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

Kevin Liautaud*, Matthieu Barbier, Michel Loreau

Centre for Biodiversity Theory and Modelling, Theoretical and Experimental Ecology Station, UMR 5321, CNRS and Paul Sabatier University, 09200 Moulis, France

**Correspondence : kevin.liautaud@gmail.com, ORCID : https://orcid.org/0000-0001-6164-8415*

Abstract

Abrupt changes in species composition, also known as ecotones, have generally been interpreted as the result of abrupt changes in the environmental conditions or physiological thresholds. The possibility that ecotones might arise from ecological niche construction by ecosystem engineers has received less 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.

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

1 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), but the mechanisms responsible for these patterns in natural settings remain largely unknown. Interspecific interactions have been identified as important factors influencing species distribution and abundance along environmental gradients (Choler et al., 2001; Terborgh and Weske, 1975). Positive interactions between species, but also competition (Liautaud et al., 2019), are among potential explanations for the concurrent appearance or disappearance of a set of species, leading to discrete communities. Abrupt boundaries in species composition, also called "ecotones" (Kent et al., 1997), can coincide with abrupt boundaries 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 this case, it is generally assumed that the shift in abiotic conditions is 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.

Simultaneous abrupt shifts in both abiotic and biotic variables can arise when a species substantially modifies its environment to its own benefit, thus creating a species-environment feedback (Jones et al., 2010; Jiang and DeAngelis, 2013), a process also known as "ecological niche construction" (Kylafis and Loreau, 2008, 2011). Examples 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).

Biodiversity is the missing connection between discrete community patterns and ecological niche construction. Many studies have highlighted the role of particular species in shaping either their abiotic or biotic environment, such as ecosystem engineers (Jones et al., 1997, 1994) or nurse

species (Niering et al., 1963). But biodiversity has been shown to be a key factor influencing different aspects of ecosystem functioning, such as productivity and stability (Loreau and Hector, 2001; Hooper et al.; Yachi and Loreau, 1999; Loreau and de Mazancourt, 2013). The diversity and interactions of ecosystem engineers, which have only rarely been studied (Sternberg et al., 2007; Jiang and DeAngelis, 2013; Bearup and Blasius, 2017), might thus be an important factor influencing the emergence of ecotones.

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 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. 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 Model and methods

2.1 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 [1] . For a given location k, the population dynamics of species i is given by:

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

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:

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

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

This 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:

$$\frac{dE_k}{dt} = \mu(B_k - E_k) + \sum_i m_i \frac{N_{i,k}}{K_i^{\max}}(C_i - E_k) \tag{3}$$

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.

2.2 Potential landscape and alternative equilibria

To predict the long-term spatial patterns created by dynamics (1) and (3), 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 :

$$\frac{dE_k}{dt} = \mu(B_k - E_k) + \sum_i m_i \frac{K_i(E_k)}{K_i^{\max}}(C_i - E_k) \tag{4}$$

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

$$\frac{dE_k}{dt} = -\frac{d}{dE_k}U(E_k) \tag{5}$$

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:

$$U(E_k) = U_E(E_k) + U_{sp}(E_k) \tag{6}$$

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

$$U_E(E_k) = \frac{\mu}{2}(E_k - B_k)^2 \tag{7}$$

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

$$U_{sp}(E_k) = -\sum_i m_i T_i^2 \exp\left[-\frac{(E_k - C_i)^2}{2{T_i}^2}\right] \tag{8}$$

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

$$\gamma_i = \frac{m_i}{\mu} \tag{9}$$

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 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 mesure of the net effect of species 2 on species 1 :

$$I_{12} = \frac{N_{1b} - N_{1a}}{N_{1a}} \tag{10}$$

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.

3 Results

3.1 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 enviromnent optimum becomes the single stable equilibrium in the system.

3.2 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 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.

3.3 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.

3.4 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).

4 Discussion

Whether changes in species composition are gradual or not along environmental gradients has been the subject of a long-standing debate in ecology (Clements, 1916; Gleason, 1926).

Several studies identified the occurrence of discontinuities in species composition -i.e ecotones -, associated with discontinuities in the environment (Kitayama, 1992; Tuomisto and Ruokolainen, 1994; Kessler, 2000). In such cases, the changes in composition were generally considered as mere consequences of changes in the environment (McIntosh, 1967; Kent et al., 1997). The question of whether these associated discontinuities might be the result of ecological niche construction (Kylafis and Loreau, 2008, 2011) has rarely been investigated. Ecological niche construction has been documented in a wide range of ecosystems (De longe et al., 2008; van Breemen, 1995; Stanton et al., 2014). Several studies showed that ecological niche construction - i.e species-environment

feedbacks - can lead to the emergence of ecotones along spatial environmental gradients (Gilad et al., 2004; Meron et al., 2004; Bearup and Blasius, 2017; Jiang and DeAngelis, 2013)

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. These results

are in contrast with 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, a community behaves in some ways similarly to a species and could be compared to a superorganism (Clements, 1916). 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 leads to an increase in total biomass, in agreement with theory and empirical results (Loreau and Hector, 2001; Tilman, 2001). 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. 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. 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.

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.

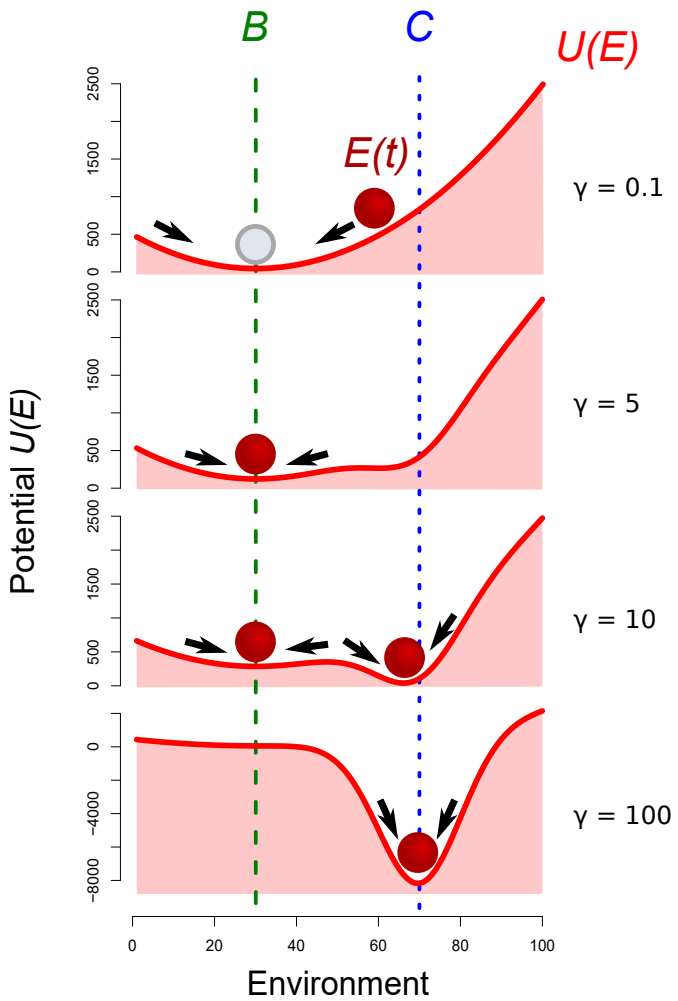

Figure 1: Representation of the environment as a potential under the action of physical processes and an ecosystem engineer. The ball representing the environmental state $E(t)$ follows the arrows down the slope until it reaches an equilibrium value, corresponding to a minimum of the potential function $U(E)$ (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 ($\gamma = 100$).

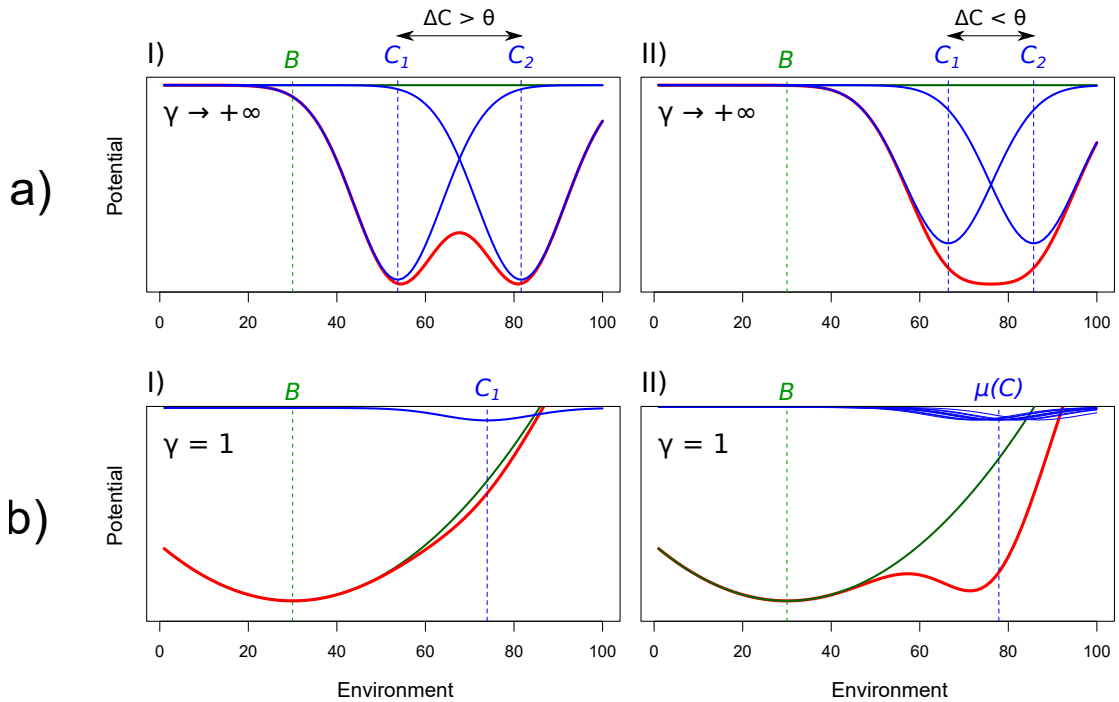

Figure 2: Influence of the similarity in species' environmental optima (ΔC) and diversity (S) on the potential landscape. Blue and green curves show the contributions of species ($U_{sp}(E)$) and environment ($U_E(E)$), respectively, to the potential $U(E)$ (red curve). a) : Influence of strong ecosystem 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 ($\gamma = 1$).

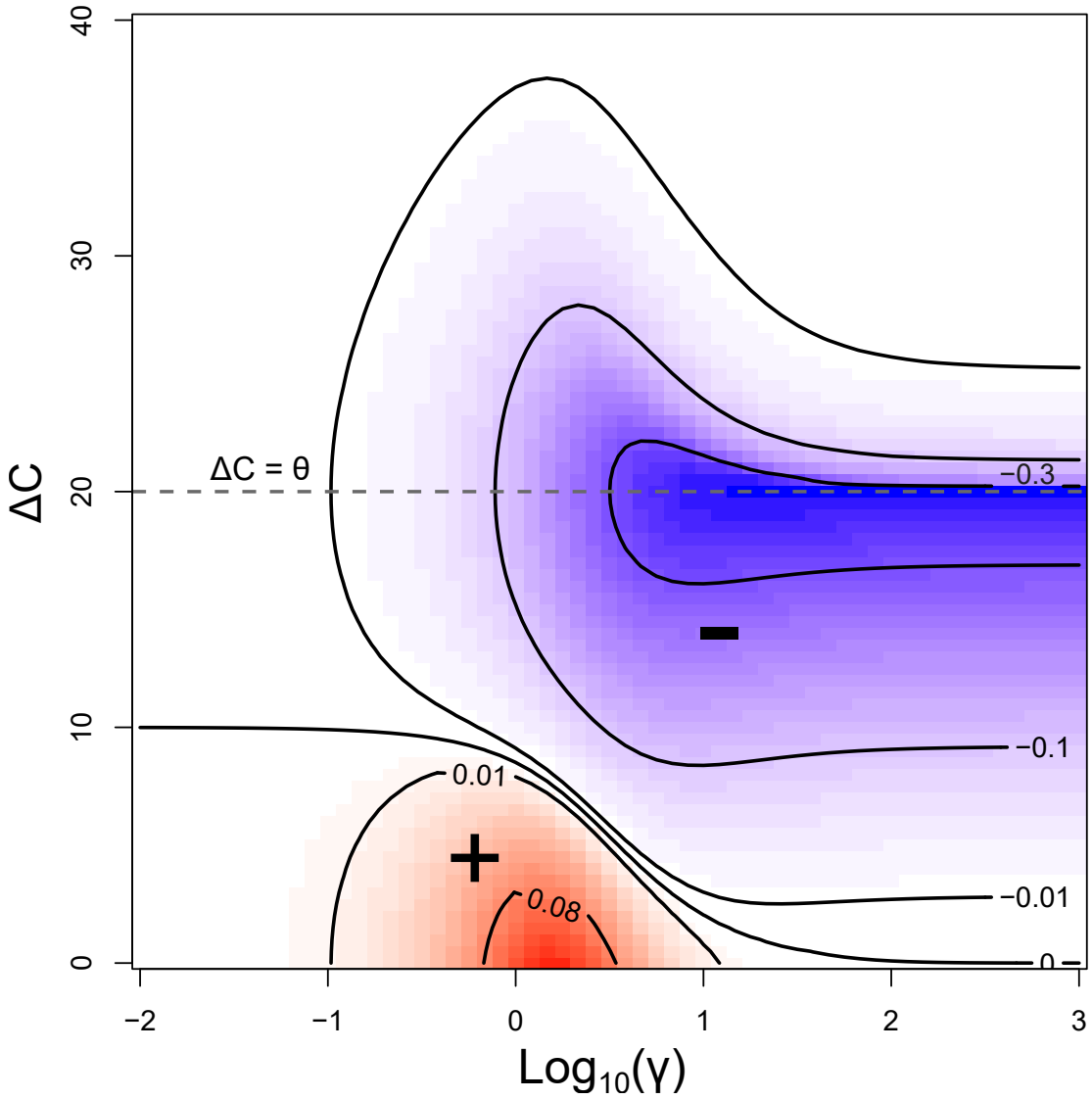

Figure 3: Emerging net species interactions as a function of the similarity of species' environment optima (ΔC), and niche construction strength (γ). Parameter values for which net competitive interactions (-) are observed are depicted in blue, whereas net mutualistic interactions (+) are depicted in 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). the 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 ($C_1 = 40$, $C_2 = C_1 + \Delta C$, $E_{t=0} = B = 50$).

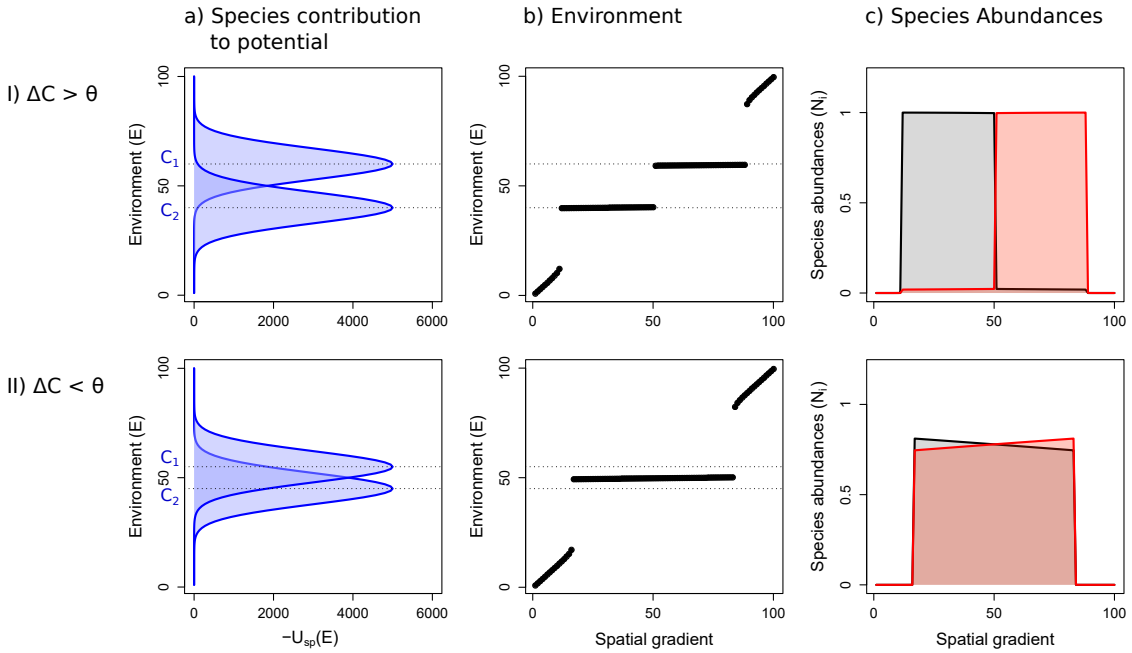

Figure 4: Influence of the similarity in ecosystem engineers on species distributions and the environment along a spatial gradient. We show results for : I) a difference in species' environmental optima ΔC larger than the threshold θ, II) a difference in species' environmental optima ΔC smaller than 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 ($\gamma = 10$).

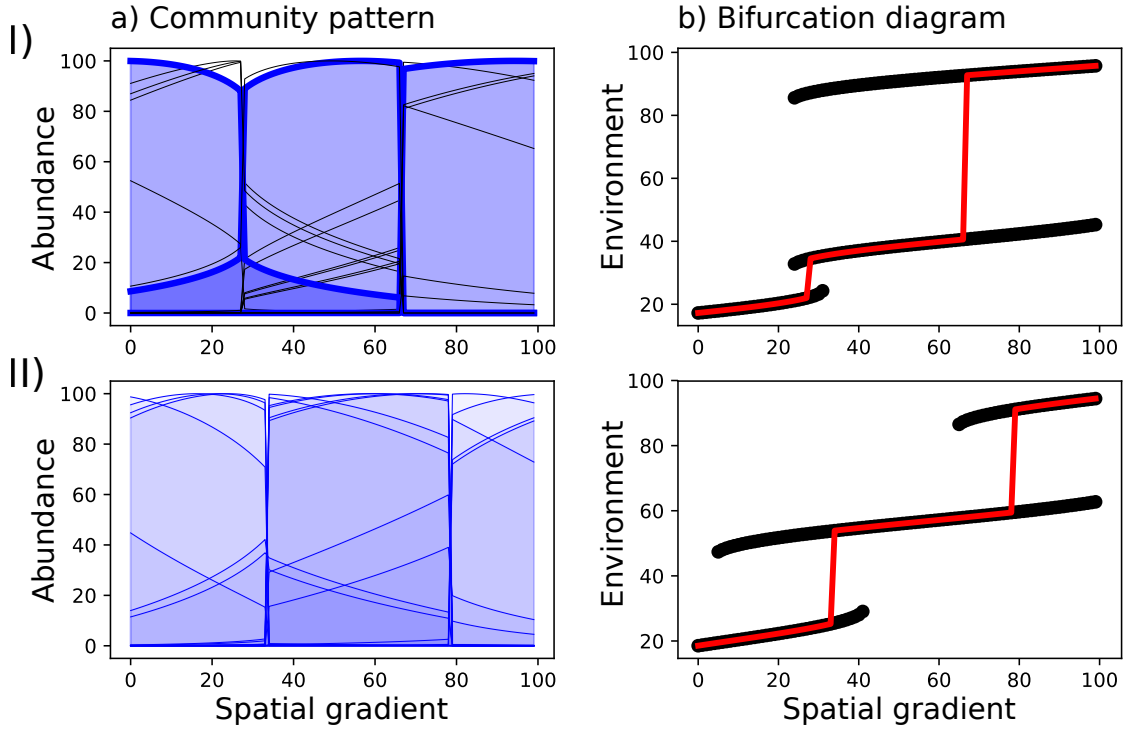

Figure 5: Species abundances along a spatial gradient (a) and bifurcation diagrams (b) in the case where: I) both strong ecosystem engineers ($\gamma = 10$, bold blue curves) and non-engineers ($\gamma = 0$, black curves) are present, II) numerous weak ecosystem engineers ($\gamma = 2$, blue curves) 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.

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References

Abrams, P. (1983). The Theory of Limiting Similarity. *Annual Review of Ecology and Systematics*, 14(1):359–376.

Armas, C. and Pugnaire, F. I. (2005). Plant interactions govern population dynamics in a semi-arid plant community. pages 978–989.

Bearup, D. and Blasius, B. (2017). Ecotone formation induced by the effects of tidal flooding: A conceptual model of the mud flat-coastal wetland ecosystem. *Ecological Complexity*, 32:217–227.

Braun-Blanquet, J. (1928). L'origine et le developpement des flores dans le massif central de France avec apergu sur les migrations des flores dans l'Europe sud-occidentale. Cont. and to be cont. *Ann Soc Linneenne Lyon*, (74):80–97.

Callaway, R. M., Brooker, R. W., Choler, P., Kikvidze, Z., Lortie, C. J., Michalet, R., Paolini, L., Pugnaire, F. I., Newingham, B., Aschehoug, E. T., Armas, C., Kikodze, D., and Cook, B. J. (2002). Positive interactions among alpine plants increase with stress. *Nature*, 417(6891):844–8.

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., Garcia, A., Pringle, R. M., and Palmer, T. M. (2015). Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Science Advances*, 1(5):e1400253–e1400253.

Choler, P., Michalet, R., and Callaway, R. M. (2001). Facilitation and Competition on Gradients in Alpine Plant Communities. *Ecology*, 82(12):3295–3308.

Clements, F. E. (1916). *Plant succession; an analysis of the development of vegetation,*, volume 45. Carnegie Institution of Washington,, Washington,.

De longe, M., D'odorico, P., and Lawrence, D. (2008). Feedbacks between phosphorus deposition and canopy cover: The emergence of multiple stable states in tropical dry forests. *Global Change Biology*, 14(1):154–160.

Dekker, S. C., Rietkerk, M., and Bierkens, M. F. (2007). Coupling microscale vegetation-soil water and macroscale vegetation-precipitation feedbacks in semiarid ecosystems. *Global Change Biology*, 13(3):671–678.

Ellison, A. M., Mukherjee, B. B., and Karim, A. (2010). Testing Patterns of Zonation in Mangroves : Scale Dependence and Environmental Correlates in the Sundarbans of Bangladesh Published by : British Ecological Society Stable URL : http://www.jstor.org/stable/2648341. *Society*, 88(5):813–824.

Gilad, E., Von Hardenberg, J., Provenzale, A., Shachak, M., and Meron, E. (2004). Ecosystem engineers: From pattern formation to habitat creation. *Physical Review Letters*, 93(9):1–4.

Gleason, H. A. (1926). The Individualistic Concept of the Plant Association. *Bulletin of the Torrey Botanical Club*, 53(1):7.

Gonzalez, A., Lambert, A., and Ricciardi, A. (2008). When does ecosystem engineering cause invasion and species replacement? *Oikos*, 117(8):1247–1257.

Hedberg, O. (1955). Altitudinal zonation of the vegetation on the east african mountains. In *Proceedings of the Linnean Society of London*, volume 165, pages 134–136. Wiley Online Library.

Hemp, A. (2006). Continuum or zonation? Altitudinal gradients in the forest vegetation of Mt. Kilimanjaro. *Plant Ecology*, 184(1):27–42.

Holling, C. S. (1973). Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, 4(1):1–23.

Hooper, D. U., Chapin III, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A. J., Vandermeer, J., and Wardle, D. A. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, 75(1):3–35.

Jiang, J. and DeAngelis, D. L. (2013). Strong species-Environment feedback shapes plant community assembly along environmental gradients. *Ecology and Evolution*, 3(12):4119–4128.

Jones, C. G., Gutiérrez, J. L., Byers, J. E., Crooks, J. A., Lambrinos, J. G., and Talley, T. S. (2010). A framework for understanding physical ecosystem engineering by organisms. *Oikos*, 119(12):1862–1869.

Jones, C. G., Lawron, J. H., and Shachak, M. (1997). Positive and negative effects of organisms as physical ecosystem engineers. *Ecology*, 78(7):1946–1957.

Jones, C. G., Lawton, J. H., and Shachak, M. (1994). Organisms as ecosystem Organisms engineers. *Oikos*, 69(3):373–386.

Kéfi, S., Rietkerk, M., van Baalen, M., and Loreau, M. (2007). Local facilitation, bistability and transitions in arid ecosystems. *Theoretical Population Biology*, 71(3):367–379.

Kent, M., Gill, W. J., Weaver, R. E., and Armitage, R. P. (1997). Landscape and plant community boundaries in biogeography. *Progress in Physical Geography*, 21(3):315–353.

Kessler, M. (2000). Altitudinal zonation of Andean cryptogam communities. *Journal of Biogeography*, 27(2):275–282.

Kitayama, K. (1992). An altitudinal transect study of the vegetation on Mount Kinabalu, Borneo. *Vegetatio*, 102(2):149–171.

Kitayama, K. and Mueller-Dombois, D. (1992). Vegetation of the wet windward slope of Haleakala, Maui, Hawaii. *Pacific Science*, 46(2):197–220.

Kylafis, G. and Loreau, M. (2008). Ecological and evolutionary consequences of niche construction for its agent. *Ecology Letters*, 11(10):1072–1081.

Kylafis, G. and Loreau, M. (2011). Niche construction in the light of niche theory. *Ecology Letters*, 14(2):82–90.

Levin, S. A. (1970). Community Equilibria and Stability, and an Extension of the Competitive Exclusion Principle. *The American Naturalist*, 104(939):413–423.

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. *Ecology Letters*, 0(0).

Lieberman, D., Lieberman, M., Peralta, R., and Hartshorn, G. S. (1996). Tropical Forest Structure and Composition on a Large-Scale Altitudinal Gradient in Costa Rica. *The Journal of Ecology*, 84(2):137–152.

Loreau, M. and de Mazancourt, C. (2013). Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. *Ecology Letters*, 16(SUPPL.1):106–115.

Loreau, M. and Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, 412(6842):72–76.

Mac Arthur, R. (1969). Species packing, and what competition minimizes. *Proceedings of the National Academy of Sciences*, 64(4):1369–1371.

MacArthur, R. and Levins, R. (1967). The Limiting Similarity, Convergence, and Divergence of Coexisting Species. *The American Naturalisthe American Naturalist*, 101(921):377–385.

MacArthur, R. H. (1972). *Geographical ecology : patterns in the distribution of species*. Princeton University Press, Princeton.

McIntosh, R. P. (1967). The continuum concept of vegetation. *The Botanical Review*, 33(2):130–187.

Meron, E., Gilad, E., Von Hardenberg, J., Shachak, M., and Zarmi, Y. (2004). Vegetation patterns along a rainfall gradient. *Chaos, Solitons and Fractals*, 19(2):367–376.

Niering, W. A., Whittaker, R. H., and Lowe, C. H. (1963). The Saguaro: A Population in Relation to Environment. *Science (New York, N.Y.)*, 142(3588):15–23.

Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N., Raven, P. H., Roberts, C. M., and Sexton, J. O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, 344(6187).

Ray, S. and Ren, D. (2012). On the upper bound of the number of modes of a multivariate normal mixture. *Journal of Multivariate Analysis*, 108:41–52.

Robertson, C. and Fryer, J. (1969). Some descriptive properties of normal mixtures. *Scandinavian Actuarial Journal*, 1969(3-4):137–146.

Soliveres, S. and Maestre, F. T. (2014). Plant-plant interactions, environmental gradients and plant diversity: A global synthesis of community-level studies. *Perspectives in Plant Ecology, Evolution and Systematics*, 16(4):154–163.

Stanton, D. E., Huallpa Chávez, J., Villegas, L., Villasante, F., Armesto, J., Hedin, L. O., and Horn, H. (2014). Epiphytes improve host plant water use by microenvironment modification. *Functional Ecology*, 28(5):1274–1283.

Sternberg, L. D. S. L., Teh, S. Y., Ewe, S. M., Miralles-Wilhelm, F., and DeAngelis, D. L. (2007). Competition between hardwood hammocks and mangroves. *Ecosystems*, 10(4):648–660.

Terborgh, J. and Weske, J. S. (1975). The Role of Competition in the Distribution of Andean Birds. *Ecology*, 56(3):562–576.

Tikhonov, M. (2016). Community-level cohesion without cooperation. *Elife*, 5:e15747.

Tilman, D. (2001). Diversity and Productivity in a Long-Term Grassland Experiment. *Science*, 294(5543):843–845.

Tuomisto, H. and Ruokolainen, K. (1994). Distribution of Pteridophyta and Melastomataceae along an edaphic gradient in an Amazonian rain forest. *Journal of Vegetation Science*, 5(1):25–34.

van Breemen, N. (1995). How Sphagnum bogs down other plants. *Trends in Ecology & Evolution*, 10(7):270–275.

Vazquez G., J. A. and Givnish, T. J. (1998). Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantlan. *Journal of Ecology*, 86(6):999–1020.

Vega-Álvarez, J., García-Rodríguez, J. A., and Cayuela, L. (2018). Facilitation beyond species richness. *Journal of Ecology*, (August):1–13.

von Hardenberg, J., Meron, E., Shachak, M., and Zarmi, Y. (2001). Diversity of vegetation patterns and desertification. *Physical Review Letters*, 87(19):198101–1–198101–4.

Wallace, B. (2013). *On the critical points of Gaussian mixtures*. PhD thesis.

Whittaker, R. H. (1956). Vegetation of the Great Smoky Mountains. *Ecological Monographs*, 26(1):1–80.

Wilson, J. B. and Agnew, A. D. Q. (1992). Positive-feedback Switches in Plant Communities.

Yachi, S. and Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proceedings of the National Academy of Sciences*, 96(4):1463–1468.