anthropogenic pressures (Isbell et al., 2015; Oliver et al., 2015), and decreases the temporal variability of key ecosystem functions (Wang and Loreau, 2016; Yachi and Loreau, 1999). These roles of biodiversity are now recognized as crucial in the maintenance of ecosystem services (Isbell et al., 2011), such as food providing, nutrient cycling or water regulation (Mace et al., 2012).

Ecosystems respond in different ways to environmental or anthropogenic perturbations. In most cases, their response is gradual, whether it is linear or nonlinear (Qin et al., 2013; Walther, 2010). In some cases, however, abrupt shifts in community composition and ecosystem functioning occur (Scheffer et al., 2001; Scheffer and Carpenter, 2003). These abrupt shifts generally arise when feedback loops involving species and the abiotic environment are present within the system (Kéfi et al., 2016; Scheffer, 2009). Shallow lakes provide a classic example of such abrup shifts, as they can dramatically shift from a clear to a turbid state due feedback loops involving the aquatic vegetation, planktonic algae and nutrient suspension (Scheffer et al., 1993; Carpenter et al., 1999). Dramatic changes in fish abundance caused by anthropogenic pressures are also observed in ocean's

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[1] This work represents a collaboration with Egbert van Nes, Marten Scheffer and Michel Loreau. In preparation

ecosystems (Conversi et al., 2015), as illustrated by the collapse of cod populations in the Baltic sea (Möllmann et al., 2009). These abrupt shifts can have deep implications for the survival of some species and for the maintenance of key ecosystem functions that can be beneficial to human activities, as illustrated by collapses in fisheries (Pinsky et al., 2011).

Recently, much progress has been made in our understanding of the role of biodiversity in ecosystem functioning. Little is known, however, about the role biodiversity might play in protecting ecosystems against collapses. Despite their common interest in the influence of environmental changes on ecosystems, the research fields of Biodiversity-Ecosystem functioning (BEF) on the one hand, and of critical transitions on the other hand, have been historically separated. Several examples, however, suggest that abrupt shifts in ecosystem functioning can result from a loss in species diversity. In Lake Victoria, a major decrease in cichlids' fish biomass and diversity was followed by an abrupt change in community composition. Nile Perch abundance suddenly increased, although this species had been introduced 30 years earlier (Downing et al., 2012). In a Caribbean coral reefs, the successive extinctions of grazer fish and urchins species resulted in an abrupt eutrophication of the ecosystem (Hughes, 1994).

A notable effect of biodiversity on ecosystem functioning is the increase in community productivity, through *complementarity and selection effects* (Loreau and Hector, 2001; Tilman, 2001). The maintenance of a sufficient level of species' biomass or abundance can enable the persistence of important ecosystem processes, in the case where the community faces environmental perturbations. This is notably the case in tropical forest ecosystems, where a decrease in tree cover can lead to savannah or treeless states (Van Nes et al., 2014). In this case, a high tree cover limits the fire expansion, thus promoting the persistence of a forest state. Likewise, tropical cloud forests are thought to be protected from fires occurring in adjacent pines forest thanks to high abundances and diversity of epiphytic species that maintain high humidity levels (Martin et al., 2011, 2007). Other theoretical studies suggest that a sufficient diversity and biomass of ecosystem engineers that modify the environment can produce and maintain species-environment feedbacks (Liautaud et al., 2019a), and thus influence ecosystem functioning.

In this study, we focus on the effect of biodiversity in protecting an ecosystem against collapse, through its effect on community biomass. We investigate the role of biodiversity in the presence of two perturbations types: 1) a press perturbation and 2) fluctuations in environmental conditions. In the current global change context, human activities are exerting increasing pressures on the Earth's ecosystems. The gradual increases in air temperature and atmospheric CO_2 (Masson-Delmotte et al., 2018) as well as the ocean acidification (Doney et al., 2009) are examples among others. To understand the consequences of such pressures on the risk of ecosystem collapse, we first investigate the role species richness might have on the ecosystem resistance to a press. Ecosystems are also experiencing stochastic fluctuations in environmental conditions. A higher variability in climatic conditions, with the occurrence of more frequent extreme events (Masson-Delmotte et al., 2018), is notably expected in the context of current global warming. We therefore study how species' response diversity can buffer the impacts of stochastic environmental perturbations.

To investigate the effects biodiversity can have on the risk of collapse, we use a competition Lotka-Volterra model, combined with an Allee effect on total biomass. We first show that biodiversity increases the critical press intensity leading to collapse in the case of an environmental press. We then show that an increase in response diversity decreases the system's propensity to collapse in the presence of stochastic perturbations. Our work shows the potential importance of biodiversity in the protection of ecosystems facing various environmental and anthropogenic perturbations. We stress that current biodiversity loss could lead to abrupt changes in ecosystem functioning and composition, with potential impacts for human well-being.

3.2 Model and Methods

3.2.1 Model

Competitive systems have commonly been used to study the effect of biodiversity on ecosystem functioning, because they address biodiversity within a trophic level explicitly (Gross and Cardinale, 2005; Loreau, 2010). We therefore study the dynamics of a pool of n competing species, with a combined Allee effect. The dynamics of species i is described by a modified Lotka-Volterra model :

$$\frac{dN_i}{dt} = r_i N_i \left(1 - \frac{\sum_j \alpha_{ij} N_j}{K_i}\right)\left(\frac{\sum_j N_j}{T} - 1\right) + p \tag{3.1}$$

where N_i represents the species i's biomass, r_i is its intrinsic growth rate, and α_{ij} is the competition coefficient of species j on species i. We only consider symmetrical competitive interactions, with $\alpha_{ij} = \alpha_{ji}$, which facilitates the persistence of all species at equilibrium. T is the threshold in total species' biomass under which species' growth rates become negative (Allee effect). The growth rate of species i, $\frac{dN_i}{dt}$, is thus influenced by the total biomass within the community.

To study the influence of species diversity on the risk of ecosystem collapse in a changing environment, we add a perturbation term p to the equation. In our study, this perturbation can take two different forms :

1) $p = -m.N_i$: an environmental press is exerted on the species, with m the press intensity

2) $p = \sigma.u_i.N_i$ in the presence of environmental stochasticity. u_i denotes a standard white-noise source. In discrete time, $u_i(t)$ would be a normally distributed random variable with zero mean and unit variance. It is drawn independently at each time step, but may be correlated between species (Arnoldi et al., 2019; Loreau and de Mazancourt, 2013). Parameter σ is the environmental standard deviation.

3.2.2 Analytical analyses and numerical simulations

Environmental press

We first study the case in which the perturbation takes the form of a press on species' abundances : $p = -m.N_i$. The aim is to determine the influence of diversity on the critical press value $m = mc$ leading to collapse.

Carrying capacities and intrinsic growth rates are set equal for all species ($K_i = K = 0.5$, $r_i = r = 1$) in the main text, but we relax these assumptions in the Supporting Information. Competition coefficients α_{ij} are drawn from a uniform distribution $\alpha \sim U(0, a)$. We only consider weak interaction strength to ensure the persistence of all species at equilibrium : $a = [0, 0.01, 0.1, 0.2]$. The dynamics is run with an initial pool of $S = 20$ species until $t = 1000$, and we verify that an equilibrium is reached. A species is then removed and the dynamics is run again until $t = 1000$. Species removal is repeated until reaching a diversity of $S = 1$. *At each step of the species removal process, species' initial biomass are set equal to the previous equilibrium biomass.*

For each species i, critical press value can be analytically calculated with :

$$mc_i = \frac{W_i}{N_i^*} \frac{(T - \sum_j (N_j^*))}{\sum_j W_j^2} \tag{3.2}$$

where W_j is calculated from the Jacobian matrix J, with : $W_j = \sum_i J_{ij}$. The Jacobian matrix J is estimated numerically with the package 'rootSolve' in the R software (R Core Team, 2016). See Appendix I for calculation details. For each diversity level, we estimate the critical press vector leading to ecosystem collapse $\vec{mc}$, using a linear approximation around the equilibrium. Vector $\vec{mc}$ represents the vector with minimum norm that leads to collapse. Its components - *i.e* specific press intensities - can differ among species ($mc_i \neq mc_j$). In our simulations, predicted press $\vec{mc}$ is overestimated by a factor λ, when compared to the observed press leading to collapse. However, the scaling with model parameters is preserved, and we show in the Appendix that prefactor $\lambda = 4$ in the case of equal interactions. For a given diversity level S, we take the averaged specific critical press $\hat{mc} = \mu(\vec{mc})$ as an estimator of press intensity leading to collapse. Results are averaged over 20 simulation runs. In the Appendix, we also show results obtained with a uniform press estimator mu, whose components are equal ($mu_i = mu$). In this case, mu represents the press intensity that is common to all species and lead to collapse.

Stochastic environmental perturbations

In this section, perturbation p is a stochastic environmental noise. Species' responses to noise can be correlated, with $cor(p_i, p_j) = \rho_{ij}$. In the case where $\rho = 0$, there are no correlations in species' responses to perturbation: response diversity is high. In contrast, when $\rho = 1$, all species respond in the same direction to a perturbation: response diversity is zero. The aim of this part of the study is to understand how response diversity can protect the ecosystem against a collapse in the presence of environmental noise. We therefore study the influence of correlation ρ on :

- 1) the coefficient of variation (CV) of total biomass over time. This metrics is used as an estimator of the system's total biomass variability. The higher the total biomass CV, the higher the probability of collapse by crossing the Allee threshold.

$$CV = \frac{\sigma_B^*}{\sum_i (N_i^*)} \tag{3.3}$$

, where $\sum_i (N_i^*)$ is the total biomass at equilibrium (in the absence of noise), and σ_B^* is the standard deviation of total biomass of a community exposed to environmental noise. σ_B^* is analytically estimated using linear approximation around equilibrium (Arnoldi et al., 2016), for different values of species' correlation response ρ :

$$\sigma_B^* = \sqrt{\sum (C^*)} \tag{3.4}$$

, where C^* is the long-term covariance matrix in species biomass, with :

$$C^* = \hat{J}^{-1}(C^e) \tag{3.5}$$

J is the Jacobian matrix, and C^e the covariance matrix of instantaneous species' responses to noise :

$$C^e_{ij} = cov(p_i, p_j) = \rho_{ij} N_i N_j \sigma^2 \tag{3.6}$$

- 2) the Collapse-Time (CT), i.e the time at which biomass becomes zero. It is an estimator of the system's propensity to collapse in a given time interval. The smaller the collapse-time, the smaller the system's ability to maintain a non-zero biomass. In this study, metrics CV and CT are used as estimators of the system's resistance to environmental perturbations.

The collapse-Time CT is recorded from numerical simulations, using the Euler–Maruyama method :

$$N_i(t+\delta t) = N_i(t) + r_i N_i \left(1 - \frac{\sum_j \alpha_{ij} N_j}{K_i}\right)\left(\frac{\sum_j N_j}{T} - 1\right)\delta t + N_i \sigma u_i(t)\sqrt{\delta t} \tag{3.7}$$

The dynamics is run for different levels in $cor(u_i, u_j) = \rho$. For a given correlation level ρ, all species pairs have equal correlation values, with $\rho_{ij} = \rho$. In our simulations, environmental standard deviation σ is set to 1, carrying capacities and intrinsic growth rates are set equal for all species ($K = 1$, $r = 1$), and competition coefficients are drawn from a uniform distribution between 0 and 0.2. The Allee threshold T is set to 1 in the main text, but we show results with different values in the Appendix. For different levels of correlation ρ, we performed 50 simulation runs and recorded the system collapse-time for each. We then plot histograms of collapse-time distribution.

3.3 Results

3.3.1 Environmental press

Diversity directly impacts the critical environmental press at which the system collapses. When biodiversity is high, high press intensities are necessary to generate collapse (Fig 1, A & B). In contrast, when few species remain in the community, a weak environmental press can lead to ecosystem collapse (Fig 1, A & B). In the case where the Allee threshold of total biomass is high ($T = 4$, Fig 1, B)), successive species extinctions can lead to ecosystem collapse without a press ($\hat{mc} = 0$, Fig.1, B). Figure 2 shows a strong correlation between the critical environmental press $\hat{mc}$ and total biomass. When species diversity is high, total biomass is high and a strong environmental press is necessary to generate a collapse. By contrast, when diversity is low, total biomass is low and the system collapses with low press levels. The competitive interaction strength also influences the critical press at which a collapse is observed. For a given biodiversity level, systems with weak interactions cope with a higher environmental press than do systems with strong interactions.

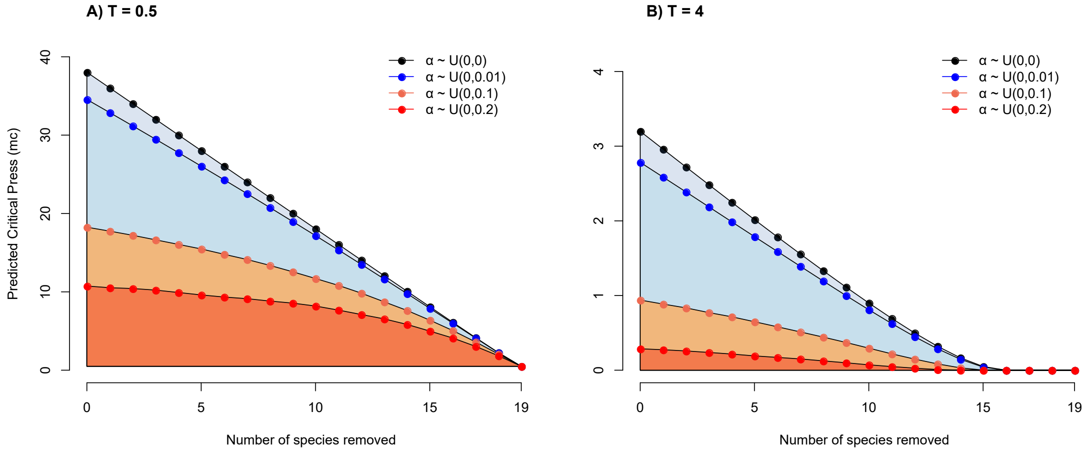

Figure 3.1: Influence of diversity loss on the predicted critical press $\hat{mc}$ leading to ecosystem collapse. Two levels in total biomass Allee threshold are described : A) $T = 0.5$, B) $T = 4$, for which four levels in maximal competitive interactions are investigated, from no competitive interactions ($A \sim U(0, 0)$), to moderate interaction strength ($A \sim U(0, 0.2)$). For a given competition strength level, persistence of the community (non-zero biomass) is observed for parameters values (S, $\hat{mc}$) below the curve. In contrast, collapse is predicted to occur for parameter values above the curve.

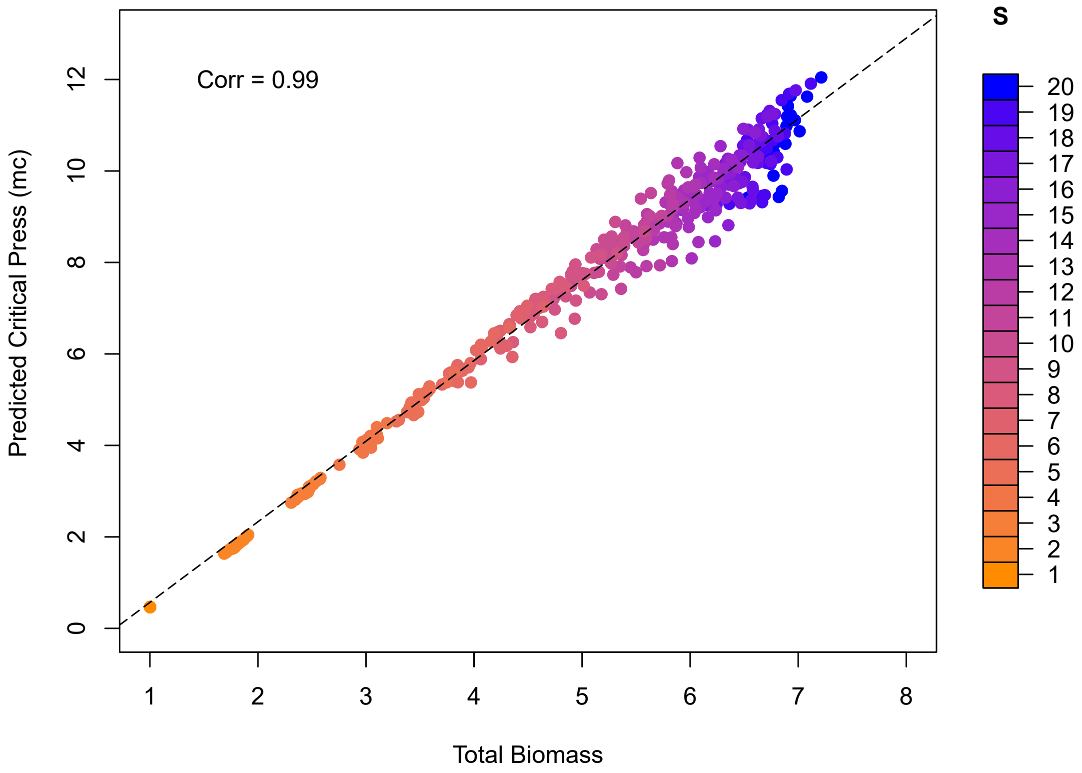

Figure 3.2: Relationship between predicted critical press value ($\hat{mc}$, y-axis) and total biomass (x-axis), for different species diversity levels. Dotted line represents the linear regression curve. Results were obtained using the species-removal process described in the "Model and Methods" section, with 20 simulation runs. Competition coefficients were drawn from a uniform distribution between 0 and 0.2

3.3.2 Stochastic environmental perturbations

In the presence of environmental stochasticity, the correlation of species' responses to noise ρ influences the system's propensity to collapse. Here we show results obtained with parameters values : $r = 1$, $\sigma = 1$, $T = 1$, $\alpha \sim U(0, 0.2)$. When there is no correlation in species responses to noise $\rho = 0$), we do not observe ecosystem collapse between $t = 0$ and $t = 1000$ (Fig 3, a). In this case, total biomass fluctuates through time, but it never reaches zero-biomass within the time period considered. In contrast, when the correlation ρ increases, ecosystem collapses are observed ($CT < 1000$, Fig 3, a & b), and become earlier as ρ increases. Finally, when correlation is high $\rho = 1$, with all species responding in the same direction to noise, all systems collapse early (Fig. 3, d). Results obtained with different parameters values are shown in the Appendix.

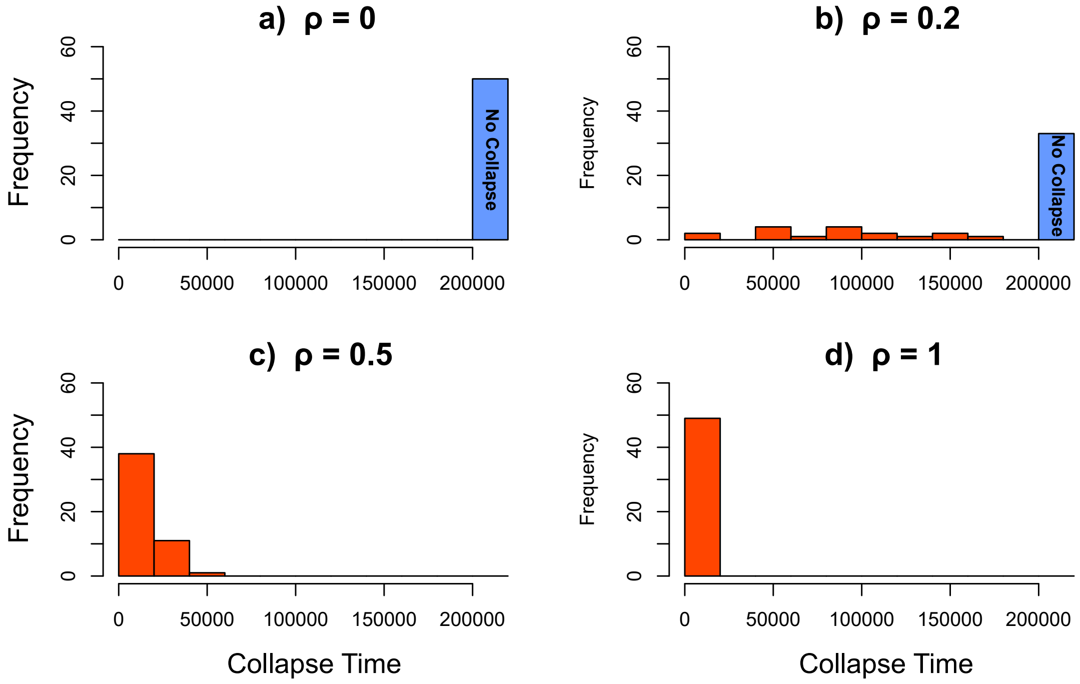

Figure 3.3: Distribution of collapse-time CT for four different values of correlation in species' instantaneous response to noise ρ. x-axis : time at which the system collapses, y-axis : number of simulation runs (frequency). Blue bars indicate that no collapses were observed within the time period considered. For each level of correlation ρ, 50 simulation runs were performed. Parameters values : $r = 1$, $\sigma = 1$, $T = 1$, $\alpha \sim U(0, 0.2)$

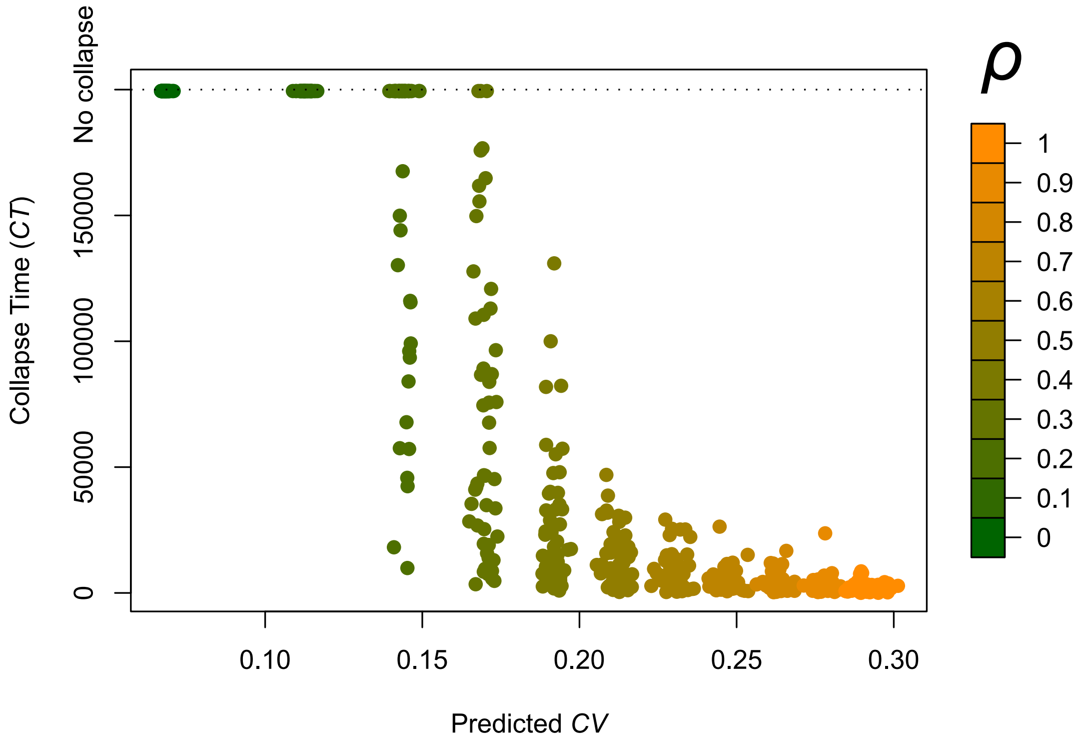

Figure 3.4: Relationship between the observed Collapse Time (CT, y-axis), and the predicted coefficient of variation in total biomass (CV, x-axis), for different levels of correlation in species response to noise ($\rho = 0$ to $\rho = 1$). The "saturating effect" observed for high values of ρ is due to the absence of collapse within the time-period studied (but see Fig.3). Parameters values : $r = 1$, $\sigma = 1$, $T = 1$, $\alpha \sim U(0, 0.2)$

Figure 4 shows how the system's variability is influenced by parameter ρ, and how it is related to Collapse-Time CT. When the correlation of species responses is low, the predicted coefficient of variation in total biomass is low. In this case, fluctuations in total biomass are of low amplitude. When correlation ρ increases, CV increases, which means that the magnitude of fluctuations in total biomass increases (Fig. 4). We observe a negative relationship between the observed Collapse-Time CT and the analytically predicted coefficient of variation in total biomass CV. The higher the correlation in species response ρ, the smaller the predicted coefficient of variation CV.

3.4 Discussion

In this work, we showed that biodiversity can play a critical role in protecting ecosystems against collapse in stressful environments. In particular, we showed that two distinct diversity features - *species richness and response diversity* - will act, depending on the perturbation type.

In our model, an increase in species richness leads to an increase in total productivity through a complementarity effect, which is consistent with theoretical predictions and field experimental results (Tilman, 2001; Loreau and Hector, 2001; Hooper et al.). This increase in total community biomass leads to an increase in the critical press value leading to ecosystem collapse. A high species diversity thus increases ecosystem resistance to a press. A consequence is that, for a given press value, a loss in species diversity leads to a decrease in ecosystem resistance. If too many species go extinct, total biomass decreases and can go below the Allee threshold. In our model, the system will therefore shift to a zero-biomass state. In natural systems, however, a similar shift can lead to an alternative state with a different community composition. For instance, a decrease in cichlid fish diversity and biomass in Lake Victoria (Downing et al., 2012) resulted in an abrupt change in community composition, with a fish community dominated by the Nile Perch.

In the presence of stochastic environmental perturbations, diversity acts on ecosystem resistance through the diversity of species' responses. In this case, species responding in different directions have a buffering effect on the total biomass, as attested by a decrease in the coefficient of variation of total biomass. This leads to a decrease in the system's propensity to collapse by crossing the Allee threshold. This buffering effect of response diversity has been empirically and theoretically studied and is known as the ”insurance effect” (Yachi and Loreau, 1999). In this study, we show that the insurance effect can also protect an ecosystem against a critical transition. These results are in line with the work of Isbell et al. (2015), who showed that diversity increases the resistance of ecosystem productivity to climatic extremes. In systems where biomass is critical to maintain important ecosystem functions, biodiversity can thus play an important protecting role against a collapse.

In this study, an ecosystem collapse occurs when the total biomass crosses a critical threshold. We did not model the mechanisms leading to ecosystem collapse, such as the presence of feedbacks between species and their environment (Liautaud et al., 2019a). In natural systems, however, biodiversity loss is expected to result in ecosystem collapse when important feedbacks loops are involved in ecosystem functioning. Feedback loops are an important condition for the emergence of abrupt transitions in perturbed environments (Kéfi et al., 2016; Scheffer, 2009), and the threshold that we used in this study can result from the operation of such feedback loops. When biomass is involved in the maintenance of such loops, a decrease in response diversity or species richness can result in a collapse if total biomass is not high enough. A decrease in cloud mountain forest diversity, for instance, can lead to a weaker resistance to fire perturbations (Martin et al., 2007, 2011) because tree and epiphyte plant biomass promotes high humidity levels through various feedbacks. In the case of forest-savannah ecosystems, plant-fire feedbacks are modified when tree cover becomes too low, and the system can shift into a flammable state (Van Nes et al., 2014). In lake Victoria, cichlid species were able to contain the Nile perch invasion, notably by eating its eggs. A decrease in cichlid diversity then suppressed this control exerted on the perch's early life stages, which resulted in perch invasion. In a more theoretical framework, Liautaud et al. (2019a) showed that a high diversity of species modifying their environment can result in the emergence of substantial species-environment feedbacks that strongly influence community composition and the abiotic environment. If diversity decreases, total biomass decreases, and feedback loops are no longer maintained, leading to abrupt changes in species composition. Ecosystems in which strong feedback loops between species, or between species and their environment, might therefore be particularly sensitive to diversity loss. Thus, species-environment feedbacks should be included in models to understand the effects of biodiversity loss on ecosystem functioning.

This might help conservationists to identify communities and ecosystem types in which biodiversity loss can lead to abrupt transitions.

In the current context of climate change, environmental press and stochasticity are already affecting ecosystems. Perturbations such as increases in ocean water and air temperatures and ocean acidication are among the causes of current biodiversity loss. Climate change is also expected to lead to a higher variance in climatic conditions, with the occurrence of more frequent extreme events. These disturbances, in addition with other causes such as habitat fragmentation, are deeply affecting the Earth's biodiversity. In this study, however, we stress that biodiversity loss itself can reinforce the effects these perturbations have on ecosystems. We showed that decrease in species richness and response diversity can decrease ecosystem resistance. Current biodiversity loss, in interaction with other anthropogenic perturbations, could thus deeply impact numerous ecosystem functions and lead to ecosystem collapses in the worst-case scenarios. A number of studies have already showed that biodiversity loss can impact ecosystem functioning and key ecosystems services that benefit humans (Isbell et al., 2011; Balvanera et al., 2006; Cardinale et al., 2012). Our work further suggests that these changes might be abrupt, and that the maintenance of high diversity levels could be critical for the maintenance of key ecosystem functions.

3.5 Appendix

Analytical determination of critical press m for equal competition strength

In the absence of any press, the dynamics is described by :

$$\frac{dN_i}{dt} = rN_i\left(1 - \frac{\sum_j^S \alpha_{ij}N_j}{K}\right)\left(\frac{\sum_j^S N_j}{T} - 1\right) \tag{3.1}$$

For equal interaction strength : $\alpha_{ij} = \alpha$, and $\alpha_{ii} = 1$, we can define : $\nu = \sum_j^S N_j$,

Then, $\sum_j^S \alpha_{ij}N_j = \frac{\nu}{S} + \frac{S-1}{S}\alpha\nu$, with $\alpha_{ii}N_i = \frac{\nu}{S}$

We thus get :

$$\frac{d\nu}{dt} = r\nu\left(1 - \frac{A\nu}{K}\right)\left(\frac{\nu}{T} - 1\right) \tag{3.2}$$

with $A = \frac{1}{S}\left(1 + (S-1)\alpha\right)$

In the presence of press, the dynamics becomes :

$$f(\nu) = \frac{d\nu}{dt} = r\nu\left(1 - \frac{A\nu}{K}\right)\left(\frac{\nu}{T} - 1\right) - m\nu \tag{3.3}$$

0 is a trivial solution of $f(\nu)$. Otherwise, equation $f(\nu = 0)$ has a single non-null solution when:

$$m = r\left(\frac{(AT + K)^2}{4ATK} - 1\right) \tag{3.4}$$

Estimation of critical press vector $\vec{m}$

Dynamics around equilibrium

We define $\Delta\vec{N}(t) = \vec{N}(t) - \vec{N}^*$, with $\vec{N}(t)$ the vector of species' biomass at time t, and $\vec{N}^*$ the vector of species biomass at equilibrium in the absence of external press.

Around equilibrium, we can approximate the dynamics by :

$$\frac{d\Delta\vec{N}(t)}{dt} = J\vec{x}(t)$$

, with J the Jacobian matrix.

In the presence of an external press $-\vec{m}N$:

$$\frac{d\Delta\vec{N}(t)}{dt} = J\vec{x}(t) - \vec{m}\vec{N}$$

When $\dfrac{d\Delta\vec{N}(\infty)}{dt} = 0$ (New equilibrium in a presence of a press $\vec{m}$, $\vec{N} = \vec{N}_{Eqm}$), then :

$$J\Delta\vec{N}(\infty) = \vec{m}\vec{N}$$

$$\Leftrightarrow J(\vec{N}_{Eqm} - \vec{N}^*) = \vec{m}\vec{N}$$

$$\Leftrightarrow \vec{N}_{Eqm} - \vec{N}^* = J^{-1}(\vec{m}\vec{N})$$

The aim is to calculate critical press value m_c leading to collapse. This corresponds to :

$$\sum_i \Delta N_i = T - \sum_j N_j^*$$

Case in which press intensities mu_i are equal for all species (uniform)

In the case where $mu_i = mu$

$$\Delta N_i = \sum_j J_{ij}^{-1} mu N_j^*$$

$$\Rightarrow \sum_i \Delta N_i = mu \sum_i \sum_j J_{ij}^{-1} N_j^*$$

$$\Rightarrow mu = \frac{T - \sum_j N_j^*}{\sum_i \sum_j J_{ij}^{-1} N_j^*}$$

Critical press $\vec{mc}$ in the general case

In this case, the components of vector $\vec{mc}$ are not necessarily equal. We determine the press vector $\vec{mc}$ with minimal norm leading to collapse.

We define $M_i = mc_i N_i^*$

$$\Delta\vec{N} = J^{-1}\vec{M}$$

$$\sum_i \sum_j J_{ij} M_j = T - \sum_j N_j^*$$

If we define $W_j = \sum_i J_i j$

$$\sum_j M_j W_j = T - \sum_j N_j^*$$

$$\Leftrightarrow \vec{M}\vec{W} = T - \sum_j N_j^*$$

The press is minimized if $\vec{M} = a\vec{W}$

$$\Leftarrow a\vec{W}\vec{W} = T - \sum_j N_j^*$$

$$\Leftarrow a = \frac{T - \sum_j N_j^*}{\vec{W}\vec{W}}$$

and $\vec{M} = a\vec{W}$

$$\Rightarrow \vec{M} = \vec{W}\frac{T - \sum_j N_j^*}{\vec{W}\vec{W}}$$

With $M_i = mc_i N_i$, we obtain :

$$mc_i = \frac{W_i}{N_i^*}\frac{T - \sum_j N_j^*}{\sum_j W_j^2}$$

which gives in vectorial form :

$$\vec{mc} = \frac{\vec{W}}{\vec{N^*}}\frac{T - \sum_j N_j^*}{\vec{W}\vec{W}}$$

The press value obtained here is an overestimation of exact critical press leading to collapse. With this estimated critical press, the scaling with parameters is preserved (α, T,etc.). the value of the prefactor λ, however, depends on the model features (see estimation of λ in the case of equal interactions in the next section).

Estimation of prefactor λ for equal competition strengh

For equal interaction strength. J is the jacobian matrix of system described by Eq (3.2)

$$J = \frac{\partial}{\partial \nu}\left[r\nu\left(1 - \frac{A\nu}{K}\right)\left(\frac{\nu}{T} - 1\right)\right]_{\nu=\nu^*} \tag{3.5}$$

$$J = r\nu^*\frac{\partial}{\partial \nu}\left[\left(1 - \frac{A\nu}{K}\right)\left(\frac{\nu}{T} - 1\right)\right]_{\nu=\nu^*} \tag{3.6}$$

We can deduce from Eq (3.2) that : $\nu^* = \dfrac{K}{A}$

$$\Rightarrow J = r\,\frac{AT - K}{AT} \tag{3.7}$$

Around equilibrium ,

$$\Delta\nu = -J^{-1}(-m\nu^*) = \frac{AT}{r(AT - K)}m\nu^* \tag{3.8}$$

$$\Rightarrow \Delta\nu = \frac{m}{r}\frac{KT}{AT - K} \tag{3.9}$$

Collapse is predicted to occur when

$$\Delta\nu = T - \nu^* = T - \frac{K}{A} = \frac{AT - K}{A} \tag{3.10}$$

With (9) and (10), we thus obtain :

$$m = r\frac{(K - AT)^2}{AKT} \tag{3.11}$$

, which represents an overestimation (prefactor $\lambda = 4$) of the analytical result (Eq 3.4).

Additional numerical analyses

Influence of biodiversity loss on uniform critical press ($\vec{mu}$)

In the main text, we show the influence of biodiversity loss on critical press $\vec{m}$, by taking the press value $\vec{mc}$ with minimal norm that result in a collapse. We here show the results when taking the uniform vector press $\vec{mu}$, with $mu_i = mu$.

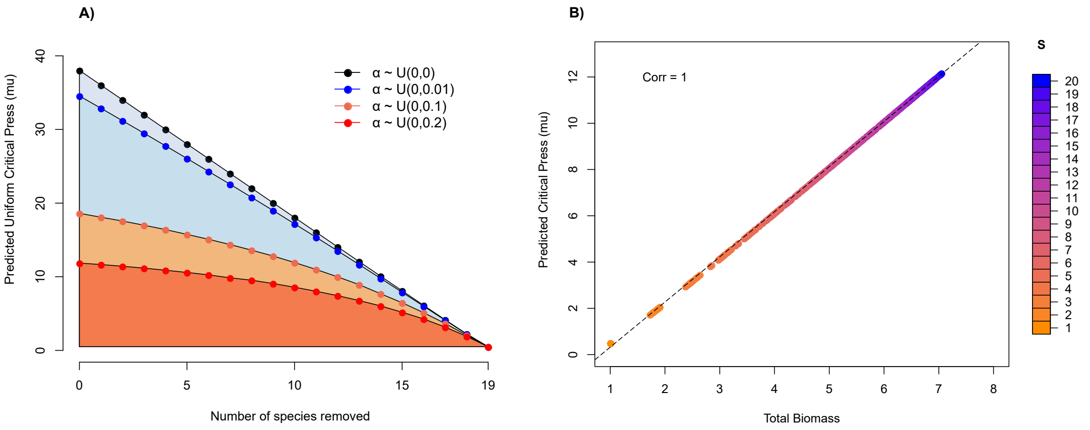

Figure A1: A) Influence of diversity loss on the predicted uniform critical press mu that results in community collapse. B) Relationship between predicted uniform critical press value (mu, y-axis) and total biomass (x-axis), for different diversity levels.

Influence of biodiversity loss on critical press for non-equal carrying capacities K_{max}

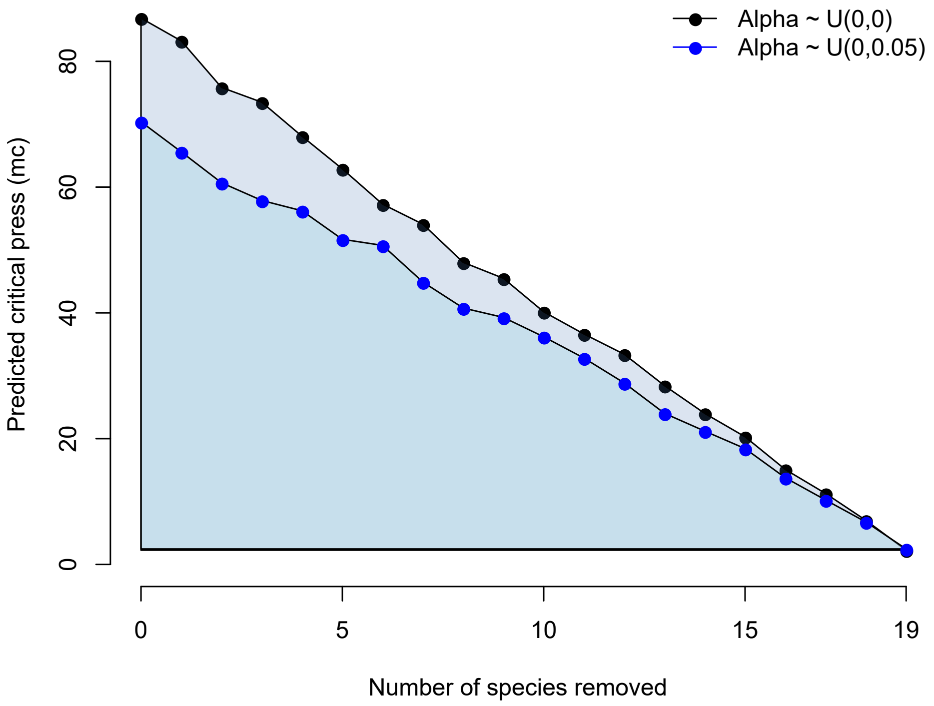

Figure A2: Influence of diversity loss on the predicted critical press mc that results in community collapse. Maximal carrying capacities K_{max} are drawn from a uniform distribution between 1 and 3. Two levels in maximal competitive interactions are investigated, from no competitive interactions ($A \sim U(0,0)$), to weak interaction strength ($A \sim U(0,05)$

Conclusion and General Discussions

This thesis aimed to understand the conditions under which communities respond either gradually or abruptly to environmental changes. I will first discuss the main contributions of our work in 1) identifying the ecological processes resulting in the emergence of various spatial community patterns, and 2) in illustrating the role biodiversity can play in protecting an ecosystem against collapse when environment changes in time. I will then discuss more general questions, such as the contribution of theoretical ecology in the study of ecosystem responses to environmental changes. I will then discuss the limitations in comparing theoretical and experimental results, by taking the example of spatial patterns in plant communities. The importance of various positive feedback types on the emergence of discrete community patterns will then be outlined with examples from various ecosystem types. Lastly, I will discuss the potential implications of our findings to understand and predict ecosystem responses to current global changes.

Main contributions

From continuum to zonation. What are the drivers of community patterns along spatial environmental gradients ?

In the two first chapters of this thesis, our objective was to determine the causes leading to different community patterns across space when environment changes gradually. We had set aside the cases in which 1) abrupt changes in environmental conditions, 2) presence of physiological thresholds or 3) human activities could have influenced species' distributions.

In the first chapter, we concentrated on the role competition and dispersal can play on the emergence of various community patterns. Competition has been shown to influence species distribution (MacArthur, 1972; Robertson, 1996; Choler et al., 2001; Terborgh and Weske, 1975), but the conditions under which various spatial patterns can emerge had not been investigated in detail. Notably, a long-standing debate opposed supporters of individualistic (Gleason, 1926; Wilson and Sober, 1989) and organismic (Clements, 1916; Wilson and Sober, 1989) views of nature, which predict gradual or rather discontinuous changes in spatial community patterns, respectively. In this study, we showed that the strength and variance of competition deeply influence spatial community patterns. In the case of weak and uniform interactions, we showed that changes in species' abundances and community composition are gradual. In contrast, when the community includes both strong and weak competitors, discrete communities emerge in space, separated by sharp boundaries where a high species turnover is observed. We showed that these abrupt changes are caused by the presence of alternative stable states in the system. This multistability results from the emergence of positive indirect interactions among species, that are otherwise in direct competition. Furthermore, we showed that a large range of intermediate patterns can emerge, in the case of intermediate conditions in competition. Thus, we stressed that competition theory can encompass the individualistic and organismic views of nature and place them in a broader context, where they appear as two limiting cases along a continuum of community patterns. We also showed that dispersal tends to homogenize species composition and smooth out the patterns that result from competition. This study is the first to identify the theoretical conditions in competition and dispersal that result in different community patterns along an environmental gradient.

In the second chapter, we focused more precisely on rapid spatial changes in community composition, *i.e* ecotones. We investigated how the diversity of ecosystem engineers -*i.e* species that modify their abiotic environment - can influence the emergence of ecotones. We showed that the contribution of biodiversity to ecotone emergence is different depending on the intensity of ecosystem engineering. In the case where species are weak ecosystem engineers, the main contribution of biodiversity to community organisation is through species richness. In this case, a single engineer is not able to modify its environment, and create a discontinuity. When many weak engineers are present, however, they are able to collectively modify the environment to their collective benefit, creating a discontinuity in the environment and in community composition. In contrast, when engineers are strong, the contribution of diversity will be through differences in species' environmental optima. These differences will influence the number of ecotones and their location along the gradient. In the cases of ecosystem engineering, the abrupt changes in community composition also result from the presence of alternative stable states in the system.

These two studies highlight the role of interactions among species, and between species and their environment in the emergence of various spatial community patterns. We show that the emergence of discrete patterns is associated with the existence of positive feedback loops, whether they result from indirect interactions within the community, or from species-environment feedbacks. These positive feedback loops can generate alternative stable state that result in abrupt changes in community composition.

How can biodiversity protect ecosystems against a collapse ?

In this study, we illustrated three ways in which biodiversity can protect an ecosystem against collapse. First, we showed in chapter two that many weak ecosystem engineers are able to collectively modify their abiotic environment. This collective environmental modification results in the emergence of alternative stable states, that can generate abrupt changes in community composition in space, but also in time. In the case of a decrease of ecosystem engineer richness, species-environment feedbacks may no longer be maintained. The system could thus shift to another state, with different environmental conditions and community composition.

In Chapter 3, we illustrated how biodiversity can protect an ecosystem against collapse, through its effect on community biomass. In our model, an increase in species richness leads to an increase in total productivity through a complementarity effect, which is consistent with theoretical predictions and field experimental results (Tilman, 2001; Loreau and Hector, 2001; Hooper et al.). In the case of an environmental press exerted on the ecosystem, we showed that this increase in total community biomass leads to an increase in the critical press value leading to ecosystem collapse. A high species diversity thus increases ecosystem resistance to a press. A consequence is that, for a given press value, a loss in species diversity leads to a decrease in ecosystem resistance. In the case where the system shows multistability, a loss in species richness can generate an abrupt shift from a state to another one. In the presence of stochastic environmental fluctuations, diversity also acts on ecosystem resistance, through species' response diversity. In this case, species responding in different directions have a buffering effect on total biomass, that lead to a decrease in the system's propensity to shift from a state to another one (by crossing a threshold in biomass). This buffering effect of response diversity has been empirically and theoretically studied and is known as the ”insurance effect” (Yachi and Loreau, 1999). In this study, we showed that the insurance effect can also protect an ecosystem against a critical transition.

Biodiversity can thus play a critical role in protecting ecosystems against collapse in stressful environments. This is notably the case in ecosystems for which strong feedback loops between species, or between the species and their environment are observed. If they are strong enough, these feedback loops can lead to multistability, which may result in the emergence of abrupt transitions when environment changes. Current biodiversity loss, in interaction with other anthropogenic perturbations, could thus deeply impact numerous ecosystem functions and lead to ecosystem collapses in the worst-case scenarios.

The contribution of theoretical ecology in the study of ecosystem responses to environmental changes

The study of ecosystem responses to environmental changes has been addressed in a large number of fields of research in ecology, from plant ecology to microbiology. Numerous ecological processes can influence the responses of ecosystems to environmental changes and are common to different ecosystem types. Competition, mutualism or niche construction can be observed in plant communities as well as in microbial or benthic marine ecosystems. Their consequence on the response of ecosystems in time or space might thus be similar. A theoretical approach can thus help to group together processes occurring in different ecosystems within the same conceptual framework. This approach contrasts with an idiosyncratic view of ecological systems. In this work, our goal was to investigate the existence of simple and general laws or principles that can influence ecosystem responses in space or time and provide general results that can be used by researchers from various disciplines.

In natural settings, a myriad of factors can influence the response of ecosystems to changes in their environment. Abiotic factors and interactions between them, the nature and intensity of interspecific interactions as well as interactions between species and their environment are likely to influence the magnitude and nature of ecosystem responses. In field and experimental studies, it can be particularly hard to identify and discriminate the different processes leading to a pattern. In contrast, a theoretical approach allows one to isolate one or a limited number of factors, and to investigate their effects on an ecological phenomenon. In the first chapter of this study, we concentrated specifically on the role of competition in the emergence of different spatial patterns. Our theoretical approach allowed us to identify under which conditions different outcomes are expected. While competition is not the only factor influencing species distributions and community patterns in nature, our study allowed us to understand and predict the specific contribution that interspecific competition can have on community patterns. Our resulting predictions are complemented with the findings of the second chapter, where we instead investigated the role that the diversity of ecosystem engineers can have on spatial community patterns.

A theoretical approach also allows exploration of situations that cannot be studied with experiments or field observations. Empirically, estimating the influence of competition or niche construction on ecosystem responses in space or time can be particularly difficult, due to several limitations. These constraints can be physical (time and space required, isolation of abiotic factors), financial, technical (how to estimate interaction strength between species?), or ecological (how to get a species pool with enough species and desired interaction features?). In our study, theory allowed us to explore a large range of conditions in the interactions between the species and their environment, and their consequences on community patterns. Some of these theoretical predictions are testable, as it could be the case for interspecific competition. Indeed, several methods were developed to measure interaction strengths (Laska and Wootton, 1998; Wootton and Emmerson, 2005), even though they are restricted to small spatial scales. In the case of ecosystem engineering, however, little work has been done to measure engineering intensity, and a theoretical approach can thus provide insights into the contribution of this ecological process to ecotone emergence, or point towards potential indirect signatures of ecosystem engineering, such as mangrove -hardwood forest ecotones.

Theory also allows one to explore conditions that are rarely, if ever, observed in nature. Thus, in chapter 1, theory allowed us to explore a large range of conditions on competition, and make predictions on the resulting community patterns. All these patterns, however, might not be observed in nature because these conditions are rarely met in natural systems.

By freeing us from purely pragmatic constraints, a theoretical approach can allow digging deep into non-obvious, indirect and unintuitive phenomena that would be hard if not impossible to tackle and understand from raw data.

Limitations in comparing theoretical and experimental results : the case of spatial vegetation patterns

One pattern, various potential causes

Since the beginning of the 20th century, a large number of studies have focused on community patterns along environmental gradients, with diverging results regarding their nature. Gradual changes in species composition and abundance (Lieberman et al., 1996; Vazquez G. and Givnish, 1998; Smale, 2008; Whittaker, 1956), as well as abrupt changes (Kitayama and Mueller-Dombois, 1992; Dech and Maun, 2005; Hemp, 2006) have been observed. The mechanisms leading to these different patterns, however, are particularly hard to identify in the field. Abrupt changes in composition along environmental gradients can result from numerous ecological processes, as well as interactions between humans and natural ecosystems. For instance, the sharp treelines that are currently observed in European mountains result from human-nature interactions in most of cases. In these ecosystems, animals grazing is encouraged at the expense of the forest (Speed et al., 2011; Treml et al., 2016). Along environmental gradients, abrupt changes in composition can also result from the occurrence of physiological thresholds, such as physiological constraints due to chemical properties of the soil in forest ecosystems (Peppler-Lisbach and Kleyer, 2009), and temperature thresholds in marine ecosystems (Schils and Wilson, 2006).

In some cases, abrupt changes in community composition are associated with rapid changes in environmental conditions (Tuomisto and Ruokolainen, 1994; Kessler, 2000). A simple hypothesis to explain these abrupt changes, then, that changes in environmental conditions are responsible for changes in species composition and abundance (McIntosh, 1967; Kent et al., 1997). Several studies, however, showed that the modification of environment by ecosystem engineers can lead to the emergence of rapid changes in species composition and in the environment (Jiang and DeAngelis, 2013; Sternberg et al., 2007; Bearup and Blasius, 2017). We showed in this theoretical work how the diversity of engineers can result in the emergence of such patterns, but also govern their magnitude and location along the gradient. It can be particularly complex, however, to differentiate cases in which environmental changes cause species turnover from cases where ecological niche construction leads to the coincidence of these boundaries, based on empirical observations. A thorough knowledge of the species' ecology and ecosystem functioning is generally necessary to identify the role that niche construction can play in the emergence of an ecotone. This is notably the case for the emergence of ecotones in tidal ecosystems (Bearup and Blasius, 2017), or in mangroves (Sternberg et al., 2007).

In the first chapter of this study, we showed that competition can result in various pattern of community organisation along spatial environmental gradients. Competition was shown to play a role in species distributions (MacArthur, 1972; Robertson, 1996; Choler et al., 2001; Terborgh and Weske, 1975). Our study, however, is the first to show that competition can lead to the emergence of abrupt changes in space, with many species affected. As mentioned above, it can be very difficult to identify the role of competition in the emergence of various patterns from field observations. This is due, in particular, to the difficulty of estimating the strength of interactions, as we discuss in the next section.

From theoretical predictions to in situ measurements

Among the various causes that influence spatial community patterns, we focused in this study on the role of interactions between species (in particular interspecific competition) and between species and their environment (ecological niche construction). Not only does the nature of these interactions (competitive, mutualistic) play an important role, we also showed that their intensity and variance do too. The estimation of the strength of biotic and abiotic interactions in complex systems, however, is quite a complex task. In the last decades, several methods were developed to assess the strength of species interactions in experiments or in nature (Laska and Wootton, 1998; Wootton and Emmerson, 2005). But these studies did not consider as many species as there are in tropical mountain forests for instance, where a lot of studies on vegetation changes were carried out. The species richness of these ecosystems, as well as the technical difficulties in applying the methods described in these studies represent a major limitation in linking theory to observations. Moreover, we assumed in the first chapter that interspecific competition between two species does not change along the environmental gradient. For various environmental conditions, the effect of a species on another species' growth rate is exerted through a change in their respective carrying capacities, but the value of the competition coefficient is assumed to remain constant. Even when interaction strength can be estimated at a given location, the potential influence of the environment on the interaction intensity makes it challenging to test empirically our theory along environmental gradients. The same conclusion can be drawn for the estimation of ecological niche construction intensity, for which very few studies have been carried out.

The multiple methods used to assess boundaries in species distribution

The study of community changes in space has interested many researchers from various areas of research in ecology. Many of these studies, however, were carried out by plant ecologists, for historical but also technical reasons. Indeed, it is relatively easy to define transects and study the presence/absence of plant species in space, as compared with marine or soil communities. Even in plant ecology, however, numerous methods have been used to assess the gradualism/abruptness of changes. The objectives of these studies also diverge among various ”schools” in the study of plant distribution. Among the methods widely used during the 20th century, we can mention phytosociological analysis, which aims at classifying vegetation types depending on the co-occurrence of species. For instance, Kitayama and Mueller-Dombois (1992) detected distinct ”vegetation types” along an altitudinal transect, using the Braun-Blanquet classification. This approach, however, is based on the assumption that plant associations can be classified and grouped into discrete units. This assumption might bias analyses, by assuming that discrete ”groups” of plant communities should be present in nature. In addition, phytosociological analyses generally do not focus on the ecological processes that lead to different community patterns. Instead, they rather concentrate on classifying them into different ”associations” (Hemp, 2006; Ewald, 2003).

In 2011, a comparison of six methods to detect altitudinal boundaries in plant composition was carried out (Bach and Robbert Gradstein, 2011), with diverging results. These methods were based on the co-occurrence of species (phytosociological analysis), statistical analyses such as ordination, cluster, parsimony analyses and structure-based classification, or the calculation of species turnover indices (Jaccard index). Not all methods detected boundaries, and their location along the gradient were different depending on the method selected. The multiplicity of methods and the diversity of estimators used to estimate the magnitude of changes in composition make the comparison between empirical and theoretical results difficult, as well as the comparison between empirical results in various ecosystem types.

Positive feedback loops and abrupt community changes in space

As mentioned above, many processes can lead to the emergence of abrupt changes in species composition in space. In this study, however, all abrupt changes observed in species composition resulted from the presence of positive feedback loops. In chapter 1, these feedbacks emerged from direct competition between species, whereas they emerged from species-environment interactions in chapter 2. Here, I review the different types of feedback loops that can lead to the emergence of discrete patterns in space.

One of the simplest cases is the presence of a single species that interacts with its environment -*i.e* ecosystem engineering - as described in the second chapter. In this case, the presence of one or several individuals at a given location can improve their environmental conditions, such as water availability and nutrient retention. In turn, this local improvement of conditions can fuel the species' growth and maintenance. In locations where the species is absent, the environment stays unfavourable and prevents its growth. This is notably observed in harsh environments such as deserts and arid ecosystems, where water and nutrient retention by plants creates discrete community patterns (Meron et al., 2004; Gilad et al., 2004; von Hardenberg et al., 2001; Kéfi et al., 2007). Similar processes can occur in the presence of several ecosystem engineers, that have a similar influence on their abiotic environment. In this study, we showed how the collective action of ecosystem engineers on their abiotic environment can promote the emergence of species-environment positive feedbacks, which result in discrete patterns of species distribution .

The modification of environmental conditions can also promote the establishment of other species, that are "nursed" by the engineer (Niering et al., 1963; Molenda et al., 2012). In this case, species turnover can be magnified by the appearance of an engineer in space and of its associated ”nursed” species (which would not be present otherwise), as we discussed in the second chapter.

More complex dynamics can also exist. Stanton et al. (2014), for instance, showed that epiphytic species can improve micro-environmental conditions for the host plant. The epiphytic species benefits from the support of a tree, and in turn improves the water-use of its host.

Feedback loops between species and their environment can also include perturbation events that create sharp boundaries in species composition. For instance, the dynamics of forest-savannah ecosystems is though to be governed by fire dynamics (Staver et al., 2011a,b). Zones with a high forest cover are little flammable, and are little impacted by fires. In contrast, savannahs are flammable, which prevents forest establishment. This leads to the emergence of abrupt transitions between zones of regularly burnt savannah and unburnt forests. Similar observations have been made in mountain ecosystems, where humid cloud forests can be sharply replaced by pine forests along an altitudinal gradient (Martin et al., 2007). In this case, pine trees promote the occurrence of fires. In turn, fires promote the maintenance of the pine forest. In contrast, fires do not enter the cloud forest because of high humidity levels.

In the first chapter of this thesis, we also showed that feedback loops can emerge when all species are in direct competition. In this case, abrupt transitions from one community to another are observed when a substantial fraction of indirect interactions are positive. This results in a high degree of integration in the community. In space, a community can thus be abruptly replaced by another one when environment changes along a gradient, creating discrete communities separated by sharp boundaries.

Implication of our findings in a context of global changes

In all the cases described above, the occurrence of positive feedback loops result in the emergence of highly non-linear dynamics, and even of alternative stable states in the most extreme cases. In the two first chapters, we showed that such highly non-linear dynamics are responsible for the emergence of abrupt changes in species composition in space. These results are also valid in the case of temporal changes in environmental conditions.

In the case of competitive communities, abrupt changes in composition in time are expected in cases where both the average intensity and variance of competitive interactions are high. In microbial communities, (Xiao et al., 2017) showed the existence of a high heterogeneity in interaction strength. These results are consistent with theoretical (Tikhonov and Monasson, 2017; Tikhonov, 2016a) and empirical results (Rillig et al., 2015), which showed that the composition of microbial communities can rapidly shift from one state to another. This might have important consequences for human well-being, as microbial communities play a major role in numerous ecosystem services such as food provisioning (Johansson et al., 2004; Alori et al., 2017). Many other ecosystem types might include communities that are prone to shift brutally from one state to another in time. The difficulty in identifying the features of their interactions networks, however, constitute a major limitation to their identification. The discrete community patterns observed in plant communities (such as savannahs, tropical mountain forests, etc.), could, however, indicate that these communities are prone to shift abruptly from one state to another if abiotic conditions change in time.

In the second chapter, we showed that changes in environmental conditions can result in abrupt shifts from one community of ecosystem engineers to another. In this case, not only species composition and ecosystem functioning, but also abiotic environmental conditions will be abruptly modified. Ecosystems such as mangroves, where trees directly modify water salinity (Sternberg et al., 2007), could thus shift to another state if perturbed. Given the fact that mangroves supply various ecosystem services (Duke et al., 2007), such abrupt shifts can have deep implications for human-well being.

We also showed that biodiversity might play a key role in protecting ecosystems against collapse. In the case were species modify their abiotic environment, biodiversity loss can break species-environment feedback loops, and result in important changes in community composition and environmental conditions. Biodiversity can also play a key role in protecting ecosystems in which the maintenance of sufficient biomass levels is critical for the maintenance of various ecosystem functions. Species richness promotes productivity, which in turn can increase the system's resistance to an environmental press. Likewise, we illustrated how response diversity increases ecosystem resistance to environmental noise. It was shown that biodiversity can play a critical role in ecosystem functioning and the provisioning of numerous ecosystem services (Isbell et al., 2011; Balvanera et al., 2006; Cardinale et al., 2012). In this work, we showed that biodiversity loss can lead to abrupt transitions, and could thus abruptly impact critical ecosystem services.

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TITLE:
COMMUNITY STABILITY AND TURNOVER IN CHANGING ENVIRONMENTS

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SUMMARY:

The question whether communities should be viewed as superorganisms or loose collections of individual species has been the subject of a long-standing debate in ecology. Each view implies different spatial and temporal community patterns. When environment gradually changes in space or in time, the organismic view predicts that species turnover is discontinuous, while the individualistic view predicts gradual changes in species composition. The main objective of this thesis is to understand the theoretical conditions under which these various types of community response can occur. First, I study the role of interspecific competition can play in the emergence of various spatial community patterns. I investigate the theoretical conditions in competition under which smooth or discrete spatial patterns can emerge. Then, I study how interactions between species and their environment can lead to various community patterns in space. I notably show how ecological niche construction can lead to the emergence of abrupt changes in species composition and in the environment, and the role biodiversity plays therein. Finally, I focus on the role biodiversity can play against ecosystem collapse. In this section, I illustrate how diversity loss, through its effects on total biomass, can lead to ecosystem collapse.

KEYWORDS:
Theoretical ecology, Modeling, Community ecology, Community patterns, Environmental gradients, Abrupt transitions

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