



LETTER

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

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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 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.

Keywords

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

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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 & 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 (structuring 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 organisation predicts the gradual replacement of species by new species as the environment changes (Gleason 1926). In contrast, an organismic community organisation 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 & Givnish (1998) failed to find discrete plant communities along altitudinal

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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 1992; Dech & 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 & Wilson 2006; Pepller-Lisbach & 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 organisation.

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 & 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 & 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.* 2007, 2016).

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 & Weske 1975; Case & 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 & 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 2017). 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.

MODEL AND METHODS

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:

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

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 characterised 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:

$$K_{i,k} = O_i e^{-\frac{1}{2} \left(\frac{p_k - C_i}{T_i} \right)^2}. \quad (2)$$

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).

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:

$$\frac{dN_{i,k}}{dt} = rN_{i,k} \left(1 - \frac{\sum_j \alpha_{ij} N_{j,k}}{K_{i,k}} \right) + d \left(\sum_{s \neq k} (N_{i,s} - N_{i,k}) e^{-\frac{(s-k)^2}{2\sigma_d^2}} \right). \quad (3)$$

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

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's (1912) distance J_δ 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 & 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} .

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 characterises 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_k of abundances at site k for a given equilibrium. Since two distinct vectors are highly unlikely to have the same projection along a random direction (Candes & Tao 2006), we defined CSI_k as the scalar product of B_k 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:

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

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.

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 2017). 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 $t = 20\,000$, 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 nine simulations. For each of the nine 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.

RESULTS

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. 1b, 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. 1c, II & III).

In contrast, if competition between species is uniformly weak, gradual changes in species abundances and composition along the gradient are observed (Fig. 1b, I). In this case, the Gini coefficient is low, meaning that changes in species abundances are equally distributed along the gradient (Fig. 1a, I). Jaccard's distance shows a unimodal distribution of turnover, with the predominance of zero or very low

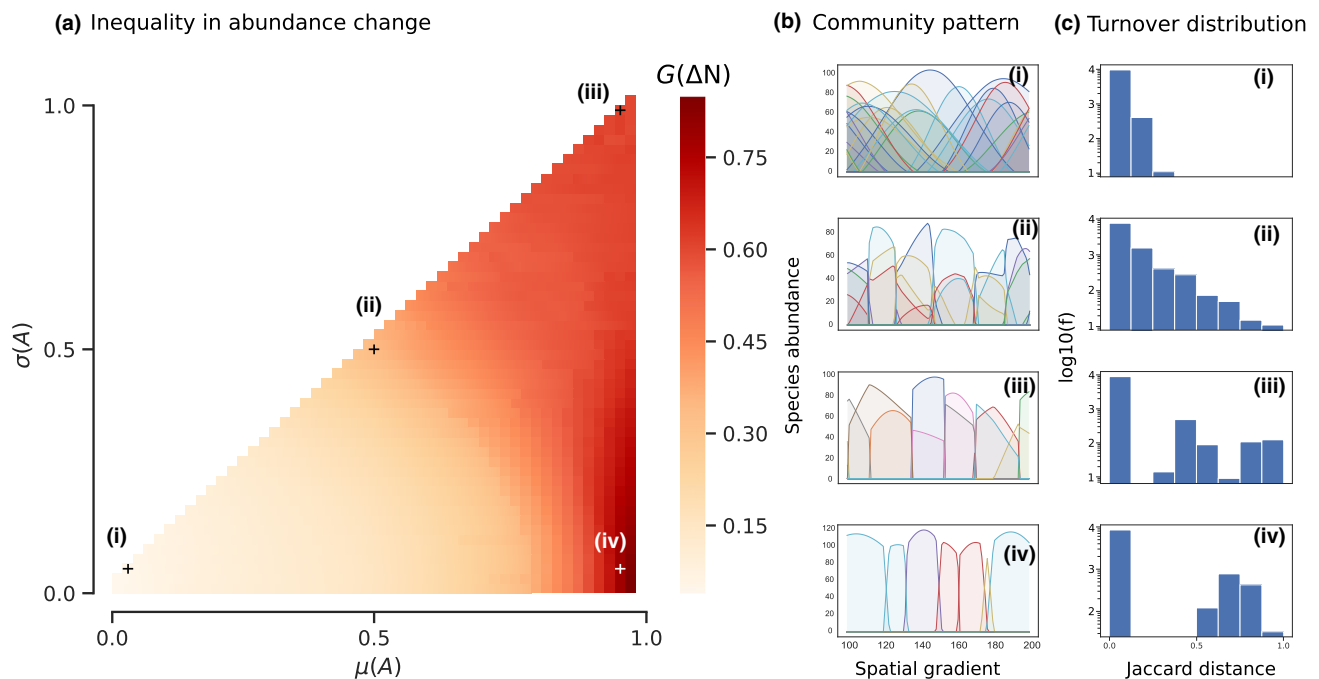


Figure 1 Effects of competition on spatial community patterns. (a) Effects of the mean, $\mu(A)$, and standard deviation, $\sigma(A)$, of competition strength on the inequality of abundance change along the gradient, $G(\Delta N)$. (b) Spatial community patterns associated with cases I, II, III and IV 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.

species turnover values, and no high species turnover values (Fig. 1c, I).

In the special case of very high mean competition 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. 1b, 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. 1a, IV), and the histogram of Jaccard's distances shows the predominance of zero turnover zones, with several medium to high turnover zones (Fig. 1c, 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. 1b, I) show gradual changes in the Community State Index (CSI) along the environmental gradient (Fig. 2a, I). Whatever the initial conditions, only one equilibrium can be reached by the local community. In contrast, bifurcation diagrams of systems with stronger competition

(Fig. 1b, II & III) show abrupt shifts in both community composition and CSI (Fig. 2a, 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. 2a, II & III). Multistability is predicted to occur only when some coefficients α_{ij} are above 1 (Bunin 2018), which is consistent with observations (Fig. 2b). In these cases, initial conditions do matter, and can lead to different communities at equilibrium. In the case of discrete single-species communities (Fig. 1b, IV), bifurcation diagrams show abrupt changes in CSI, but no alternative stable states (Fig. 2a, IV).

When both the mean and variance of competition strength are intermediate, we observe high values of the Positive Feedback Index (Fig. 3a). 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.

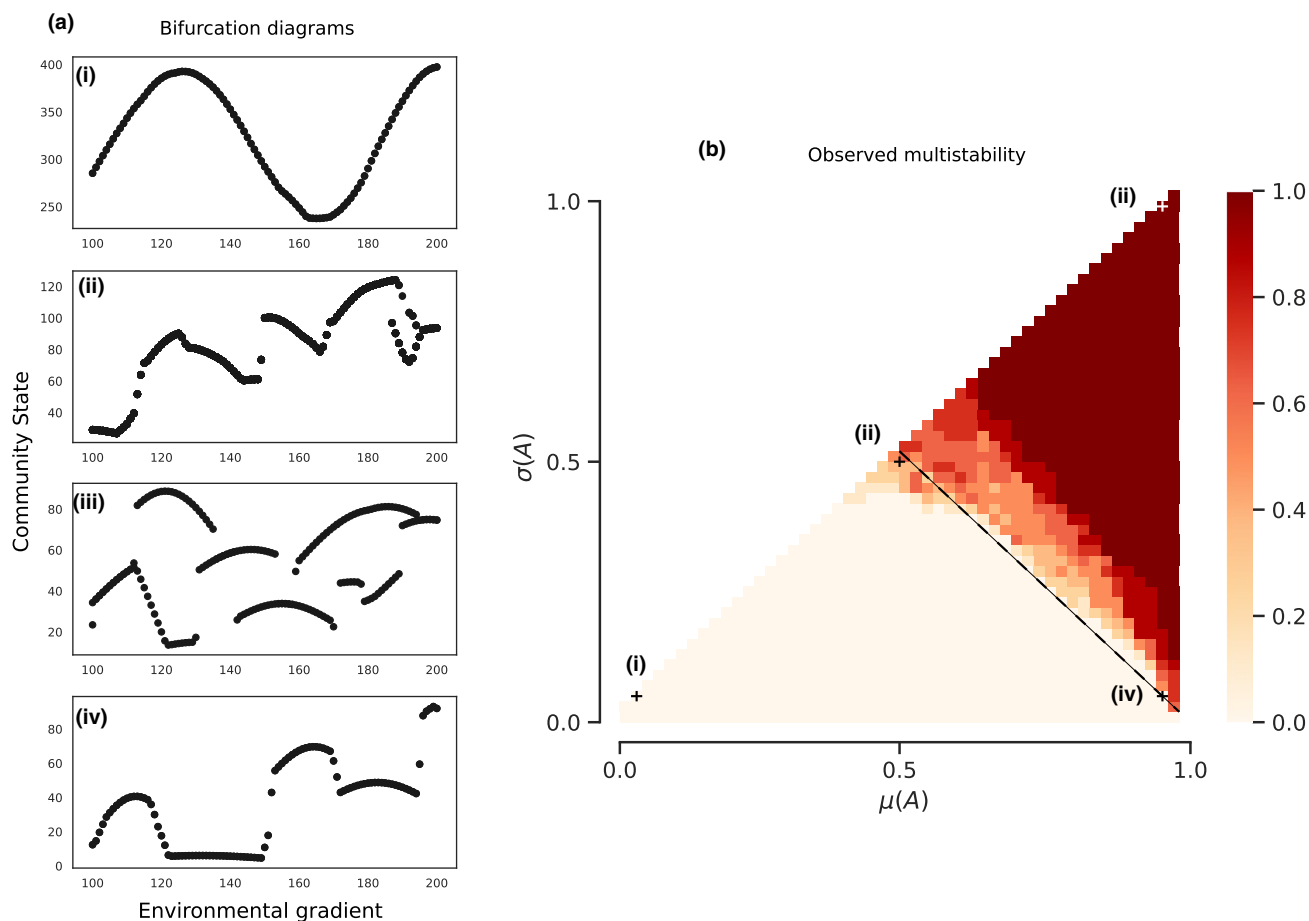


Figure 2 (a) Bifurcation diagrams obtained by the superimposition of the various community state indices (CSI) obtained from 100 simulations with different initial conditions. Each point on the bifurcation diagram represents a stable equilibrium. (b) Observed Multistability Index. This index represents the fraction of nine simulation runs for which multistability is observed. Theoretically, multistability is predicted to occur above the dashed line (Bunin 2018).

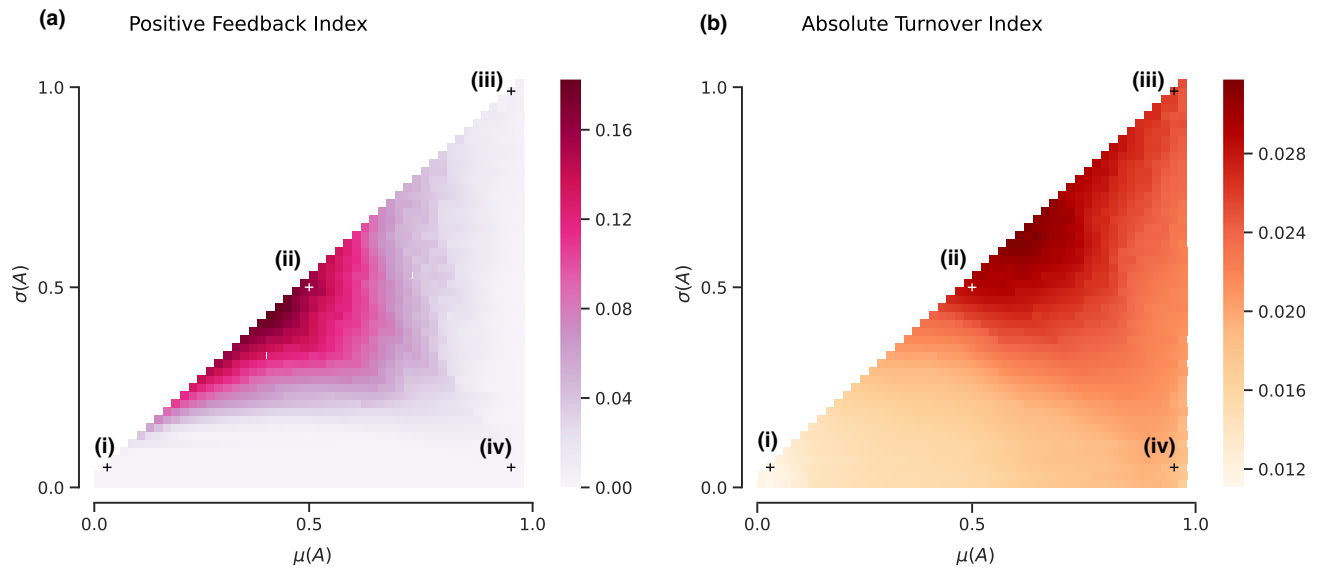


Figure 3 (a) Positive Feedback Index, which measures the fraction of indirect interactions that are positive. (b) Absolute Turnover Index, which combines two effects: (1) how many species appear or disappear in compositional shifts, and (2) how unequally these shifts are distributed along the gradient. For both indices, results are averaged over 9 simulations.

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. 1b, III). Increases in both the dispersal rate d and kernel size σ_d tend to reduce the inequality in abundance changes along the environmental gradient (Fig. 4a). Thus, there are discrete communities along the gradient when both the dispersal distance and dispersal rate are low (Fig. 4b, 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. 4b, γ).

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 & Hastings 2014) or ecological niche construction (Bearup & 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

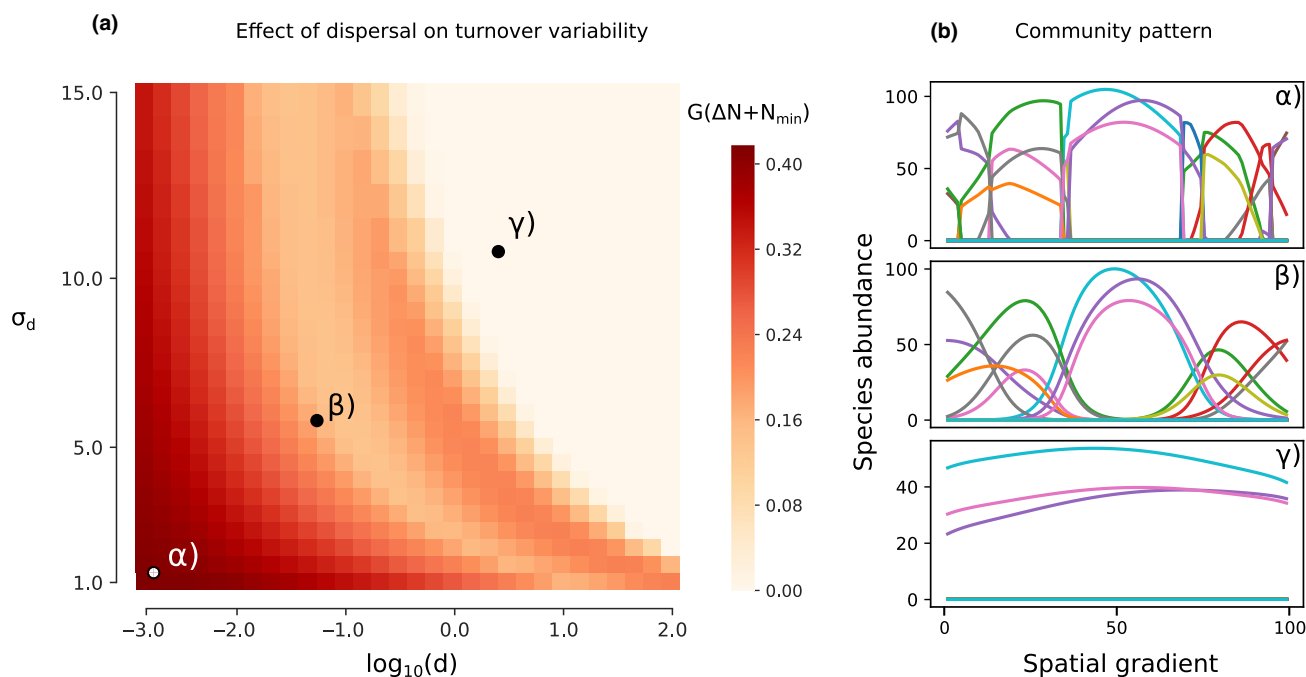


Figure 4 Effects of dispersal on spatial community patterns. (a) Effects of dispersal rate (d) and kernel size (σ_d) on inequality in abundance changes $G(\Delta N)$ along the gradient. (b) Spatial community patterns associated with cases 1, 2, and 3 in (a). At high dispersal, changes in species abundances 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 $N_{min} = 1$.

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 & Case (1976) and van Nes & 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 & 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 homogenise species composition. This recovers results from metacommunity theory showing that dispersal

decreases beta-diversity among communities (Mouquet & Loreau 2003; Leibold *et al.* 2004), a theoretical prediction that is supported by empirical studies (Forbes & Chase 2002; Kneitel & Miller 2003; Simonis & 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 & Givnish 1998) or in marine benthic organisms along depth gradients (Smale 2008), might thus reflect either a truly individualistic organisation 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 organisations.

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 (Vitousek 1997; Hoegh-Guldberg *et al.* 2007; 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 & 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 & Thuiller 2005; Araújo & 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 organisation should prevail and be taken into account to predict the responses of species and communities to environmental changes.

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AUTHORSHIP

EvN, MS and ML designed the study and the model, KL and MB performed the simulations and analysed the model, KL wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

DATA ACCESSIBILITY STATEMENT

Data available from the Repository: <https://doi.org/10.5281/zenodo.2710078>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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