

**The effects of the spatial structure of the environment on species coexistence and related consequences to local and regional community structure**

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## **ABSTRACT**

**Title:** Local and regional coexistence can be mediated by the spatial structure of the environment

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Spatial environmental heterogeneity is widely accepted and cited as a mechanism underlying the structure of ecological communities. Most empirical evidence related to the effects of environmental heterogeneity comes from assessing how local environments vary in relation to one another and how this variation affects community (and metacommunity) structure. However, similar levels of environmental variation are often structured differently in space, likely affecting species distributions and the ways in which they coexist. Yet, the spatial structure of environmental variation received very little attention. In this study, we set out for the first time a model to understand the effects of the spatial structure of the environment on metacommunity dynamics and its effects on species co-existence at local and regional levels. We built a metacommunity model in a spatially explicit landscape with spatially structured environmental conditions and a continuum of specialist to generalist species that competed for space. Dispersal mortality was set as a function of species' environmental tolerances and the environmental variation experienced during dispersal. The spatial structure of the environment was found to increase local and regional coexistence, while also selecting for more specialist species. In landscapes with strong spatial structure, patches with similar environmental values were clustered together, thus facilitating the successful colonization of suitable patches by specialist species. Conversely, weakly structured landscapes selected for generalist species. As such, increased environmental spatialization fostered niche partitioning, facilitating coexistence and, as a result, increasing local and regional diversity.

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## LIST OF SYMBOLS AND ABBREVIATIONS

Symbols & abbreviations	Definition
$a$	Autocorrelation range
$C0$	“Nugget effect”; $1 - C0$ is the autocorrelation strength
$\Sigma$	Covariance matrix of environmental values
$\sigma_{ij}$	Elements of the matrix $\Sigma$
$d_{ij}$	Euclidean distance between patches $i$ and $j$
$\bar{E}_i$	Average environmental value within patch $i$
$\mu_j$	Niche optima of specie $j$
$s_j$	Niche breadth of specie $j$
$K$	Carrying capacity
$r_{max}$	Maximum reproductive rate
$\delta$	Dispersal rate
$\delta_s$	Dispersal success
$\delta_s^m$	Dispersal success of $m$ successive dispersal
$E_{ikt}$	Intrapatch environmental values for patch $i$ at generation $t$ ( $E_{ikt} \sim N(\bar{E}_i, 0.01)$ )
$\omega_{ijkt}$	Competitive ability of species $j$ for $E_{ikt}$ (see eq. 4; Fig. 2)
$\tilde{\omega}_{ijkt}$	Relative competitive ability of species $j$ for $E_{ikt}$ (see eq. 5; Fig. 2)
$\tilde{\omega}_{ijt}$	Relative competitive ability of species $j$ for in patch $i$ at generation $t$ (see eq. 6; Fig. 2)
$r_{ijt}$	Expected reproductive rate of species $j$ for in patch $i$ at generation $t$
$N_{ijt}$	Population abundance of species $j$ for in patch $i$ at generation $t$
$\bar{s}$	Average niche breadth of the metacommunity (see eq. 9)
$SSI$	Spatial Structure Index (see eq. 10)
$\tau$	Disturbance rate
$\theta$	Strength of dispersal mortality (Not used but see model assumption in Appendix IV)

## INTRODUCTION

Spatial environmental heterogeneity (resource or non-resource) is widely accepted and cited as a mechanism underlying the structure of ecological communities (Chesson 2000, 2018). Because species vary in their responses to and abilities to handle spatial variation in their environments, heterogeneity is a central mechanism of species coexistence. Most empirical evidence related to the effects of environmental heterogeneity comes from assessing how local environments vary in relation to one another and how this variation affects community structure (e.g., direct gradient analysis, beta-diversity studies, environmental filtering; Whittaker 1967, Condit et al. 2002, Lebrija-Trejos et al. 2010, Laliberté et al. 2014). However, similar levels of environmental variation are often structured differently in space (where variation occurs) and time (when variation occurs), likely affecting species distributions and the ways they coexist. Yet, the structure of environmental variation received very little consideration in comparison to environmental heterogeneity's magnitude.

At local and regional scales, environmental heterogeneity drives community composition. At local scales, environmental heterogeneity may stabilize local species coexistence via niche partitioning. As postulated by the theory of limiting similarity (Abrams 1983), species that are too similar to one another cannot coexist locally. It follows that species' niches must sufficiently differ (e.g., use different environments) to allow species coexistence, which is referred to as niche partitioning (MacArthur 1958). However, the relationship between heterogeneity and richness is rather unimodal than simply positive. While greater environmental heterogeneity at the local scale should harbor greater number of species given that more niches are available, it also decreases the relative availability (area for spatial or frequency for temporal) associated to different types of environment. Although a greater number of species can coexist in heterogeneous environments through mechanisms such as storage effect (spatial or temporal), consisting in the ability of storing the "gains" made in favorable environments to compensate for the "losses" in unfavorable environments (Chesson 1983), a decrease in the relative frequency of favourable environments increase local extinction risk. It follows that generalist species that do well in a broader range of environmental conditions can take advantage of these niches left unoccupied by specialists that go locally or regionally extinct. As such, increase in environmental heterogeneity should first lead to an increase in local richness by hosting additional specialists, before a decrease in diversity via allowing greater number of generalist species replacing multiple

specialists. At regional scale, environmental heterogeneity (i.e. variation in environmental features among patches) allows different local communities to assemble within a metacommunity as a result of a shift in competitive dominance driven by changes in environmental conditions (Gleason 1926, Clements 1936), a process loosely referred to as environmental filtering even though it is often mediated by competition (see Kraft et al. 2015, Cadotte and Tucker 2017).

Moreover, demographic and/or spatial processes also impact local and regional coexistence. Demographic processes such as priority effect (Connell and Slatyer 1977) can give rise to multiple alternative stable states in ecological communities (Sutherland 1974, May 1977), thus promoting regional coexistence as different combinations of species (i.e., community composition) can arise even in the absence of environmental heterogeneity. Demographic stochasticity (e.g., when, by chance, population growth is higher or lower than expected), whose effect is stronger when population sizes are small, generate path-dependant community assembly (i.e., when early stages of community assembly have great impact on the resulting community even though the circumstances during early stage are no longer relevant for the community; but see Connell and Slatyer 1977) as in neutral dynamic (Hubbell 2001) or in priority effect (Urban and De Meester 2009, De Meester et al. 2016). Additionally, spatial processes can lead to local and regional coexistence (see Amarasekare 2003) through differences in species life histories such as the competition-colonization trade-off (Levins and Culver 1971, Hastings 1980) where the better colonizer can rapidly colonize newly available patches, thus producing offspring that can disperse before the stronger competitor can successfully colonize any particular patch and outcompete the first colonizing species. In addition, dispersal between patches can promote local coexistence via source-sink dynamics, in which weaker competitors survive in an unfavourable environment (sink) as long as immigration compensates its local negative growth rate (Pulliam 1988). As such, regional coexistence driven by regional environmental heterogeneity or path-dependant community assembly can in turn promote local coexistence through source-sink dynamics, though it could also lead to species homogenization across communities if dispersal is too strong (Loreau and Mouquet 1999, Amarasekare and Nisbet 2001).

Ecologists have focussed extensively on disentangling environmental and spatial drivers of ecological communities, mostly using the variation partitioning framework (Borcard et al. 1992, Peres-Neto et al. 2006, but see Brown et al. 2017 for discussion), which allows one to estimate the relative importance of these drivers in determining variation in species composition

across communities (beta-diversity across local communities within a metacommunity). In the variation partitioning framework, fraction [a] is the variation explained by environmental predictors only, fraction [c] represents the variation explained by spatial predictors only, and fraction [b] is the variation jointly explained by space and environment (spatially structured environment; Peres-Neto et al. 2012). While ecologists have focussed on the pure environmental [a] and pure spatial [c] fractions, the spatially structured fraction of the environment [b] is rarely analyzed and interpreted, but rather considered as a confounding effect resulting from the collinearity between spatial and environmental predictors. As such, relevant (and well-cited) meta-analyses for estimating the relative importance of environmental and spatial factors driving species variation within metacommunities have otherwise overlooked the importance of spatially structured environmental variation (e.g., Cottenie 2005, Soininen 2014, 2016). However, as reported by Cottenie's (2005) meta-analysis, spatially structured environment (see Appendix I for definition) explains on average 10% of community composition, while the total explanation of all fractions [a+b+c] sits at 48%. The strong emphasis on analyzing spatial and environmental drivers independently led the spatial structure of the environment to be overlooked as a mechanism underlying species coexistence within metacommunities despite the fact that in natural systems environmental variation is spatially structured (e.g., topography or climatic variables such as temperature and precipitation; Legendre 1993).

The influence of temporal (Petchey et al. 1997, Heino 1998, Heino et al. 2000, Gonzalez and Holt 2002, Wichmann et al. 2003, Schwager et al. 2006, Long et al. 2007, Ruokolainen et al. 2007, Ruokolainen and Fowler 2008), spatial (Palmqvist and Lundberg 1998, Lande et al. 1999, Robert 2009, Massie et al. 2015), or spatiotemporal (Matthews and Gonzalez 2007, Ruokolainen et al. 2009) structure of environmental variability (i.e., where the average environmental conditions over time is constant over space, but the temporal fluctuations are spatially and/or temporally autocorrelated) on extinction risk and species coexistence have been exhaustively studied. However, only few theoretical studies have investigated how the spatial structure of environmental variation per se underlie species coexistence and patterns of species composition across local communities. For instance, based on a two-species simulation model, Snyder (2008) found that the spatial structure of the environment promotes greater levels of regional coexistence than its temporal structure. Short-distance dispersal, which foster species aggregation across local communities, has been shown relevant to regional coexistence in a spatially structured

environment based on a simple two-species system (Snyder and Chesson 2003). Moreover, the spatial structure of the environmental features was found to impact species life history traits such as dispersal ability (Büchi and Vuilleumier 2012), colonization ability, survival rate (Büchi et al. 2009), as well as levels of specialization (Büchi and Vuilleumier 2012, 2014) in a multispecies simulation model. In addition, Bar-Massada et al. (2014) found that spatialized environments reduced the importance of neutral interactions in community assembly. Büchi et al. (2009; 2012; 2014) report that the effect of the spatial structure of the environment on species coexistence was contingent on species' dispersal abilities and disturbance rate, but because their simulation protocol aimed at investigating selection of life-history and/or dispersal traits rather than coexistence per se, these studies provide very little understanding of the role of spatial structure of the environment on species coexistence and related consequences to community structure.

However, despite the fact that the results of these studies (i.e., Snyder and Chesson 2003, Snyder 2008, Büchi et al. 2009, Büchi and Vuilleumier 2012, Bar-Massada et al. 2014, Büchi and Vuilleumier 2014) were contingent on dispersal, none considered dispersal costs in their simulation models, the wide evidence of its prevalence (see Bonte et al. 2012 for a review), including its importance to species coexistence (Mouquet and Loreau 2003). In other words, past models assumed that individuals emigrating from a given patch would always immigrate in another patch, thus removing the ultimate cost of dispersal (i.e., mortality). Dispersal is indeed not a risk-free process, having strong implications to fitness (Bonte et al. 2012). In addition to the fact that dispersal requires resources and time that would be otherwise allocated to other activities, dispersal also comes with mortality risks related to predation, parasitism, and energetic costs. Indeed, extreme environmental conditions experienced during dispersal can directly lead to dispersal mortality for both active (Bonnet et al. 1999, Winne and Hopkins 2006, Keefer et al. 2008) and passive (Pechenik 1999, Hiddink et al. 2002, Hiddink and Wolff 2002, Allen and McAlister 2007) dispersers. In addition, inhospitable environments may indirectly lead to higher mortality as a consequence of increased energy expenditure (Rand and Hinch 1998, Bonnet et al. 1999, Aarestrup et al. 2005, Rand et al. 2006, Winne and Hopkins 2006) or resource limitation (McConaugha 1992, Horvath and Lamberti 1999). It follows that environmental tolerance alleviates this source of dispersal mortality, hence increasing dispersal ability across heterogeneous landscapes.

The links between specialization, dispersal ability and successful colonization is widely established (Amarasekare et al. 2004) and are likely to interact strongly with the spatial structure of environmental conditions to determine how species coexist. Indeed, while generalist species can succeed in a large range of environmental conditions, specialist species have higher fitness at their niche optima, thus outcompeting generalist species and constraining them to local communities without specialists (Egas et al. 2004). However, depending on the spatial structure of the environment, dispersal limitation of specialist species may reduce their ability to reach isolated patches due to costs associated to dispersal mortality or to maintain viable populations in sub-optimal sites via source-sink dynamic, which may in turn reduce the regional persistence of specialists given that sink populations often benefit from recolonization from source populations following a disturbance (Frouz and Kindlmann 2001). As such, accounting for species' dispersal abilities is essential to understand how the spatial structure of the environment underlies species coexistence.

Here, we investigate for the first time the effects of the spatial structure of the environment on metacommunity dynamics and its effects on species coexistence at the local and regional levels, as well as the selection of ecological specialization. This investigation was conducted using a metacommunity simulation model that considered mortality as a function of the dispersing environment. We used a multispecies model in which selection among species can occur, as our focus is not only on species coexistence, but also on how selection of specialization levels affects species coexistence. A two-species or "few-species" model is more fitted to study coexistence mechanisms, but does not necessarily allow an understanding of how the level of spatialization of the environment mediates the coexistence of specialist versus generalist species, which ultimately may result in the number of species that can coexist locally and regionally.

Considering that larger spatial range (i.e., the distance over which environmental values are more similar than expected by chance) and stronger spatial autocorrelation lead to smaller environmental differences between neighbouring sites (Appendix I), we predict that (1) larger spatial ranges and stronger spatial autocorrelation lead to higher specialization because dispersers face very little environmental heterogeneity; (2) smaller differences among patches (i.e. larger and stronger spatial autocorrelation) should promote connectivity between patches, leading to higher local coexistence (i.e., greater number of species) via source-sink dynamics. As a result, we predict that (3) stronger spatial autocorrelation should homogenise communities in their

species composition, leading to reduced beta diversity among local communities and consequently lower regional diversity.

## **METHOD**

### **General simulation framework**

We used a spatially explicit metacommunity model in a lattice landscape of  $40 \times 40$  patches structured by spatial environmental variability. Our model included a continuum of specialist to generalist species that competed for space in a locally (spatially-structured) heterogeneous environment based on the matching of their niche with local environmental conditions. Individuals dispersed among patches within the landscape and could disperse multiple steps within the same dispersal event. Individual dispersal mortality was based on the matching between the species niche (that the individual belonged to) and the local environmental conditions of the patches visited by the individual during dispersal. Spatially structured environmental variation was simulated based on a spherical variogram model. Ten types of spatially structured landscapes determined by two variogram parameters (spatial range and nugget) combined against 6 simulation scenarios as a function of dispersal and disturbance (see simulation dynamics for details) were replicated 30 times each, leading to a total of 1800 simulations ( $30 \times 6 \times 10$ ; see Table 1 for list of parameters used). The model and analyses were implemented in R version 3.5 (R Core Team 2013).

### **Landscape structure**

We simulated metacommunities consisting of 1600 local communities by considering a  $40 \times 40$  lattice with periodic boundaries (torus) across all simulations. For the sake of simplicity, we considered a single environmental variable. We investigated nine different spatial structures for the environment in which three levels of autocorrelation strength (low, medium, and high) combined with three levels of autocorrelation range (short, medium, and long) (see Fig. 1). To generate a spatialized environment, we first conditioned a spatial covariance matrix  $\Sigma$  to follow the commonly used spherical variogram model with a given range ( $\alpha = \{3, 10 \text{ or } 20\}$ ) and a given autocorrelation strength ( $C0 = \{0, 0.33 \text{ or } 0.66\}$ ; i.e., the “nugget effect”) as follows:

$$\Sigma = [\sigma_{ij}] = \begin{cases} (1 - C0) * (1 - \frac{3d_{ij}}{2a} - 0.5 \left(\frac{d_{ij}}{a}\right)^3), & \text{if } 0 < d_{ij} \leq a \\ 0, & \text{if } d_{ij} > a \\ 1, & \text{if } d_{ij} = 0 \end{cases} \quad (\text{eq. 1})$$

where  $\sigma_{ij}$  are the elements of the covariance matrix  $\Sigma$ ,  $d_{ij}$  is the Euclidean distance between patches  $i$  and  $j$ ,  $a$  is the spatial range and  $1 - C0$  is the strength of the autocorrelation.

To generate an environmental variable that is a random sample from a given spatial covariance matrix, we used a multivariate random normal generator assuming a mean of zero and the covariance matrix as  $\Sigma$  (mvrnorm function from the MASS R package). The environmental variable was standardized to mean zero and unit variance so that only the spatial structure of the environment varied across scenarios and their replicates. For each simulation replicate within and across different spatial structures (variogram models), we generated a new spatialized environmental variable. Although we considered a torus for the dispersal landscape, the environmental variable was generated in a finite landscape due to computational constraints in using a two-dimensional Gaussian random field generator (used for generating spatialized variables in a torus) for such a large lattice across 1800 landscapes. As such, the method used here to generate spatialized environments may induce slight discrepancies in the spatial structure of the environment when transported to a torus (i.e., when landscape edges are brought together to form the torus). To measure whether considering a finite landscape for the environment (i.e., an edge effect) and a torus landscape for species dispersal affected our results, we also analyzed them based on a central lattice of  $30 \times 30$  and found that results were extremely consistent with the results based on the original  $40 \times 40$  lattice. Finally, we also considered a non-spatialized environment ( $10^{\text{th}}$  spatial structure;  $C0 = 1$  and  $a = 0$ ). The environmental values at each patch will serve later on to set the average of intrapatch environmental heterogeneity (see section *Reproductive phase*).

## Species

For each simulation, a total of 250 species was considered as the metacommunity pool (i.e., species pool). Each species  $j$  was characterized by its niche optima  $\mu_j$  that determined in which environmental values (conditions) the species performed best, and a niche breadth  $s_j$ , which determined the level of specialization (here a Gaussian density function of environmental

values around the niche optima). All species reproduced asexually once before dying (semelparous), thus removing competition among generations. Niche optima and niche breadth for each species were drawn from a standard normal distribution  $N(0,1)$  and a lognormal distribution  $\ln(-2.75, 0.75^2)$ , respectively. The distribution of niche optima was designed to match the distribution of environmental values, while the lognormal distribution was used for niche breadth because it generates a greater number of specialist species relative to generalists. Given that specialists have narrower niches, many are needed to fulfill the environmental space and avoid gaps. If an equal number of specialists and generalists were created, it would either lead to high niche overlap between generalists, or large gaps between specialists' niches. Moreover, the distribution of niche breadths in vertebrates globally follows a distribution very similar to a lognormal distribution (Donelle et al., in prep). Note that initial simulations indicated that species with mean and variances for niche optima and breadth distributional values outside of range considered here rarely, if ever, persisted relative to the environmental variation considered in our simulations. This is not a restriction of our simulations per se but rather than scaling the distribution of species niche relative to the way environmental variation was generated, we used a larger metacommunity pool but kept the distribution of species niche constant.

### **Simulation dynamics**

The simulation dynamics was composed of two distinctive and consecutive life-history events –dispersal followed by reproduction – and was run for 500 generations. Local carrying capacity ( $K = 1000$ ) and maximum reproduction rate ( $r_{max} = 5$ ) were fixed across scenarios. Initial conditions were set so that each species were expected to be present in 25% of the patches, and 25% of the species were expected to be present in each patch, while the expected size of each community was  $K/2$ . More precisely, each species in each patch had a 25% probability of having an initial population size drawn from a Poisson distribution with mean 8 (for  $k = 1000$ ). Note that preliminary results showed no qualitative differences in metacommunity dynamics between simulations carried over a on longer number of generations (1000 and 5000 generations) or on different  $r_{max}$  (3 and 10) and  $K$  (100 and 10000 individuals) values or with different initial species' prevalence (all species present in all patches).

### Dispersal phase

At the beginning of each generation  $t$ , each individual had a probability  $\delta$  to leave the focal patch (disperse) towards one of the eight nearest (neighbouring) patches. Dispersal success  $\delta_s$  for a given species  $j$  arriving into a given patch  $i$  was set as:

$$\delta_s = e^{\frac{-(\bar{E}_i - \mu_j)^2}{2s_j}} \quad (\text{eq. 2})$$

where  $\bar{E}_i$  is the average environmental value within patch  $i$  as generated in the *Landscape* section; remember that  $\mu_j$  is niche optima and  $s_j$  is niche breadth for the  $j^{\text{th}}$  species. Any individual that survived a previous dispersal event could undergo further dispersal events with the same  $\delta$  probability each time step. The dispersal phase ended once every individual that dispersed has either settled in a patch or died during dispersal. As such, any given individual can disperse multiple times within the same generation (time step). In our model, the compounded dispersal success of all successive individual dispersal events can be interpreted as establishment success. Therefore, the compounded establishment probability  $\delta_s^m$  (for any given individual) after  $m$  dispersal steps is:

$$\delta_s^m = \delta^m * \prod_{i=1}^m e^{\frac{-(\bar{E}_i - \mu_j)^2}{2s_j}} \quad (\text{eq. 3})$$

where  $\bar{E}_i$  (as previously defined) is the average environmental value within patch  $i$  at the  $m^{\text{th}}$  dispersal step. We investigated three different levels of dispersal rate ( $\delta = \{0.1; 0.25; 0.5\}$ ).

### Reproductive phase

Note that every individuals of given species had the same reproductive rate. For simplicity, we refer to it as species reproductive rate. The local reproductive rate for each species was based on their relative competitive ability based on a Gaussian response to environmental conditions. Note, however, that if we were to assume that environmental conditions were homogenous and constant through time within any given individual patch, patches would be dominated by a single species (though different species among patches). This dominant specialist would be one whose niche optimum is very close to the otherwise constant environmental value, following the competitive exclusion principle (Hardin 1960). To generate local spatio-temporal stochastic environmental heterogeneity (see *Model assumptions* section for further discussion), for each patch  $i$  in generation  $t$ , we created 10 within patch environmental values ( $k = [1,10]$ ) drawn from a normal distribution centered around the original environmental value  $\bar{E}_i$  and with a variance of 0.01 ( $E_{ikt} \sim N(\bar{E}_i, 0.01)$ ). As such, intrapatch variance (heterogeneity) in

environmental conditions was set at 1% of total environmental variance across the entire landscape (i.e., variance of the environment was set to unity as described earlier), but note that results (not reported here) were qualitatively similar whether local variance was set to 0.1%, 1% or 5% of the total variance. As such, the competitive ability ( $\omega$ ) for the  $j^{\text{th}}$  species within a patch  $i$  for the  $k^{\text{th}}$  intrapatch environmental value at time  $t$  was:

$$\omega_{ijkt} = \frac{1}{s_j \sqrt{2\pi}} * e^{-\frac{(E_{ikt} - \mu_j)^2}{2s_j^2}} \quad (\text{eq. 4})$$

and its relative competitive ability ( $\tilde{\omega}$ ) across all species was:

$$\tilde{\omega}_{ijkt} = w_{ijkt} / \sum_{j=1}^{250} N_{ijt} * \omega_{ijkt} \quad (\text{eq. 5})$$

where  $N_{ijt}$  is the abundance of species  $j$  at generation  $t$  in patch  $i$ . Note that  $\tilde{\omega}_{ijkt}$  is zero for all species if the patch is empty. Consequently, the relative competitive ability of species  $i$  within patch  $j$  was:

$$\tilde{\omega}_{ijt} = \sum_{k=1}^{10} \tilde{\omega}_{ijkt} / 10 \quad (\text{eq. 6})$$

Defining the local relative competitive ability as the mean of relative competitive ability instead of the relative mean competitive ability allowed for niche partitioning (see Fig. 2 for details). Note that  $\tilde{\omega}_{ijt}$  can be interpreted as the proportion of resources (here space set by  $K$ ) captured by an individual of species  $j$  at generation  $t$  in patch  $i$ . Therefore, reproductive rate of any given individual is the product of  $\tilde{\omega}_{ijt}$  and the carrying capacity  $K$ . However, to avoid excessive reproduction in absence of competition (e.g., after a disturbance), the per capita reproductive rate ( $r_{ijt}$ ) was capped at  $r_{max}$  as follow:

$$r_{ijt} = (\tilde{\omega}_{ijt} * K) * \frac{r_{max}}{r_{max} + (\tilde{\omega}_{ijt} * K)} \quad (\text{eq. 7})$$

Finally, the population size at any given next generation ( $t+1$ ) was drawn from a Poisson distribution with a mean given by the product of the reproductive rate and population size:

$$N_{ij(t+1)} \sim P(r_{ijt} * N_{ijt}) \quad (\text{eq. 8})$$

For the scenario in which we considered disturbance, at the end of the reproductive phase, each local community (i.e., within a patch) had a probability  $\tau = 0.01$  of being killed by disturbance. Note that  $\tau = 0$  in the scenario without disturbance.

## Simulation output

For each simulation, measures of specialization, diversity and spatial structure was recorded at each 100 generations (results reported in Appendix V) and main results were generated on the basis of the last generation ( $t=500$ ). We calculated the average niche breadth of the resulting metacommunity (regional level) because it is a driver of niche processes related to environment such as interspecific competition and niche partitioning, as well as spatial processes given the that greater niche breadths should increase the success of species to disperse (see eq. 2 on dispersal success). As such, the average niche breath allows us to make a better link between the types of species that are selected in any particular spatial structure for the environment and the resultant species coexistence dynamics. Average niche breadth  $\bar{s}$  of the metacommunity was measured as the geometric mean of species' niche breadth weighted by the (surviving) species' regional abundance.

$$\ln(\bar{s}) = \frac{\sum_{j=1}^{250} \sum_{i=1}^{1600} \ln(s_j) * N_{ij}}{\sum_{j=1}^{250} \sum_{i=1}^{1600} N_{ij}} \quad (\text{eq. 9})$$

where  $N$  is the (local) abundance at patch  $i$  for the  $j^{\text{th}}$  species. We used the geometric mean to preserve the ratio between niche breadths given that a 0.1 difference in niche breadth is small for a species with a niche breadth of 1, but quite large for a species with a niche breadth of 0.1.

Species richness and evenness are intrinsically related (Jost 2010) and metrics that consider both in a single index were used here as they directly relate to the capacity of species to coexist within patches (alpha diversity) and in entire metacommunities (regional diversity). While local and regional coexistence are directly related to the alpha and gamma components of diversity (Jost 2007), the interpretation of the beta component in the context of coexistence is less straight forward. The beta component can be interpreted as the diversity in community composition among patches, which informs on the importance of dispersal to local community assembly as high dispersal between communities leads to mass effects and homogenization (low beta diversity). Conversely, low dispersal induces variation among community composition as some species are not able to reach optimal patches. Note that this interpretation of beta diversity is straightforward in our context as the distribution of environmental values and of species' niche parameters ( $\mu_j$  and  $s_j$ ) were kept constant across simulations (i.e., the expected number of optimal patches per species is the same) but this may not be the case in natural metacommunities.

Diversity metrics (alpha, beta, and gamma diversity) were measured using the entropy approach based on Hill's number (Hill 1973) as described in Jost (2007). Given that in our simulations individuals and species only differed by their niche optima and breadth, we chose the second order of Hill's number ( $q = 2$ ), which gives equal weights to all individuals rather than giving greater weights to either more rare or common species. Note that in this framework, the beta component represents the information gained from individual communities in relation to the whole metacommunity (Marcon et al. 2014). The analyses were conducted using the `entropart` package in R (Marcon and Hérault 2015).

Finally, to investigate the effects of the spatial structure of the environment on diversity metrics (i.e., coexistence patterns) and on regional (metacommunity) average niche breadth  $\bar{s}$  (eq. 9), we used an index of spatial structure to serve as predictor of the four response variables (alpha, beta, and gamma diversity, as well as metacommunity's average niche breadth  $\bar{s}$ ). Using a single continuous variable as a predictor instead of the 20 fixed parameters (10 landscapes types and two variogram parameters – including a non-spatialized variable) simplified the presentation of results and analyses but see Appendix VI for boxplots for each of the four response variables as a function of the variogram parameters. Moreover, we also expected that *SSI* would be more sensible to the stochasticity in the spatial structure of the environment among replicates and variogram models that may be not well captured by their fixed parameters if used as predictors.

The Spatial Structure Index (*SSI*) was defined as follows:

$$SSI = -\ln \left( \sum_{i=1}^{1600} \sum_{h=1}^8 \frac{(\bar{E}_i - \bar{E}_h)^2}{1600 * 8} \right) \quad (\text{eq. 10})$$

where  $\bar{E}_i$  and  $\bar{E}_h$  are the average environmental values within patch  $i$  and  $h$ , respectively, and patch  $h$  is one of the 8 neighbouring patches of patch  $i$ . Note that this metric is a transformation of Geary's  $C$  (Geary 1954) if we consider that the spatial weights are 1 for the 8 neighbouring patches, and 0 otherwise (see Appendix II for a demonstration). As defined here, *SSI* captures the environmental differences that individuals encounter during dispersal. As such, *SSI* can be also related to landscape connectivity, as higher environmental differences between neighbouring patches lead to higher dispersal mortality (see eq. 2). As shown in Fig. 3, large values of *SSI* (one single proxy of the strength of the spatial structure of the environment) can be directly related to the strength of the spatial structure of the environment which was generated on the basis of two parameters (i.e., spatial range and spatial autocorrelation).

## Data analysis

Here we fit separate statistical models for each diversity component (alpha, beta and gamma) and regional (metacommunity) average niche breadth  $\bar{s}$  against the spatial structure of the environment (*SSI*) and dispersal rate. Each model was fit on the basis of 900 observations (i.e., 30 replicates x 10 landscape types x 3 dispersal rates) separately for dynamics with and without disturbance. We used a generalized linear model (GLM; McCullagh and Nelder 1989, Chambers and Hastie 1992) with a gamma log-link function as it can account for variance that increases with the mean found in our simulation results (Figs. 4 and 7). Note that the gamma diversity was transformed as  $1 - \textit{gamma diversity}$  to ease the fitting procedure and then transformed back (in Fig. 7) to ease interpretation. Because we were more interested in assessing the effect of dispersal rate rather than parameterizing it, we included dispersal rate as a categorical variable in the GLM particularly because we detected non-linear (and different) effects of dispersal for some response variables. Note that the interaction between dispersal rate (treated as categorical) and *SSI* was left out to simplify interpretation particularly given that its effect was negligible, explaining less than 3% of the deviance across all models. Note also that for gamma diversity and regional (metacommunity) average niche breadth  $\bar{s}$ , the fit of the model would have been slightly improved by variable transformation (either response or predictors), but for simplicity we considered all models without any additional transformation.

Subsequently, in order to assess the relative explanatory power of the spatial structure (*SSI*) and dispersal rate, we performed a sequential analysis of deviance (deviance being the generalized analog of variance) (McCullagh and Nelder 1989), where we first estimated deviance explained by *SSI* and then the additional deviance explained by adding dispersal rate as a predictor into the model (i.e., the semi-partial deviance). This procedure leads to very similar results (not shown) to variation partitioning (Borcard et al. 1992, Peres-Neto et al. 2006) because our factorial design makes dispersal rate and *SSI* nearly orthogonal; as such, their collinearity is nearly zero. Note that the residuals of the models showed no meaningful variation as a function of the strength or the range of spatial autocorrelation, thus indicating to our *SSI* index was effective in capturing all the spatial variation in the response variables.

We focused on the results of the analysis of deviance rather than the model coefficients (slopes; but see Appendix VII for a table) because we aimed at assessing the independent effects of spatial structure on coexistence (measured as patterns of variation in diversity metrics across

simulation scenarios). In addition, we do not report any significance as they are not a product of independent replication (see White et al. 2014 for a discussion). Our analysis of deviance based on GLM pseudo- $R^2$  (ratio between model with a given predictor – either *SSI* or dispersal – and its null deviance – intercept only model; see Table 2) as is a better indicator of the importance of the explanatory variable (White et al. 2014).

## RESULTS

### Specialization

Regional (metacommunity level) average niche breadth  $\bar{s}$  (a metric of specialization) at the end of the simulation (i.e., only considering the surviving species) decreased as function of the strength of the spatial structure (Fig. 4) leading to greater regional prevalence of specialist species in landscapes having stronger spatial structures (high *SSI*). *SSI* was a stronger predictor of regional average niche breadth under disturbance, explaining 81% of the variation of the average niche breadth in contrast to the 34% of the variation explained by the model without disturbance (Table 2). Higher dispersal rates led to smaller levels of regional average niche breadth only in the absence of disturbance (Fig. 4). In this case, only 40% of the variation in the regional average niche breadth was explained by dispersal rates whereas only 1% of the variation was explained in the presence of disturbance (Table 2). Finally, species at the end of the simulation were more specialized (lower regional average niche breadth) in the absence of disturbance (contrast between the two panels in Fig. 4 with and without disturbance).

### Alpha diversity

Local (alpha) diversity increased in landscapes with strong spatial structure in the environment (Fig. 5). However, the explanatory power of spatial structure (*SSI*) was lower in the absence of disturbance, where it explained 51% of the variation in alpha diversity in contrast with the models with disturbance where 81% of the variation was captured by *SSI* (Table 2). Moreover, higher dispersal rates led to an increase in local diversity. As such, dispersal rate accounted for 44% and 16% of the variation in alpha diversity for undisturbed and disturbed scenarios, respectively (Table 1). Finally, disturbance reduced alpha diversity but more so the environment had weak spatial structure (contrast between the two panels in Fig. 5 with and without disturbance).

## **Beta diversity**

Increasing the strength of the spatial structure led to a decrease in beta diversity (i.e., changes in species composition among patches) (Fig. 6). As such, in undisturbed and disturbed scenarios, *SSI* captured 53% and 79% of the deviance in beta diversity, respectively (Table 2). Beta diversity also decreased with higher dispersal rates, meaning that local communities were more similar when the dispersal rate was high. As such, dispersal rate accounted for an additional 42% and 17% for scenarios without and with disturbance, respectively (Table 2). Beta diversity was higher in the presence of disturbance. Finally, disturbance increased beta diversity but more so for weak spatial structures (contrast between the two panels in Fig. 6 with and without disturbance).

## **Gamma diversity**

In presence of disturbance, regional (gamma) diversity increased as a function of the strength of the spatial structure of the environment (*SSI*), explaining 53% of the variation in gamma diversity across simulation scenarios (Table 2 and Fig. 7; but note that the y-axis' scale changes between graphs so that effect of *SSI* in absence of dispersal could be perceptible). However, in the absence of disturbance, gamma diversity was found to decrease with *SSI* and it explained 24% of the variation. Hence, stronger spatial structure promotes regional coexistence in the presence of disturbance but hinders regional coexistence in its absence. Furthermore, in the absence of disturbance, lower dispersal rates led to higher gamma diversity, with dispersal rate explaining an additional 21% of the variation in the variation of gamma diversity (Table 2). Dispersal rate was negligible in the presence of disturbance. Finally, gamma diversity was lower in the presence of disturbance, especially for low values of *SSI* (contrast between the two panels in Fig. 7 with and without disturbance).

## **DISCUSSION**

In this study we set out for the first time to study the effects of the spatial structure of the environment on metacommunity dynamics and its effects on species coexistence at the local and regional levels. To uncover the underlying mechanisms by which the spatial structure of the environment mediates species coexistence (local – alpha and regional – gamma diversities), we also investigated how beta diversity and average niche breadth of the resulting metacommunities

varied as a function of spatial structure. Beta diversity measures how local communities are homogenized by dispersal, while niche breadth allows us to assess species' trade-offs between local competitiveness and regional persistence through dispersal.

As predicted (see Introduction), we found that the spatial structure in environmental features strongly shaped local and regional species coexistence. As we discuss here, these results can be explained by the way in which metacommunities in landscapes with strong spatialized environmental features select for species with greater levels of specialization (smaller niche breadths). This selection has strong consequences for species coexistence at the local and regional levels. While the effects of the environmental spatial structure were stronger in the presence of disturbance (likely the case of most real ecological landscapes), absence of disturbance did not change our prediction regarding the directionality of the effects, except for regional (gamma) diversity. Our model demonstrates that spatially structured environments can promote ecological specialization by reducing the costs of dispersal of specialists, thus reducing the opportunity of generalist species to become locally established and, as a result, specialist species increase their local and regional prevalence and abundance.

## **Specialization**

In agreement with our first hypothesis, metacommunities in landscapes with weak environmental spatial structure selected against species with narrow niche breadths (i.e., specialists; Fig. 4), either via regional extinction or in lowering their regional abundances, particularly under disturbance. This is because of the large range of environmental conditions that dispersing individuals experience within landscapes with weaker spatial structures (i.e., shorter range and weaker spatial autocorrelation). As such, generalist species were strongly favoured in poorly structured environments, particularly in the presence of disturbance (Fig. 4). Indeed, generalist species can better resist the negative effects of greater environmental variation during dispersal and find patches that are non-occupied by competitively superior specialists. In these cases, generalist species are able to reproduce and disperse before individuals from specialist species can colonize the patch, thus persisting regionally. Conversely, in our model, specialist species dominated spatially structured environments (i.e., larger range and stronger autocorrelation regardless of the presence of disturbance). Indeed, specialist species are better able to find optimal conditions because: 1) the costs of dispersal mortality is lower in these landscapes

in contrast to weakly spatially structured landscapes; and 2) patches with similar environmental conditions are clustered together, decreasing the dispersal mortality while tracking suitable patches. Note, however, that the relative advantage of generalists over specialists in weakly spatially structured landscapes is much greater with disturbance as it generates greater temporal opportunities for these species (i.e., unoccupied patches where generalists are able to reproduce before being occupied by a specialist with stronger competitive abilities). As such, in the absence of disturbance, opportunities for generalist species is limited to a stochastic decrease in specialist populations either caused by temporal environmental stochasticity (i.e., within patch environmental variability experienced by a given generation reduce the reproductive rate of specialists for that generation) or by demographic stochasticity (i.e., species reproduced less than expected by chance alone; eq. 8). Furthermore, in the absence of disturbance, we found regional (metacommunity) average niche breadth to decrease slightly in scenarios where dispersal rate was higher because specialist species (which dominate local patches) could invest greater number of individuals to dispersal, while such dispersal losses exposed generalists to local (and potentially regional) extinctions as they were restricted to low abundances given the absence of open niche. As such, our model was able to reproduce the well-known colonization-competition trade-off in which colonizers (generalists) benefit from unoccupied patches before being displaced by specialist competitors (Yu and Wilson 2001, Cadotte et al. 2006, Calcagno et al. 2006).

Given that the study of Büchi and Vuilleumier (2014) also focussed on selection of specialization levels as a function of dispersal rates and of the spatial structure of the environment, it is worth comparing their results with ours at some length. Note that their simulation model did not consider dispersal mortality, while ours included mortality as a function of the environmental variation experienced during dispersal. In agreement with our results, Büchi and Vuilleumier (2014) also found specialization to increase with dispersal and to decrease with disturbance. Yet, in their model, the effect of spatial structure on specialization was found to be contingent on the dispersal rate. As such, their results match ours only at low dispersal rates as individuals seldom dispersed beyond neighbouring patches, thus be subject to potential inhospitable environments in their dispersal pathways, which was detrimental to specialist species in weakly spatially structured environment. Under low dispersal rates, both model dynamics (ours and theirs) selected for more for specialist species (i.e., low average niche

breadth) as a function of the strength of the spatial structure of the environment. However, at medium and high dispersal rates, Büchi and Vuilleumier (2014) found that environments with stronger spatial structure should select for species that are slightly more generalists (i.e., greater average niche breadth) than weaker ones. Conversely, our model predicts that more specialist species should be selected by metacommunity dynamics in landscapes even at medium and high dispersal rates. Given that in Büchi and Vuilleumier (2014) did not consider dispersal costs via mortality, individuals could effectively disperse to distant favourable patches and outcompete any weaker competitors (i.e., generalist species). While specialist species dominated even in spatially random landscapes, they were outcompeted by species with slightly larger niches in landscapes with increased spatial structure as a result of dispersal mass effects (i.e., when dispersal impacts population dynamics). As such, contrary to our model, species with slightly wider niches were advantaged as they could achieve higher average population growth (in contrast to specialist species) across a well-connected cluster of neighbouring patches. However, species with very narrow niche breadths (e.g., only able to thrive in a single or very few patches, but not in neighboring patches) would eventually go locally extinct as its local competitive advantage would be overcome by an imbalance in migration (i.e., specialist species would lose many individuals due to emigration, while a more generalist competitor would receive many individuals through immigration).

The conflicting results between the study of Büchi and Vuilleumier (2014) and ours can be explained by the fact that we considered dispersal mortality, thus preventing specialists to dominate poorly structured landscapes. Furthermore, it is worth noting that their simulation framework gave an unfair advantage to specialist species as they benefited from having more dispersers (see Appendix III for an explanation), contrary to what is expected by the well-known competition-colonization trade-off (Amarasekare et al. 2004, Kneitel and Chase 2004, Cadotte et al. 2006, Nurmi and Parvinen 2011, Livingston et al. 2012). In agreement with our conclusions, empirical evidence supports that small-scale environmental homogeneity (i.e., among neighbouring patches) – as it is the case for landscapes that have a strong spatial structure – promotes evolution of specialization. Moreover, specialists are particularly at risk (e.g., local extinction and lowering abundance at regional scales) in landscapes with lower interpatch connectivity (Tischendorf and Fahrig 2000), which can be equated to weaker spatial structures in our model as similar environments are less connected.

## **Species coexistence**

As predicted, stronger spatial structure led to an increase in alpha diversity and a decrease in beta diversity. However, our prediction in which gamma diversity would decrease as a function of the strength of the spatial structure was not fully supported as its effects depended on whether metacommunity dynamics underwent disturbance or not.

### Alpha diversity

Alpha diversity increased with the strength of the environmental spatial structure (Fig. 5) as a result of increased connectivity among patches with similar environmental conditions, thus promoting niche partitioning through a rescue effect. In strongly spatially structured landscapes, patches with similar environmental conditions are more clustered together, a case that mostly benefits specialist species as dispersers were more likely to find themselves in a hospitable environment while also reducing dispersal mortality caused by adverse environmental conditions experienced during dispersal. For instance, assume a specialist species in its most optimal patch (i.e., greatest matching between species' niche and patch's environmental value); this species will also have a strong competitive ability in nearby patches given their environmental similarity among neighbouring patches. However, as this specialist species moves further away from its niche optimum towards marginal environments, its local population decreases, thus becoming vulnerable to stochastic environmental variation and local extinction. While sub-optimal environments should prevent this specialist species to succeed, strong spatial structure connects optimal and sub-optimal patches together by exchanging individuals that periodically rescue small local populations of specialist species or even recolonize marginal patches following a stochastic extinction (Brown and Kodric-Brown 1977, Eriksson et al. 2014). In contrast, in weakly spatially structured landscapes, optimal patches are not well-connected with sub-optimal patches as distance and dispersal mortality caused by environmental variation impedes the flow of migrant specialists between optimal and sub-optimal patches. As a result, these small populations of specialists undergo extinction more often, thereby leaving opened niche spaces for generalist species. It follows that (in our model), strongly spatially structured landscapes lead to increased local niche partitioning is promoted as specialist's extinction in sub-optimal (marginal) patches is prevented by rescue effect from nearby patches, allowing greater number of species (alpha diversity) to coexist locally. In contrast, weakly spatially structured landscape inhibits

rescue effect as dispersal between similar environment is hampered. This leads to the local extirpation of multiple specialist species at the benefit of one or few generalists, thus reducing local coexistence (lower alpha diversity). Moreover, disturbance exacerbated this process since that specialists were sometimes unable to recolonize their optimal patches following a disturbance, leaving generalist species with greater niche space. As such, alpha diversity decreased more rapidly in weakly spatially structured landscapes in the presence of disturbance. Conversely, higher dispersal rates promoted rescue effect, explaining the increase in alpha diversity with greater dispersal rates (Fig. 5). Note that while the rescue effect could be interpreted as a source-sink dynamic though given that there is no “sink” per se in our model, but only competitive sinks (i.e., where a species have negative growth rate because of competition), we preferred not discussing our results in terms of the source-sink dynamics.

Although we are not aware of any study that explicitly investigated how the spatial structure of the environment affects metacommunity dynamics and the resulting patterns of local and regional coexistence, there is a large body of literature across various ecological systems that support our conclusions. Both connectivity (Bornette et al. 1998, Tockner et al. 1999, Cottenie and De Meester 2003, Luoto et al. 2003) and source-sink dynamics (Amarasekare and Nisbet 2001, Codeco and Grover 2001, Mouquet and Loreau 2003) were found to promote local diversity, while higher dispersal mortality impaired it (Mouquet and Loreau 2003, Amarasekare et al. 2004). The study of Bar-Massada et al. (2014) which relies on processes similar to the one described here (i.e., greater connectivity among patches with similar environments), showed that neutral processes are less prevalent in spatially structured environments. As a corollary, one could argue that (quasi) neutral dynamics in spatially unstructured landscapes are more likely because they should be made of more generalist species that overlap in their niches (i.e., species have more equivalent niches). In addition, as it is the case in our study, higher specialization levels are associated with more diverse (meta) communities (i.e., locally and regionally) (MacArthur et al. 1966, Kolasa and Li 2003, Carnicer et al. 2008, Ravigné et al. 2009, Weiner and Xiao 2012). In our model, local patches in strongly spatially structured landscape are occupied by multiple specialist species, thus promoting niche partitioning which leads to greater local diversity in contrast to weakly structured landscapes.

### Beta and Gamma diversity

We initially predicted that environments with stronger spatial structure would lead to the homogenization of ecological communities (i.e., lower beta diversity), in turn leading to a lower regional (gamma) diversity. Although beta-diversity indeed decreased with the strength of the environmental spatial structure, gamma diversity only decreased with a decrease in beta-diversity under the absence of disturbance. In the presence of disturbance, weakly spatially structured landscapes benefited some generalists to have really large abundances at the expense of lowering specialists' abundances as discussed in the *Alpha diversity* section above. This benefit decreased gamma diversity given the unevenness in regional abundances between generalist and specialist species. However, in the absence of disturbance, generalists had reduced opportunities to increase their abundances. As such, weakly spatially structured landscapes allowed generalists to do well without them becoming dominant, while highly spatially structured landscapes led to the (quasi) exclusion of generalists, thus explaining the slight reduction in gamma diversity as the spatial structure of the environment increased (Fig. 7). Note, however, that total absence of disturbance is ecologically unrealistic, and that even weak levels of disturbance lead to an inversion of the relationship. Moreover, in agreements with our simulations under disturbance, empirical evidence indirectly supports the idea that spatially unstructured landscapes reduce gamma diversity. As such, reduced connectivity, as it is the case in weakly spatially structured landscapes, favours generalists and better disperser species (Devictor et al. 2008, Öckinger et al. 2010, Nordén et al. 2013), leading to lower regional diversity (Helm et al. 2006, Krauss et al. 2010, Staddon et al. 2010). Note, however, that regional richness decreased in strongly spatially structured landscapes as a result of exclusion of generalist species (see Fig. 8). However, we do not discuss species richness any further as it is a poor metric of diversity in the context of our simulation framework in comparison to gamma diversity given that species richness relies on the slow accumulation of extinction events which results from the random component of stochastic demographic events (i.e., the expected reproduction is never zero, but realized reproduction can be). Note that diversity metrics often consider species abundances (as we did here) as they respond rapidly to the deterministic portion of demographic processes (reproduction, competition and dispersal rate). As such, Hill's number based diversity metrics allow a closer link between metacommunity dynamics and demographic processes.

As the strength of the spatial structure of the environment decreased, populations of specialists in marginal sub-optimal patches (see *Alpha diversity* section) were extirpated to the benefit of few generalists. In general, local patch abundances of specialist populations in optimal patches were unchanged by the spatial structure, except for some cases in which the specialists were unable to recolonize following a disturbance, which benefited generalists (results not shown here). As such, species abundances varied more across patches in weakly structured landscapes and, as a consequence, as most sub-optimal populations were extirpated, specialists either achieved high abundances or went locally extinct. In addition, local populations of generalist species also varied across patches depending on the ability of a specialist species with greater fitness potential to recolonize. On the basis of the entropy-based definition of beta diversity (i.e., the amount of information gained by considering individual communities in comparison to the whole metacommunity), increased variation among local populations led to higher beta diversity among patches. Because environmental heterogeneity was fixed in our model, such an increase in beta diversity in landscapes that were weakly spatially structured indicates stronger isolation of local communities due to dispersal limitation, which is consistent with the lower beta diversity observed in the scenario with higher dispersal rate (Fig. 6). The reduction in beta-diversity as a function of the strength of the spatial structure of the environment supports our interpretation that the lack of spatial connectivity in weakly spatially structured environments reduce local (alpha) and (regional) gamma diversity. Empirical studies tend to support the conclusion that beta-diversity decreases as a function of spatial connectivity (Tockner et al. 1999, Forbes and Chase 2002, Pardini et al. 2005, Soininen et al. 2007).

## **CONCLUSION**

We have shown that the spatial structure of environmental variation can have a strong impact on diversity across scales, as well as on species' specialization. This effect results from a change in the connectivity between environmentally similar patches. In strongly spatially structured landscape, niche partitioning is promoted as populations in optimal patches can rescue populations in sub-optimal patches via dispersal, thus leading to local communities composed of multiple specialist species. As the strength of the spatial structure decreases, successful dispersal of specialist species is hindered, thus impeding the rescue of sub-optimal patches. Generalists are therefore favoured in poorly structured landscapes as they can use a wider range of environments and are more likely to survive dispersal events, thus allowing them

to take advantage of opened niche spaces resulting from specialists' dispersal limitations. The prevalence of generalists led to a decrease in local (alpha) and regional (gamma) diversity, but increased change in community composition among local communities (beta diversity). In the absence of disturbance, the effect of spatial structure is drastically reduced.

Despite the large body of literature in ecology focussing on spatial and environmental variation, their links received very little attention (but see Büchi et al. (2009; 2012; 2014), Bar-Massada et al. 2014). Our model can be expanded in several ways. For instance, while we only investigated three levels of range and three levels strength due to computational limitations, the coverage of the parameter space could be extended to investigate, for instance, how range and strength of autocorrelation interact to mediate coexistence. Instead, we combined both range and strength of autocorrelation into a single  $s$  index ( $SSI$ ), which was a strong predictor of diversity metrics and specialization level. Yet, as shown in Fig. 3, different combinations of range and strength can yield to very similar  $SSI$  values.

Our model shows that the spatial structure in environmental features mediates the selection of specialist species *versus* generalists largely due to their differential advantages related to dispersal mortality. In our model, all species were equally prone to dispersal, yet species that experienced severe dispersal mortality in a given landscape would likely evolve to reduce their dispersal rates to lessen this source of mortality (Henriques-Silva et al. 2015, Karisto and Kisdi 2017). As such, one could assume that stronger spatial structure leads to weaker covariation between specialization and propensity to disperse because the specialists' costs of dispersal are alleviated in strongly autocorrelated environments. Previous studies have looked into the effects of landscape structure on the evolution of dispersal, but they focussed on a single species and/or did not consider species specialization (North et al. 2011, Büchi and Vuilleumier 2012, Wickman et al. 2017).

In spatially structured environments, all of the intrapatch environmental variability was occupied by specialists as a result of rescue effects from nearby patches that were environmentally similar yet slightly different. One could argue that such selection for increased specialization would lead to more efficient resource use, thus producing higher levels of ecosystem functioning. Although in our framework community productivity (i.e., total reproduction per generation) was set to be independent of community composition, our model can provide some insights on this issue. An increase in ecosystem productivity with the strength of the spatial structure of environment would be consistent with the spatial insurance hypothesis (Loreau et al. 2003), as connectivity would promote the maintenance of higher levels of ecosystem functioning following disturbances.

Finally, our model leads to testable predictions in which generalist species should dominate weakly structured environments and specialists should dominate environments that are strongly structured. These differences in dominance between specialists versus generalists should then lead to differences in local and regional diversity. Note, however, that testing this prediction empirically may be complicated by the fact that different landscapes have different environmental values and may select differently for specialist versus generalist species and associated diversity patterns.

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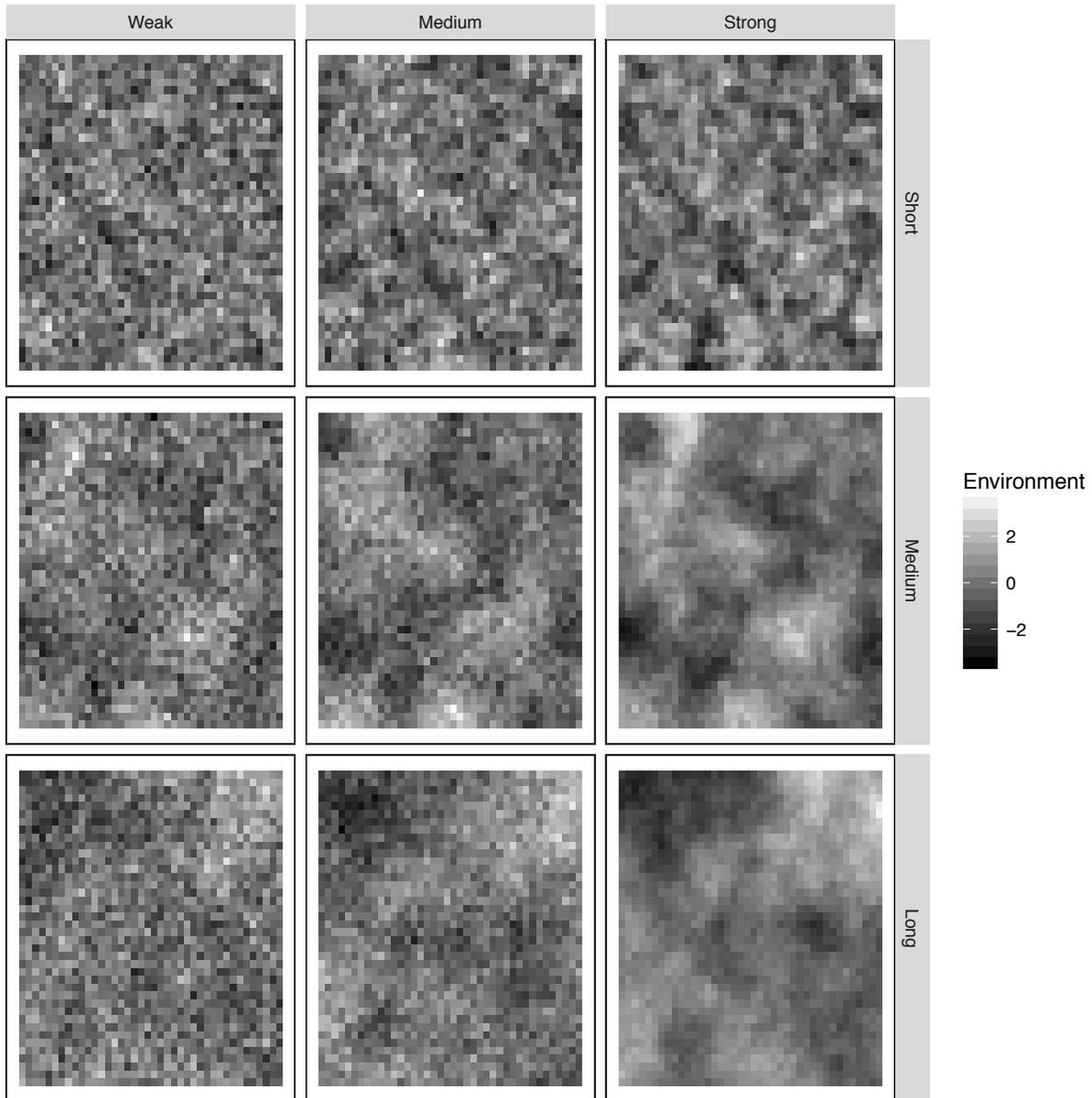
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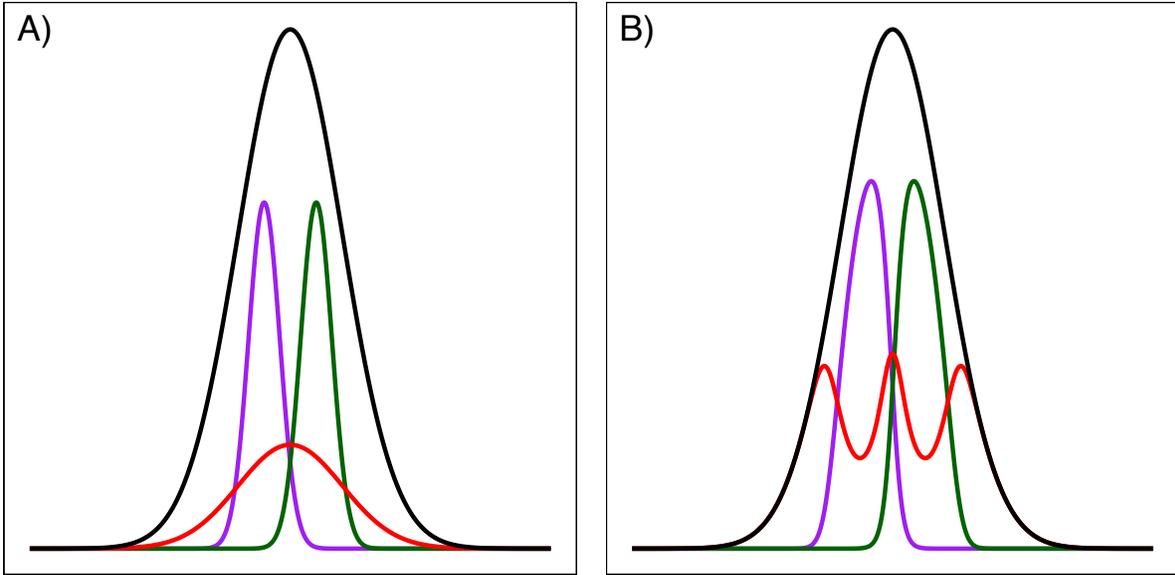
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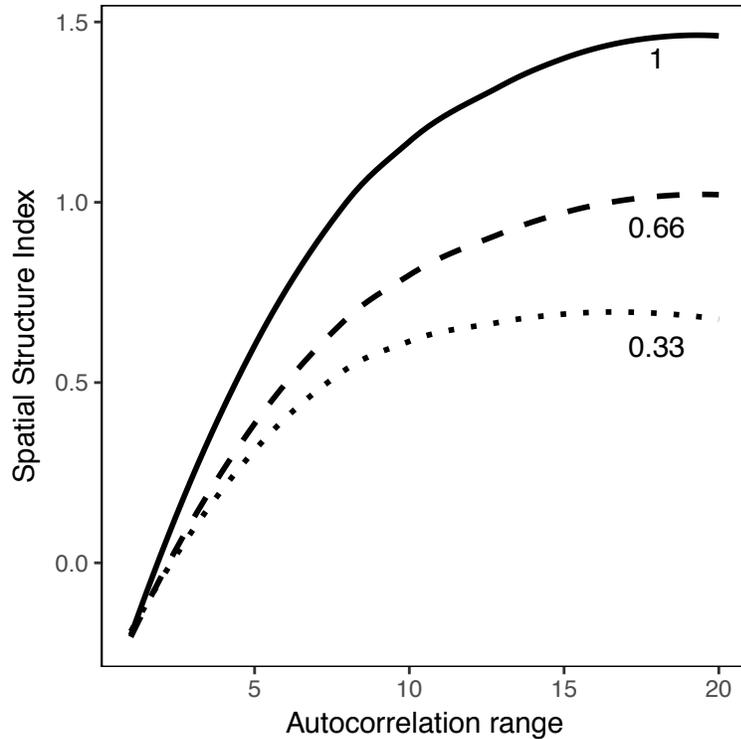
## FIGURES



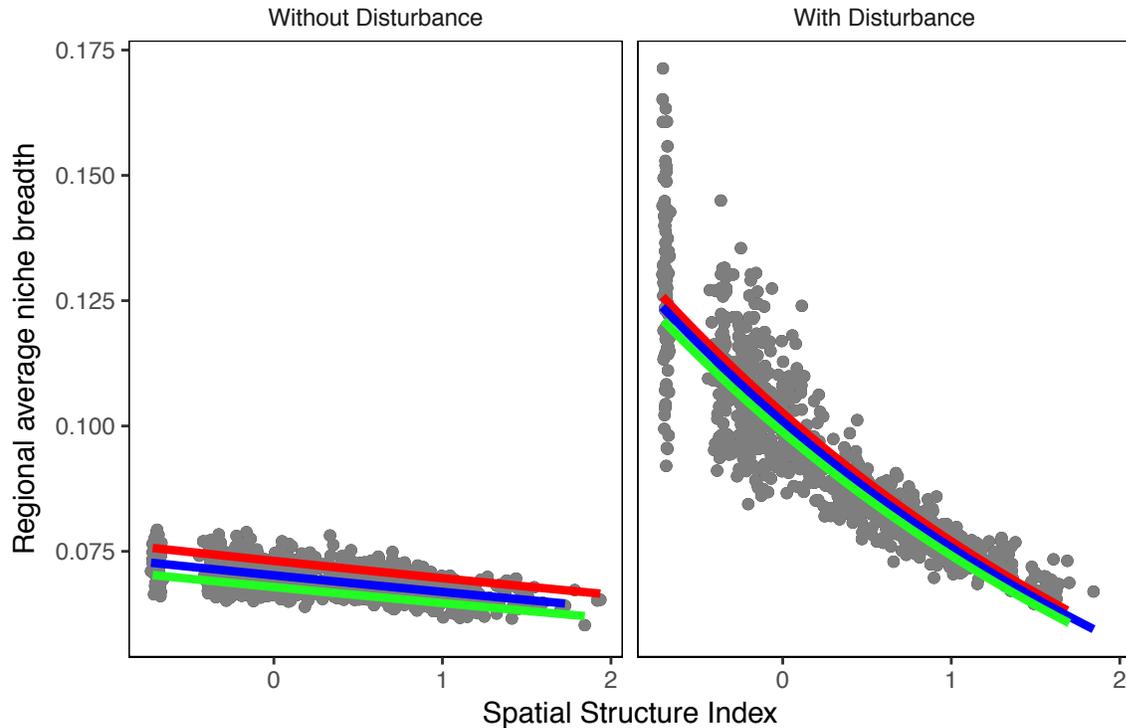
**Figure 1: Examples (one single simulation) of environmental values for each of the nine different spatially structured landscapes used in the model.** Autocorrelation strength (columns) increases from left to right, while autocorrelation range (rows) increases from top to bottom. Landscapes were generated as described in the *Landscape structure* section.



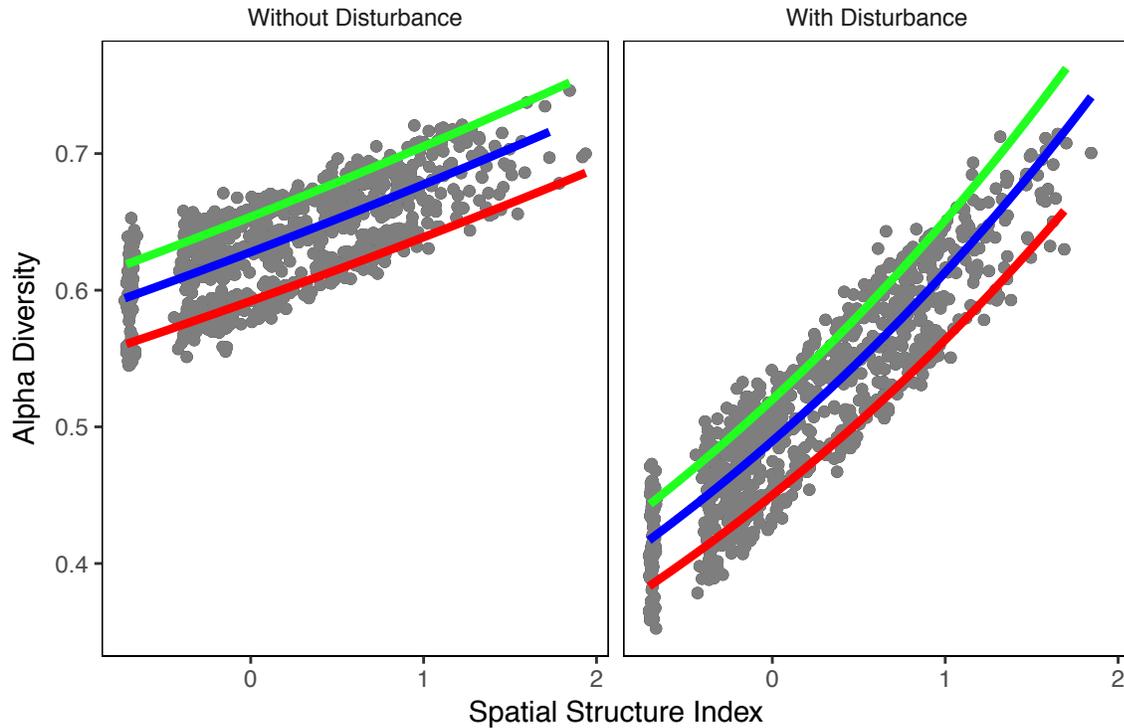
**Figure 2: Illustration of competition and determination of the mean relative competitive ability ( $\tilde{\omega}_{ijt}$ ) in our simulation framework.** In both panels, the black line represents the local environmental distribution (i.e., intrapatch environmental heterogeneity; this is the expected distribution of  $E_{ikt}$ ). In panel A, the green and purple lines represent the niche of two specialists (the competitive ability as a function of environmental values; eq. 4), while the red line represents the niche of a generalist species. In panel B, the green, purple, and red lines represent relative competitive ability as a function of environmental values for each species of panel A. Note that we here constrained the relative competitive ability to consider the local frequency of environmental values, so that the area under the curve in panel B represents the expected mean relative competitive ability  $\tilde{\omega}_{ijt}$  (eq. 6; but the actual value of  $\tilde{\omega}_{ijt}$  depends on the value of  $E_{ikt}$  that are drawn). As such, overlaps between specialists and generalists' niches have little impact on the specialist's relative competitive ability, but great impact on the generalists' relative competitive ability. However, the generalists benefit from environment unoccupied by specialists to increase their mean relative competitive ability.



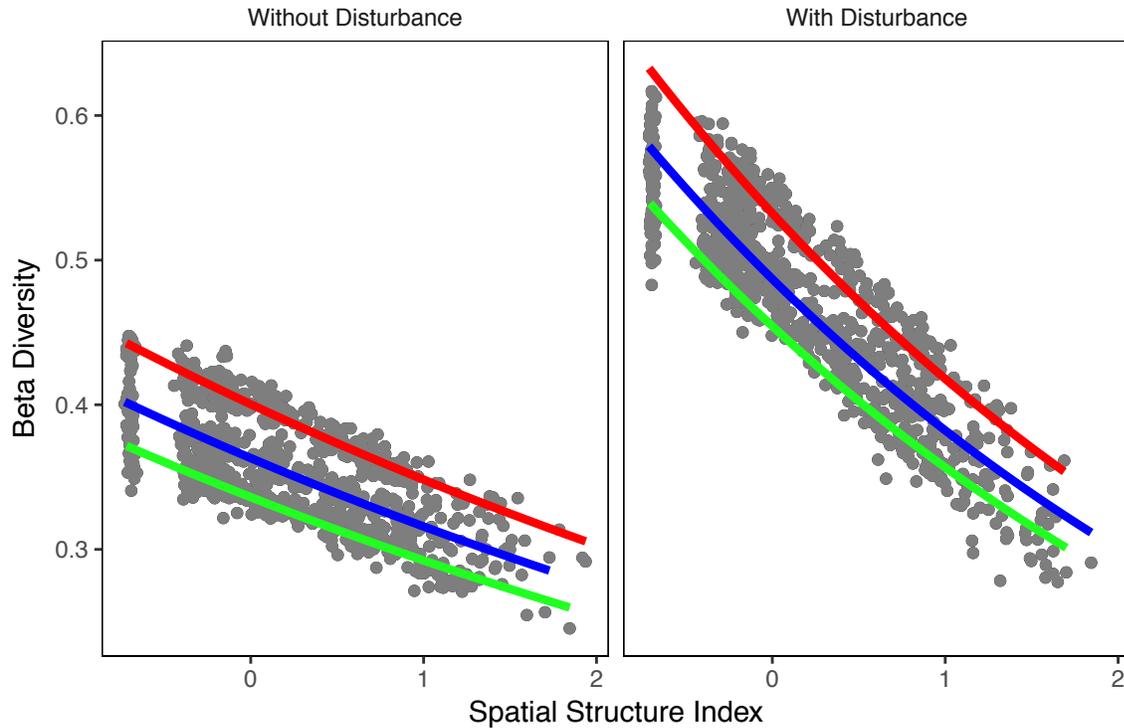
**Figure 3: Spatial Structure Index (SSI) as a function of autocorrelation range across different levels of autocorrelation strength.** The landscapes have been generated as described in the method section on a  $40 \times 40$  lattice. For each level of autocorrelation strength, 30 landscapes were generated for each of the 20 different autocorrelation ranges. Each line represents a LOESS regression for a given level of autocorrelation strength. The three levels of autocorrelation strength ( $1 - C_0$ ) used in our study ( $\{1, 0.66, 0.33\}$ ) are represented by the solid, dashed, and dotted line respectively. SSI increases with autocorrelation range and strength.



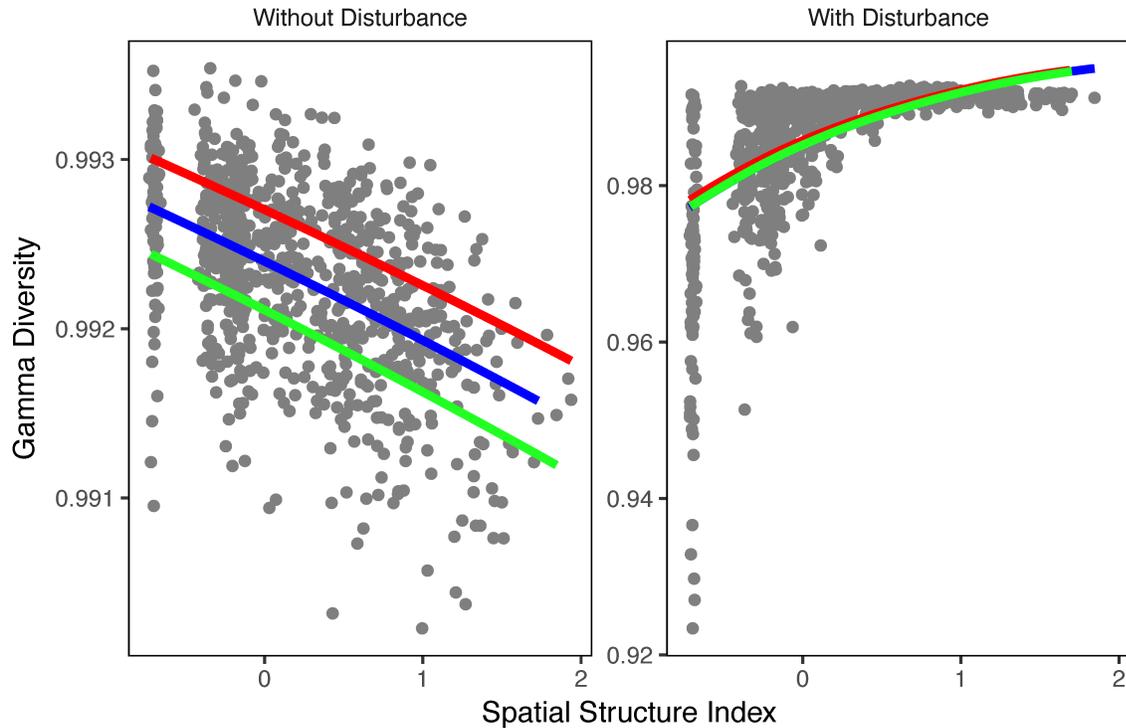
**Figure 4: Niche breadth (specialization) as a function of the spatial structure of the environment (*SSI*) with and without disturbance.** Each point (in grey) represents the regional (metacommunity) mean niche breadth of one simulation as a function of the landscape *SSI*. Larger values of *SSI* are associated with stronger spatial structure (greater ranges and stronger autocorrelations). Small values of average niche breadth indicate greater specialization. The line represents the fitted model for each level of dispersal rate. Low, medium, and high dispersal ( $\delta = \{0.1, 0.25; 0.5\}$ ) are represented in red, blue, and green, respectively.



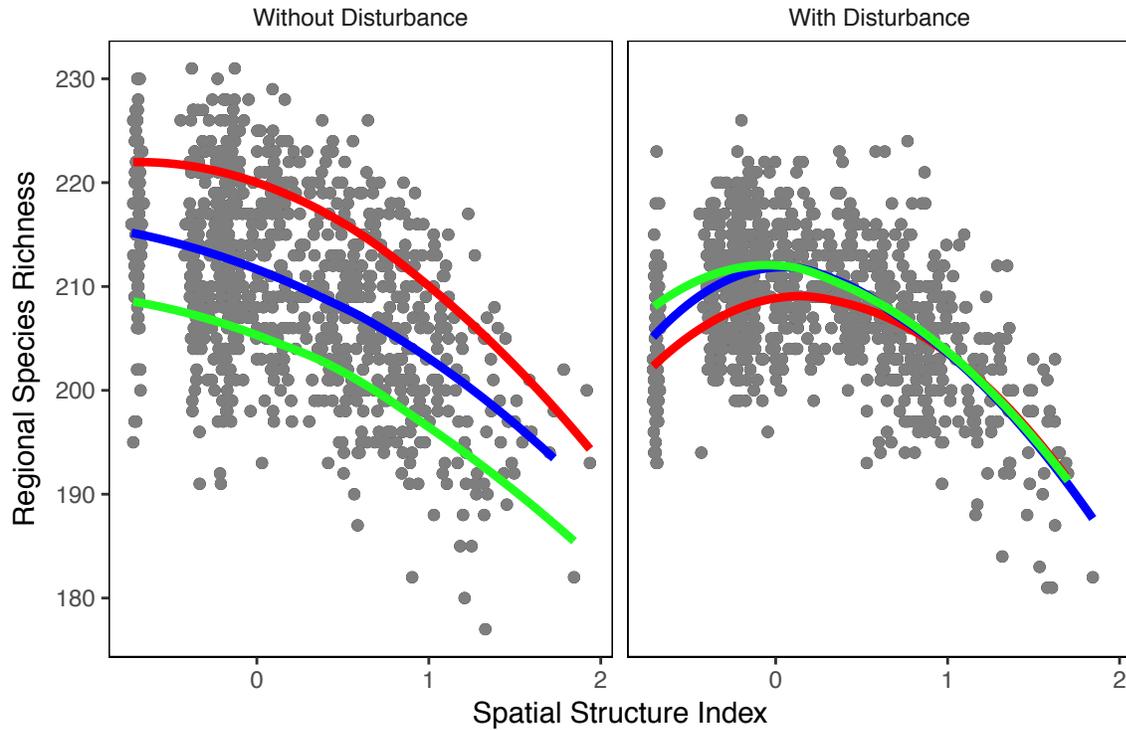
**Figure 5: Alpha diversity as a function of the spatial structure of the environment (*SSI*) with and without disturbance.** Each point (in grey) represents the regional (metacommunity) alpha diversity of each simulation (900 per panel) as a function of the *SSI* of its landscape. Larger values of *SSI* are associated with stronger spatial structure (greater ranges and stronger autocorrelations). Large values of alpha diversity indicate greater local species coexistence. The line represents the fitted model for each level of dispersal rate. Low, medium, and high dispersal rate ( $\delta = \{0.1, 0.25; 0.5\}$ ) are in red, blue, and green, respectively.



**Figure 6: Beta diversity as a function of the spatial structure of the environment (*SSI*) with and without disturbance.** Each point (in grey) represents the regional (metacommunity) beta diversity of each simulation (900 per panel) as a function of the *SSI* of its landscape. Larger values of *SSI* are associated with stronger spatial structure (greater ranges and stronger autocorrelations). Large values of beta diversity indicate greater changes among local communities. The line represents the fitted model for each level of dispersal rate. Low, medium, and high dispersal rate ( $\delta = \{0.1, 0.25; 0.5\}$ ) are in red, blue, and green, respectively.



**Figure 7: Gamma diversity as a function of the spatial structure of the environment (*SSI*) with and without disturbance.** Note that the Y-axes are on different scale. Each point (in grey) represents the regional (metacommunity) gamma diversity of each simulation (900 per panel) as a function of the *SSI* of its landscape. Larger values of *SSI* are associated with stronger spatial structure (greater ranges and stronger autocorrelations). Large values of gamma diversity indicate greater regional species coexistence. The line represents the fitted model for each level of dispersal rate. Low, medium, and high dispersal rate ( $\delta = \{0.1, 0.25; 0.5\}$ ) are in red, blue, and green, respectively.



**Figure 8: Regional species richness as a function of the spatial structure of the environment (*SSI*) with and without disturbance.** Each point (in grey) represents the regional (metacommunity) species richness of each simulation (900 per panel) as a function of the *SSI* of its landscape. Larger values of *SSI* are associated with stronger spatial structure (greater ranges and stronger autocorrelations). The line represents the LOESS regression model for each level of dispersal rate. Low, medium, and high dispersal rate ( $\delta = \{0.1, 0.25; 0.5\}$ ) are in red, blue, and green, respectively.

## TABLES

**Table 1: Parameters used in the simulation model**

Section	Parameter	Values
Landscape	Autocorrelation range ( $\alpha$ )	0*; 3; 10; 20
	Autocorrelation strength ( $1 - C0$ )	0*; 0.33; 0.66; 1
Simulation dynamics	Dispersal ( $\delta$ )	0.1; 0.25; 0.5
	Disturbance ( $\tau$ )	0; 0.01

\*Those two values generated the random landscape (i.e., the 10<sup>th</sup> spatial structure) and were not combined with the other values of landscape parameter.

**Table 2: Results of the analysis of deviance for the four response variables with and without disturbance**

Response variable	Disturbance regime	Deviance explained by <i>SSI</i>	Deviance explained by dispersal	Null deviance
Specialization	Undisturbed	34%	40%	2.08
	Disturbed	81%	1%	32.10
Alpha diversity	Undisturbed	51%	44%	3.39
	Disturbed	81%	16%	19.90
Beta diversity	Undisturbed	53%	42%	10.89
	Disturbed	79%	17%	22.46
Gamma diversity	Undisturbed	24%	21%	4.35
	Disturbed	53%	0%	242.01

## **APPENDIX I - SPATIAL STRUCTURE**

A common way to describe spatial structure is spatial autocorrelation, which is “the correlation among values of a single variable strictly attributable to the proximity of those values in geographic space” (Griffith 2003). Unless otherwise specified, in this work, the term autocorrelation refers to positive autocorrelation, and we use spatial autocorrelation and spatial structure interchangeably. Range and strength are the two parameters characterizing the autocorrelated structure. Autocorrelation range is the distance after which values are not spatially correlated, whereas autocorrelation strength refers to the magnitude of the spatial correlation between neighbouring values. In other words, weaker spatial autocorrelation leads to greater error around the patterns of autocorrelation, increasing small-scale heterogeneity. Autocorrelated landscapes can be conceptualized as a topographic map of hills and valleys (see Fig. 1). Large ranges of autocorrelation result in few large hills with smooth slopes, whereas short ranges result in many hills and valleys with steeper slopes. In this analogy, the steepness of the slope represents the average patch to patch environmental differences.

## APPENDIX II – SPATIAL STRUCTURE INDEX AND GEARY’S C

Here we show that the spatial structure index used in this study is in fact an inverse function of Geary’s C:

$$C = \frac{n - 1}{2W * \sum_i (\bar{E}_i - \bar{\bar{E}})^2} * \sum_i \sum_j w_{ij} * (\bar{E}_i - \bar{E}_j)^2 \quad (\text{eq. S1})$$

where  $n$  is the total number of patches,  $w_{ij}$  is the spatial weights matrix,  $W$  is the sum of all  $w_{ij}$ ,  $\bar{E}_i$  and  $\bar{E}_j$  are the average environmental value within patch  $i$  and  $j$  respectively, and  $\bar{\bar{E}}$  is the average environmental value across all  $\bar{E}_i$ .

Assuming that  $w_{ij} = 1$  if patches  $i$  and  $j$  are neighbours, and  $w_{ij} = 0$  if they are not, we can rewrite  $C$  as follow:

$$C = \frac{n - 1}{2W * \sum_i (\bar{E}_i - \bar{\bar{E}})^2} * \sum_i \sum_h (\bar{E}_i - \bar{E}_h)^2 \quad (\text{eq. S2})$$

where patch  $h$  is one of the 8 neighbouring patches of patch  $i$ . Given that distribution of environmental values was standardized to mean 0 and unit variance,  $\sum_i (\bar{E}_i - \bar{\bar{E}})^2 = 1$  and moving  $W$  inside the double summation,  $C$  becomes:

$$C = \frac{n - 1}{2} * \sum_i \sum_h \frac{(\bar{E}_i - \bar{E}_h)^2}{W} \quad (\text{eq. S3})$$

Now, considering that every landscape was composed of 1600 patches ( $n=1600$ ) that each had 8 neighbours, then  $W = 1600 * 8$ ,  $C$  becomes:

$$C = \frac{1600 - 1}{2} * \sum_{i=1}^{1600} \sum_{h=1}^8 \frac{(\bar{E}_i - \bar{E}_h)^2}{1600 * 8} \quad (\text{eq. S4})$$

By transforming  $C$ , we can then obtain our  $SSI$  as follow:

$$\frac{2 * C}{1599} = \sum_{i=1}^{1600} \sum_{h=1}^8 \frac{(\bar{E}_i - \bar{E}_h)^2}{1600 * 8} \quad (\text{eq. S5})$$

$$-\ln\left(\frac{2 * C}{1599}\right) = -\ln\left(\sum_{i=1}^{1600} \sum_{h=1}^8 \frac{(\bar{E}_i - \bar{E}_h)^2}{1600 * 8}\right) = SSI \quad (\text{eq. S6})$$

### APPENDIX III: BÜCHI ET AL. (2014) SIMULATION FRAMEWORK

By revisiting Büchi et al.'s (2014), we found that their simulation framework relies on an odd combination of assumptions that gives an unfair dispersal advantage to specialists. First, they implemented the specialist-generalist fitness trade-off through the reproduction parameter ( $r$ ) as follows:

$$r_j(E) = 10 * \frac{1}{\sigma_j \sqrt{2\pi}} * e^{-\frac{(E-\mu_j)^2}{2\sigma_j^2}} \quad (\text{eq. S7})$$

where the subscript  $j$  refers to the  $j^{\text{th}}$  species, while  $\mu$  and  $\sigma$  refers to niche optima and breadth, respectively, and  $E$  to the environmental value of a particular patch, with 10 being a scaling factor. As such, specialists would produce more offspring at niche optima than generalists, but generalists would produce offspring over a wider range of environment. The idea behind this trade-off is that the expected total number of offspring across all possible values of  $E$  (i.e., the indefinite integral of  $r_j(E)$ ) will always be 10 (i.e., the scaling factor) regardless of the species niche. Then, juveniles were randomly selected to bring the local community to carrying capacity. While there might be very little empirical evidence suggesting that specialist reproduction to be higher and juvenile settlement to be neutral, these two processes together would still lead to very similar local dynamics as in our simulation model.

However, in Büchi et al.'s (2014) simulation framework, dispersal occurred at the juvenile stage, therefore advantaging specialists because they produce more juveniles. Indeed, let's assume that one specialist ( $\sigma_j = 0.05$ ) and one generalist ( $\sigma_j = 0.25$ ) each dominate one patch at their niche optima. Then, each specialist would produce 80 offspring while the generalist would produce 16 offspring. Given that the dispersal rate was the same for all individuals, the specialists would have 5 times more dispersers than the generalist despite the fact that each of these species dominated a single patch each. As such, the specialist species would have a probability 5 times greater to successfully disperse to any given patch despite having the same per capita dispersal capacity. Moreover, if these two patches were equally connected, the specialist would exclude the generalist even if the specialist could not produce a single offspring in the generalist's patch. This would not be the case if dispersal occurred after selection, in which case both species would have equal dispersers, and both species would continue to dominate in their optimal patches.

## APPENDIX IV - MODEL ASSUMPTIONS AND DECISIONS

Like every simulation model, ours relies on a series of simplifications and assumptions about ecological processes. For instance, some parameters were held constant across patches (e.g., carrying capacity, disturbance rate) or across species (e.g., dispersal rate, maximum reproductive rate), while they ought to vary in natural communities. Yet, allowing these parameters to vary within a simulation would generate noise in the results, as well as unfair advantages if not coupled with appropriate trade-offs (e.g., there is no drawback in having a higher maximum reproductive rate). Also, our study considers a single environmental variable, which is a simplification of the ecological reality. In addition, we assumed dispersal to be isotropic (i.e., dispersal in every direction is equiprobable) and dispersers to be naïve (i.e., dispersers do not decide where they go) and future models could be used to investigate these more complex dispersal behaviours. However, here, we wish to further discuss some decisions that have not or rarely been made by previous metacommunity models (e.g., Loreau and Mouquet 1999, Amarasekare and Nisbet 2001, Mouquet and Loreau 2003, Büchi et al. 2009, North et al. 2011, Büchi and Vuilleumier 2012, Büchi and Vuilleumier 2014, Henriques-Silva et al. 2015).

First, our simulation framework relies on the relative local competitive ability to determine species' reproductive rates, thus assuming that only interspecific competition decrease reproductive success. As such, in the absence of interspecific competition, a species would always numerically increase (up to carrying capacity) regardless of difference between niche optima and the patch's environmental value. While this assumption could have benefited early immigrants following a disturbance as they could reproduce in a patch despite the environment value being well out of their niche given the absence of absence of competition, it would take four generations or more for a single individual to reach half of the carrying capacity as reproductive rate was capped at 5 ( $r_{max}$ ), by which time competitors would likely have immigrated, thus limiting if not stopping population growth. Therefore, this process would have very low impact on the overall metacommunity dynamics, especially given that disturbance was rather rare (i.e., expected to occur once every hundredth generations). Moreover, alternatives to implement a generalist-specialist fitness trade-off also have their limits. For instance, some studies have used the species Gaussian response to environment (eq. 4) to determine reproductive rate, and then bring the community to carrying capacity by selecting juveniles randomly (Büchi et

al. 2009, Büchi and Vuilleumier 2012, 2014). Although this would seem like a fair trade-off between specialists and generalists as the area under the curve is constant, a reproductive rate smaller than one converges toward extinction in absence of immigration, which would likely favour specialists given that they have a lesser proportion of their niche where reproductive rate is lower than one, thus questioning the equitability of such trade-off. Moreover, in total absence of competition (inter and intraspecific; i.e., infinite carrying capacity) specialists would rise to much larger abundances, as reproduction rate is compounded over multiple generations. As such, the area under the curve of reproduction rate in function of the environmental values is only constant for reproduction rate of one generation but is not for the compounded reproduction rate of multiple. Consequently, despite our assumption being a simplification of ecological reality, it seems to be a fairer trade-off than its alternatives, at least in the context of our study. In addition, change in species abundances over an environmental gradient is often mediated by competition rather than by negative effect of abiotic factor of species demography per se (see Kraft et al. (2015), and Cadotte and Tucker 2017), thus providing some basis to our assumption.

Second, given that environmental homogeneity and heterogeneity are respectively recognized as major driver of species specialization and generalization (Futuyma and Moreno 1988, Van Tienderen 1991, Brown and Pavlovic 1992), assuming complete local homogeneity is unreasonable when specialization level is part your study object. As such, we decided to implement a small level of environmental heterogeneity to avoid local domination by specialists and allow for niche partitioning, as described in the *Reproductive phase* section. Also, by doing so, generalist species can thrive on portions on local environment that was not used by the specialist (see Fig. 2). While previous simulation studies (Büchi et al. 2009, Büchi and Vuilleumier 2012, 2014) that assumed complete local homogeneity reported rapid loss of generalist at the beginning of the simulation as each patch was dominated by a single specialist, we only recorded extinction of generalist in highly structured landscape (see *Diversity patterns* section for more details). Despite being the exception rather than the norm in metacommunity model, including local heterogeneity in the model definitely improve the realism in the context of our study.

Third, dispersal mortality was implemented as a function of environmental values of patches visited during dispersal and species niche (eq. 2). As such, dispersal mortality was consistent with the species niche. Yet, whether or not species have similar environmental

tolerance when they disperse than when they compete to thrive in a patch probably depends on the ecology of the species considered, but we assumed that it is for simplicity. However, despite dispersal mortality being consistent with species niche, we implicitly assume the strength of dispersal mortality. Indeed, equation 2 could be rewritten as:

$$\delta_s = e^{\theta \frac{-(E_i - \mu_j)^2}{2s_j}} \quad (\text{eq. S8})$$

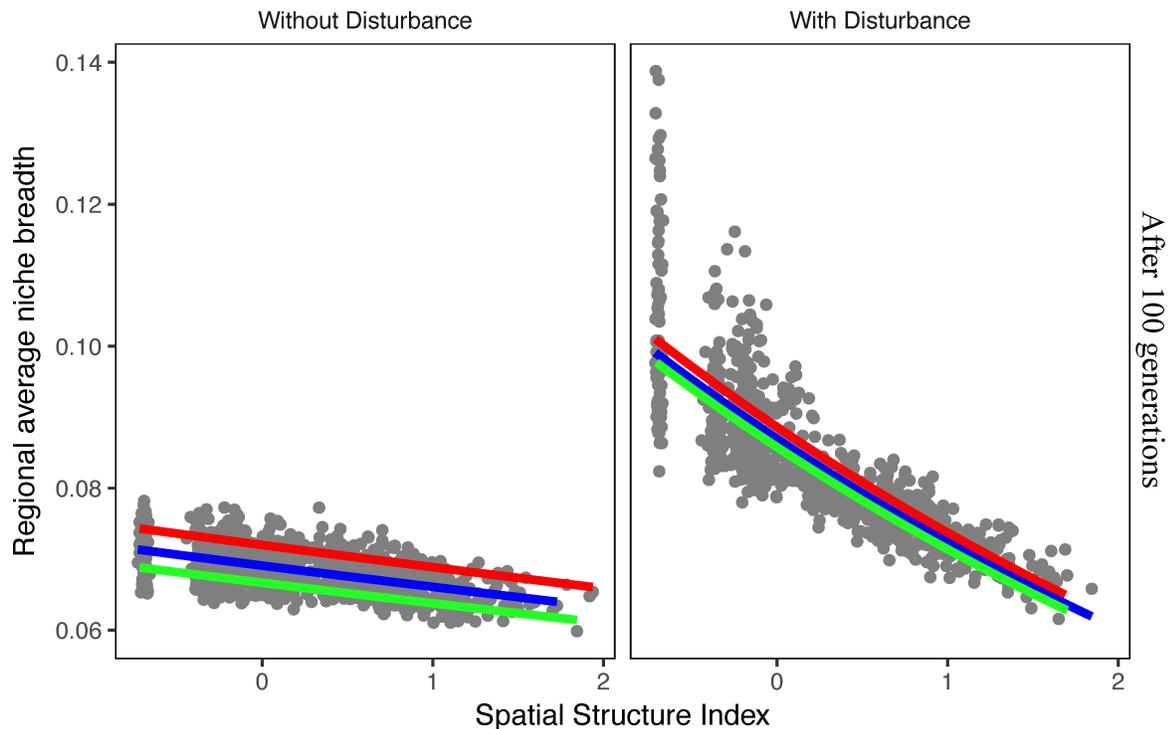
where  $\theta$  is the strength of dispersal mortality. As such, in our study we assume  $\theta$  to be 1, but this value is as arbitrary as any. In absence of dispersal mortality,  $\theta$  would take the value of zero as in previous studies (i.e., Snyder and Chesson 2003, Snyder 2008, Büchi et al. 2009, Büchi and Vuilleumier 2012, Bar-Massada et al. 2014, Büchi and Vuilleumier 2014). Though we did not explicitly examined how this parameter would impact the results of our study, we can infer that lower strength of dispersal mortality values would advantage specialists as it would alleviate their dispersal limitations without compromising their competitive advantage. Conversely, increased strength of dispersal mortality values would further impair specialists' dispersal abilities, thus advantaging generalists. Nonetheless, given that dispersal rate had no impact on the spatial structure of environment's effect as it only changed the intercept of the models, we are confident that change in the strength of dispersal mortality would not change our conclusion qualitatively although we would expect it to change the magnitude of the effect of the spatial structure of environment, with greater magnitude at stronger dispersal mortality. Even in absence of dispersal mortality, the spatial structure of environmental variable should have an impact, because connectivity between patches is not only hampered by dispersal mortality, but also by distance between patches. Still, future research should investigate how the strength of dispersal mortality affects our general conclusion that the spatial structure of the environment mediates coexistence via a change in connectivity between environmentally similar patches.

## APPENDIX V – RESULTS FROM PREVIOUS GENERATIONS

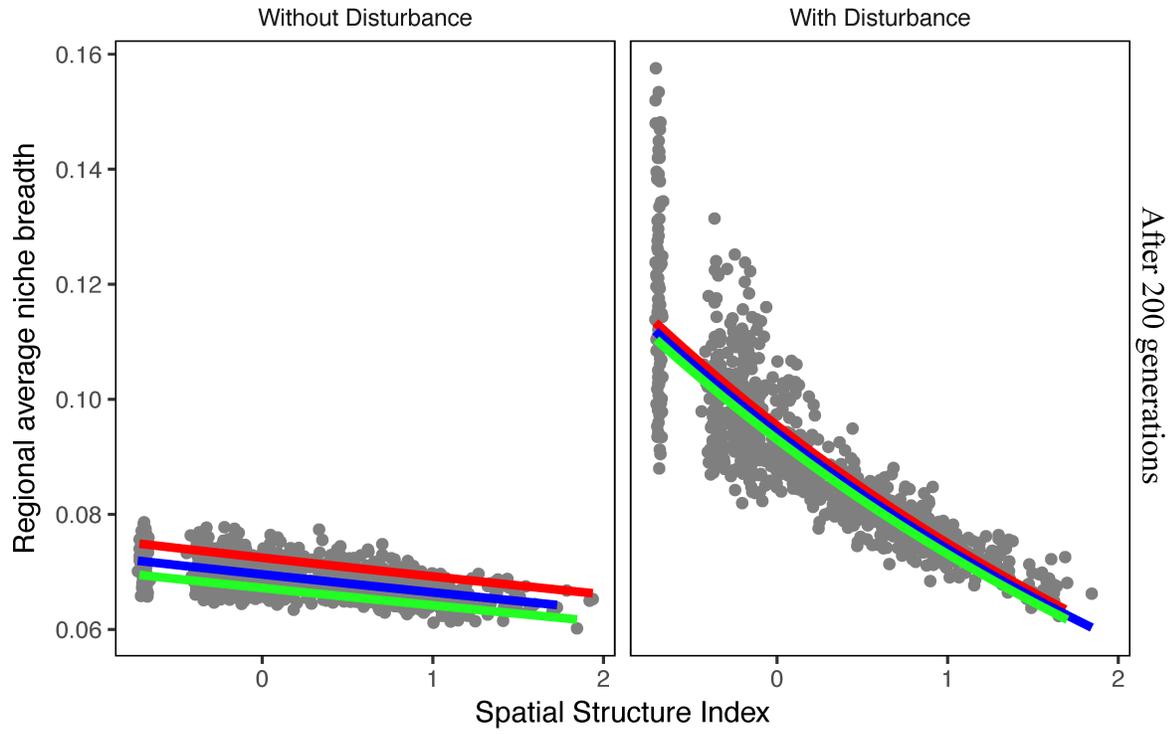
### Specialization

Here we present the analog of Fig. 4 for 100<sup>th</sup>, 200<sup>th</sup>, 300<sup>th</sup>, and 400<sup>th</sup>. The following legend, which is a copy of Fig. 4's legend, applies equally to the subsequent figures.

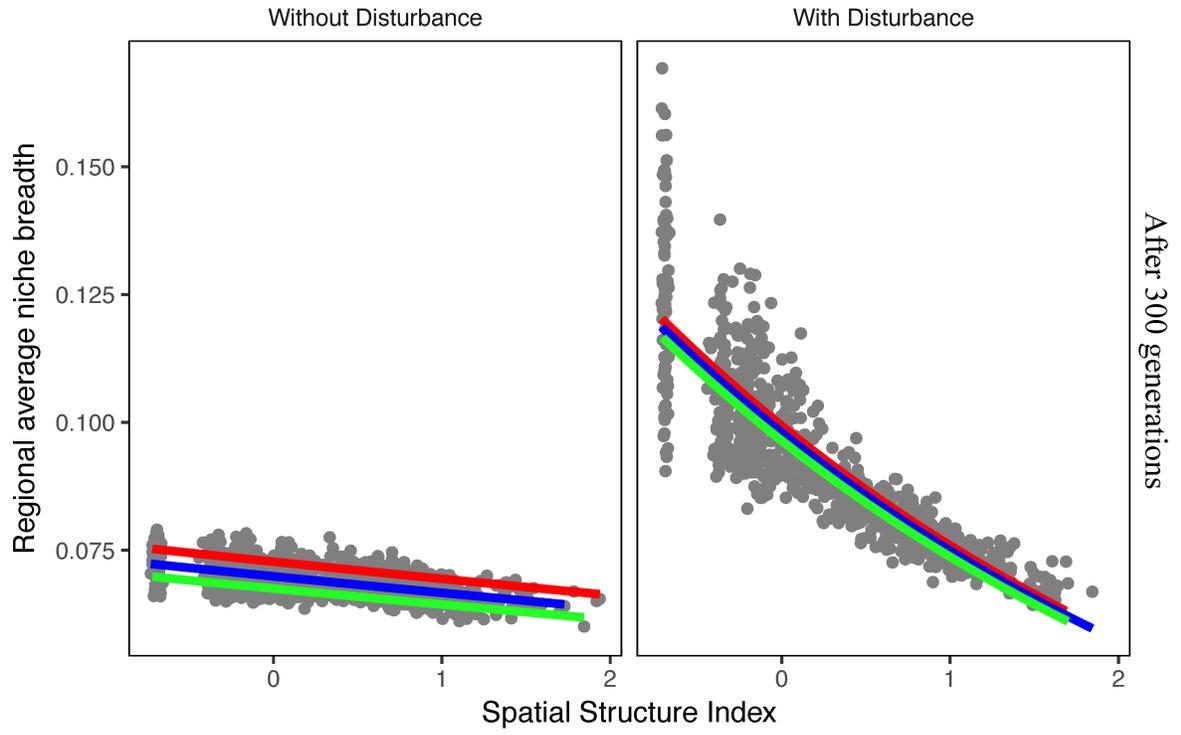
**Figure S1a-d: Niche breadth (specialization) as a function of the spatial structure of the environment (*SSI*) with and without disturbance.** Each point (in grey) represents the regional (metacommunity) mean niche breadth of one simulation as a function of the landscape *SSI*. Larger values of *SSI* are associated with stronger spatial structure (greater ranges and stronger autocorrelations). Small values of average niche breadth indicate greater specialization. The line represents the fitted model for each level of dispersal rate. Low, medium, and high dispersal ( $\delta = \{0.1, 0.25; 0.5\}$ ) are represented in red, blue, and green, respectively.



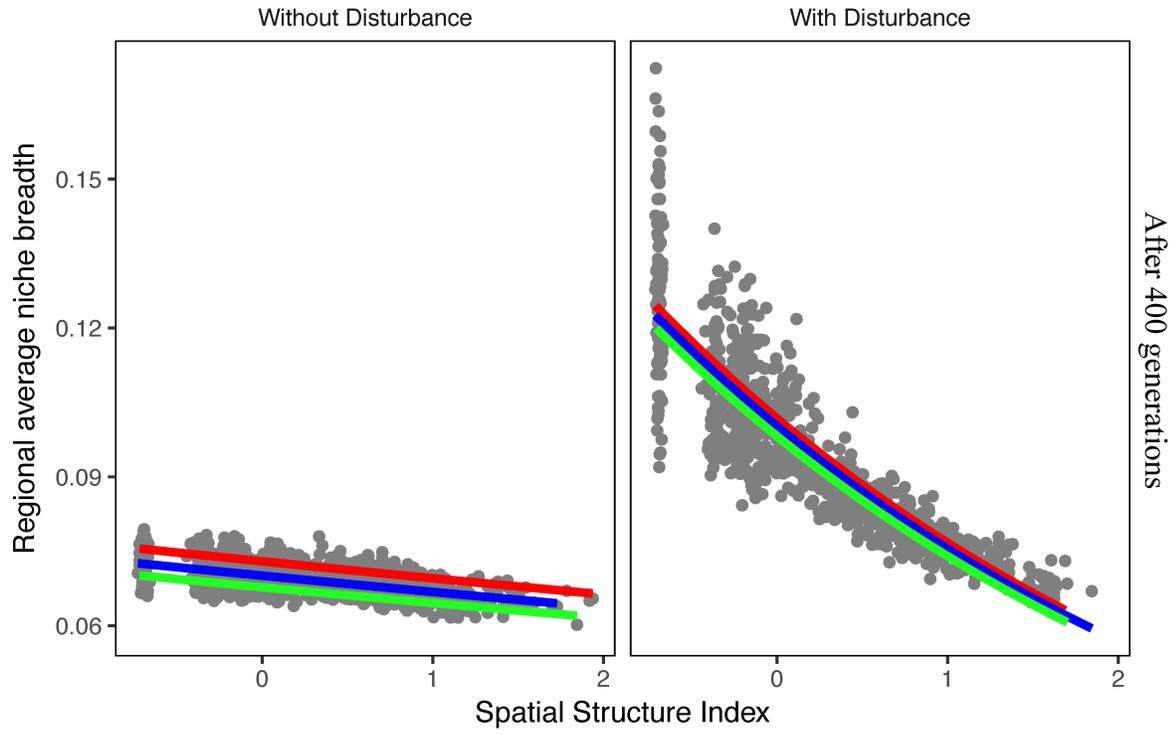
**Figure S1a**



**Figure S1b**



**Figure S1c**

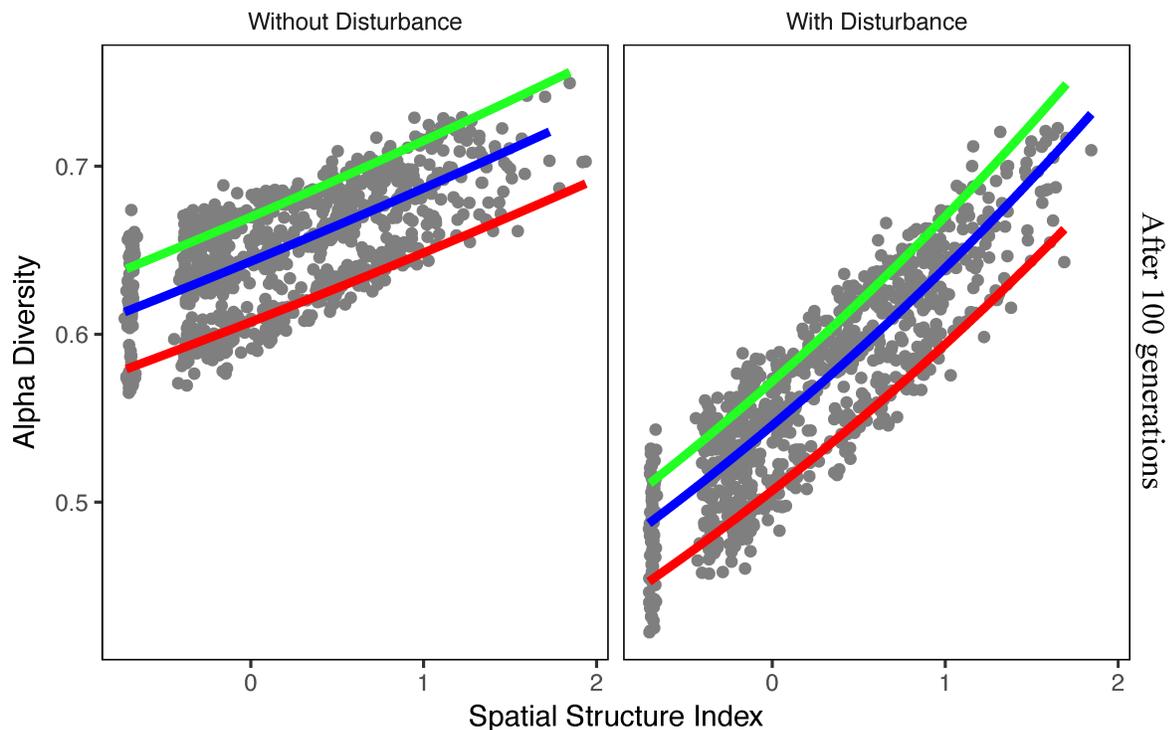


**Figure S1d**

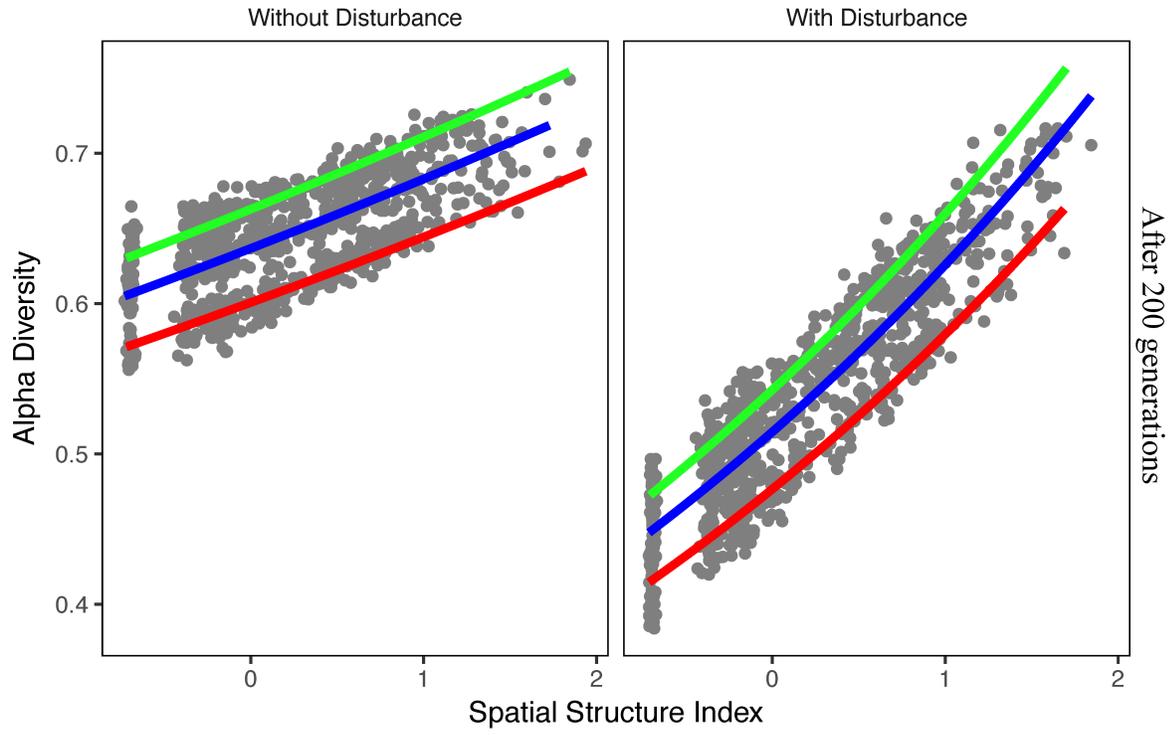
## Alpha diversity

Here we present the analog of Fig. 5 for 100<sup>th</sup>, 200<sup>th</sup>, 300<sup>th</sup>, and 400<sup>th</sup>. The following legend, which is a copy of Fig. 5's legend, applies equally to the subsequent figures.

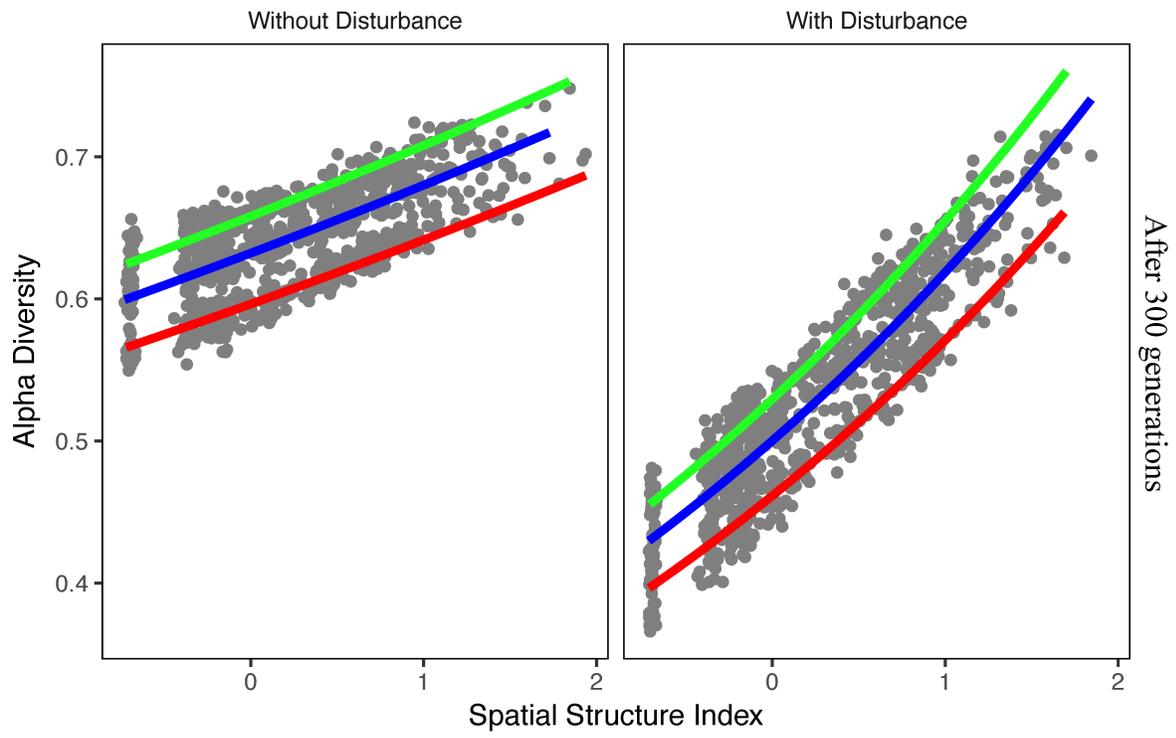
**Figure S2a-d: Alpha diversity as a function of the spatial structure of the environment (*SSI*) with and without disturbance.** Each point (in grey) represents the regional (metacommunity) alpha diversity of each simulation (900 per panel) as a function of the *SSI* of its landscape. Larger values of *SSI* are associated with stronger spatial structure (greater ranges and stronger autocorrelations). Large values of alpha diversity indicate greater local species coexistence. The line represents the fitted model for each level of dispersal rate. Low, medium, and high dispersal rate ( $\delta = \{0.1, 0.25; 0.5\}$ ) are in red, blue, and green, respectively.



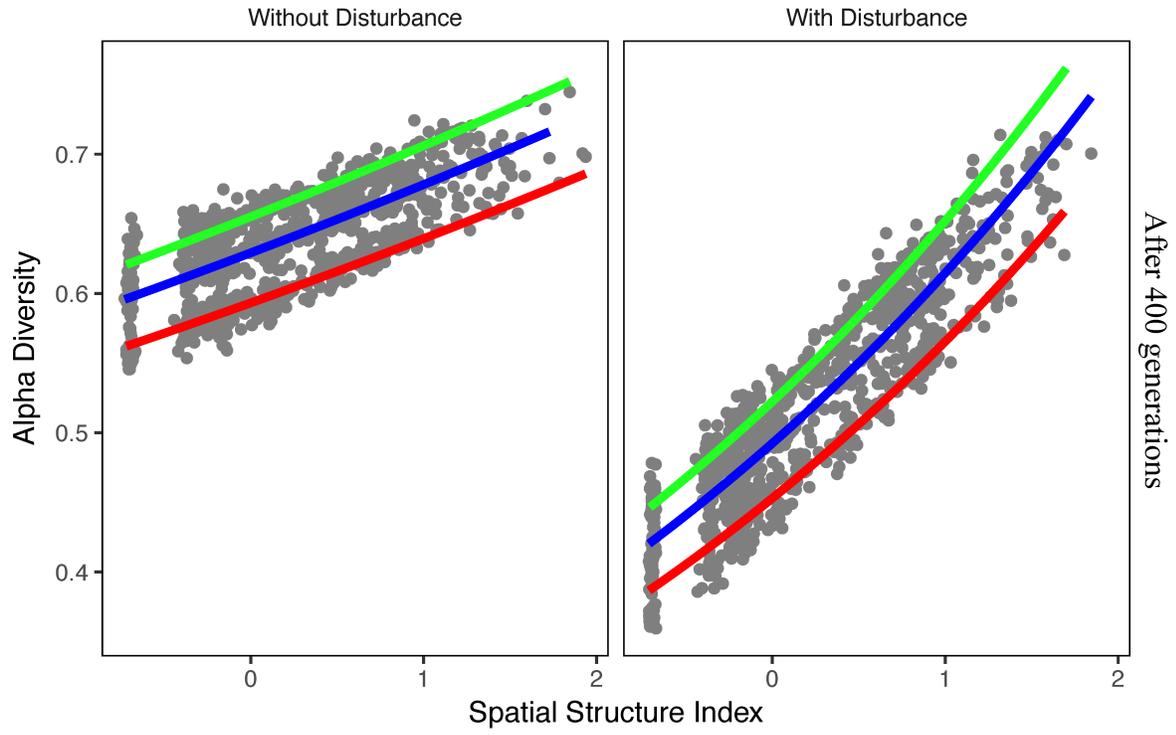
**Figure S2a**



**Figure S2b**



**Figure S2c**



**Figure S2d**

## Beta diversity

Here we present the analog of Fig. 6 for 100<sup>th</sup>, 200<sup>th</sup>, 300<sup>th</sup>, and 400<sup>th</sup>. The following legend, which is a copy of Fig. 6's legend, applies equally to the subsequent figures.

**Figure S3a-d: Beta diversity as a function of the spatial structure of the environment (*SSI*) with and without disturbance.** Each point (in grey) represents the regional (metacommunity) beta diversity of each simulation (900 per panel) as a function of the *SSI* of its landscape. Larger values of *SSI* are associated with stronger spatial structure (greater ranges and stronger autocorrelations). Large values of beta diversity indicate greater changes among local communities. The line represents the fitted model for each level of dispersal rate. Low, medium, and high dispersal rate ( $\delta = \{0.1, 0.25; 0.5\}$ ) are in red, blue, and green, respectively.

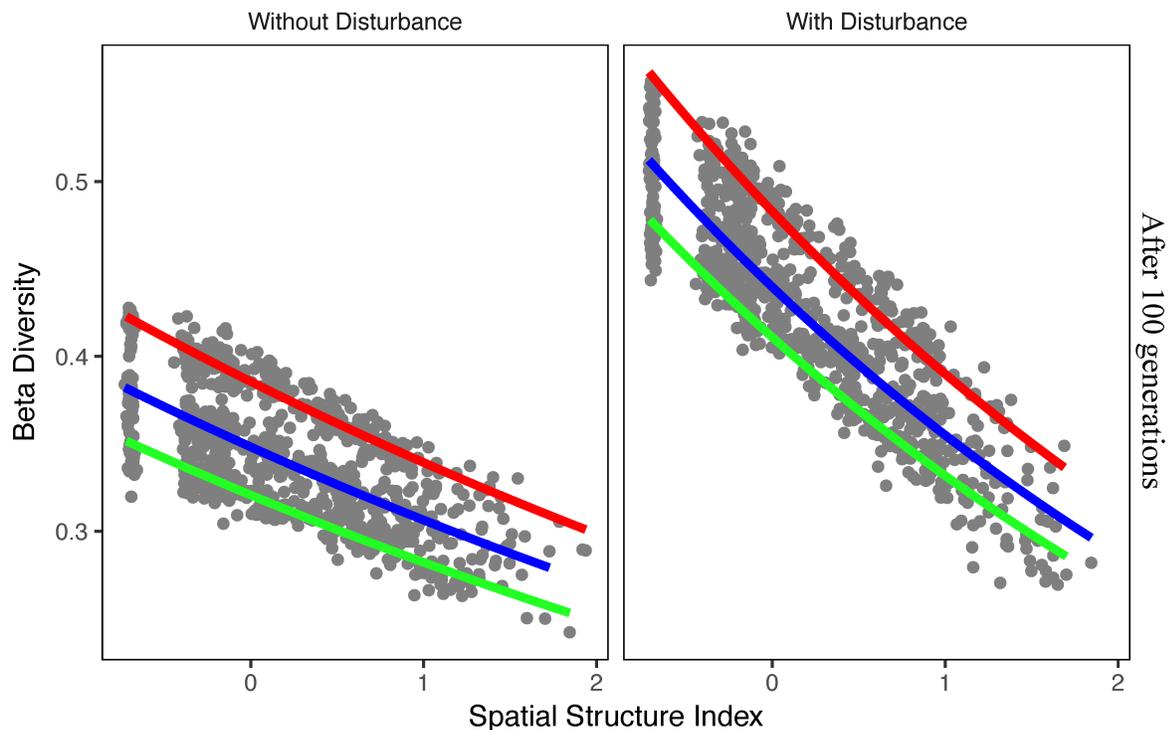
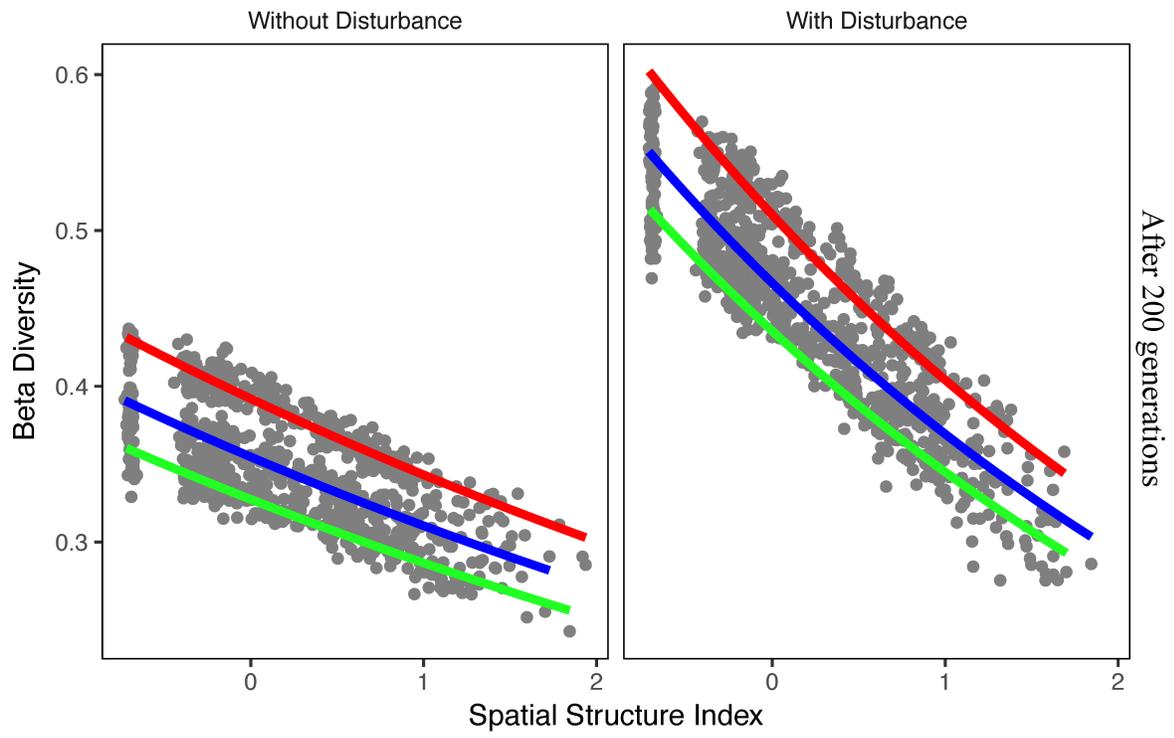
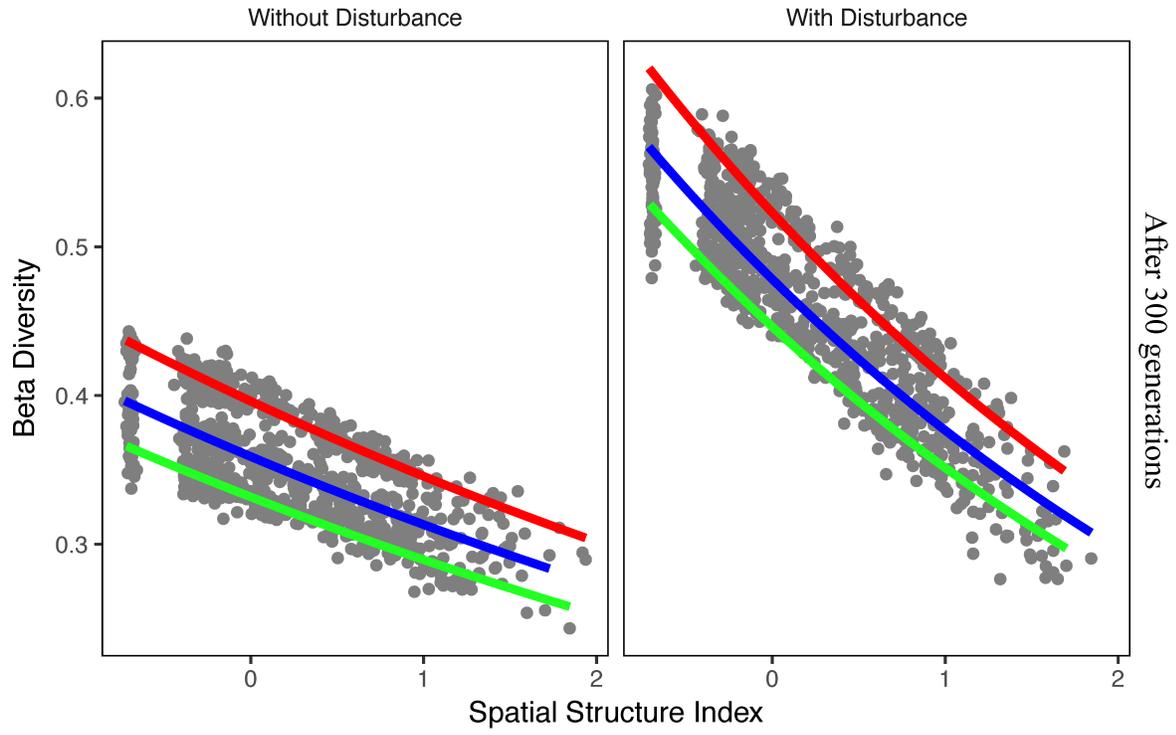


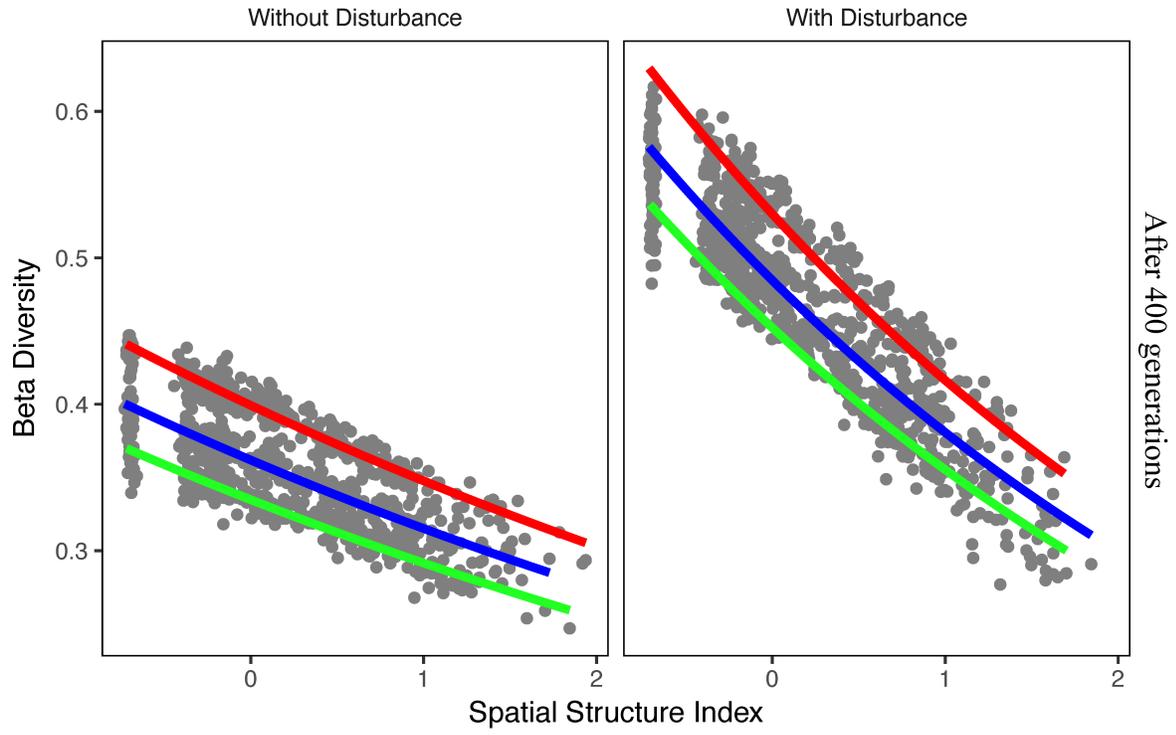
Figure S3a



**Figure S3b**



**Figure S3c**

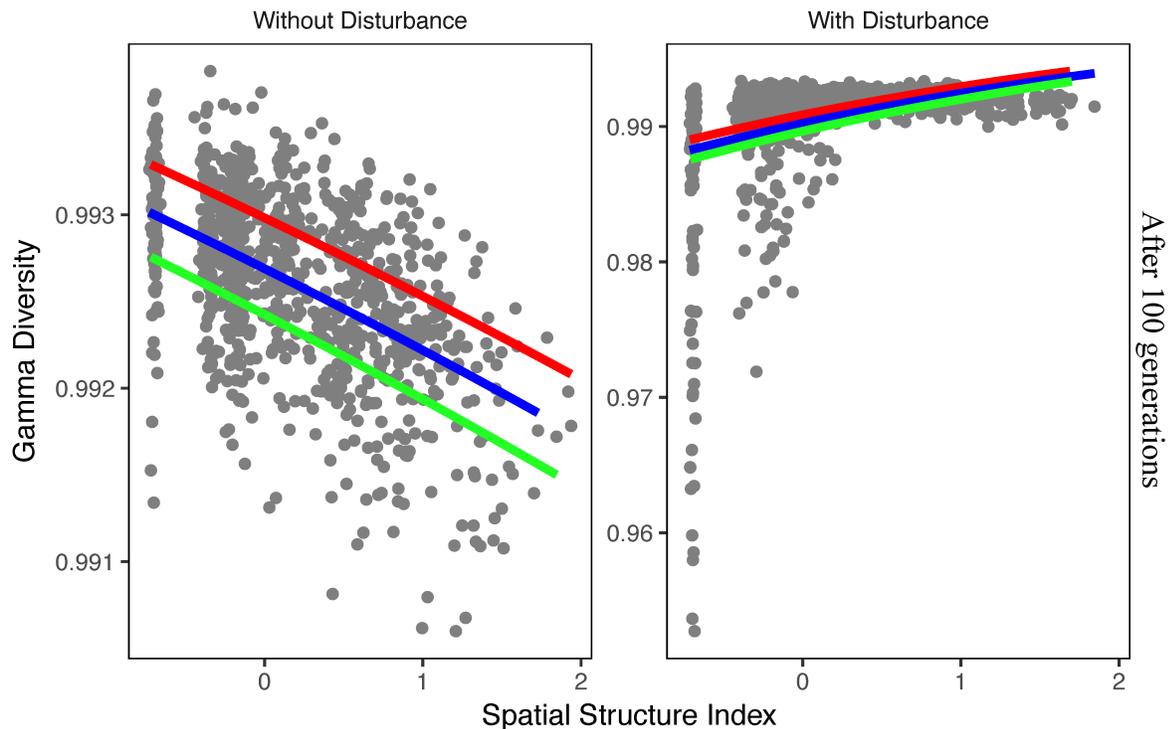


**Figure S3d**

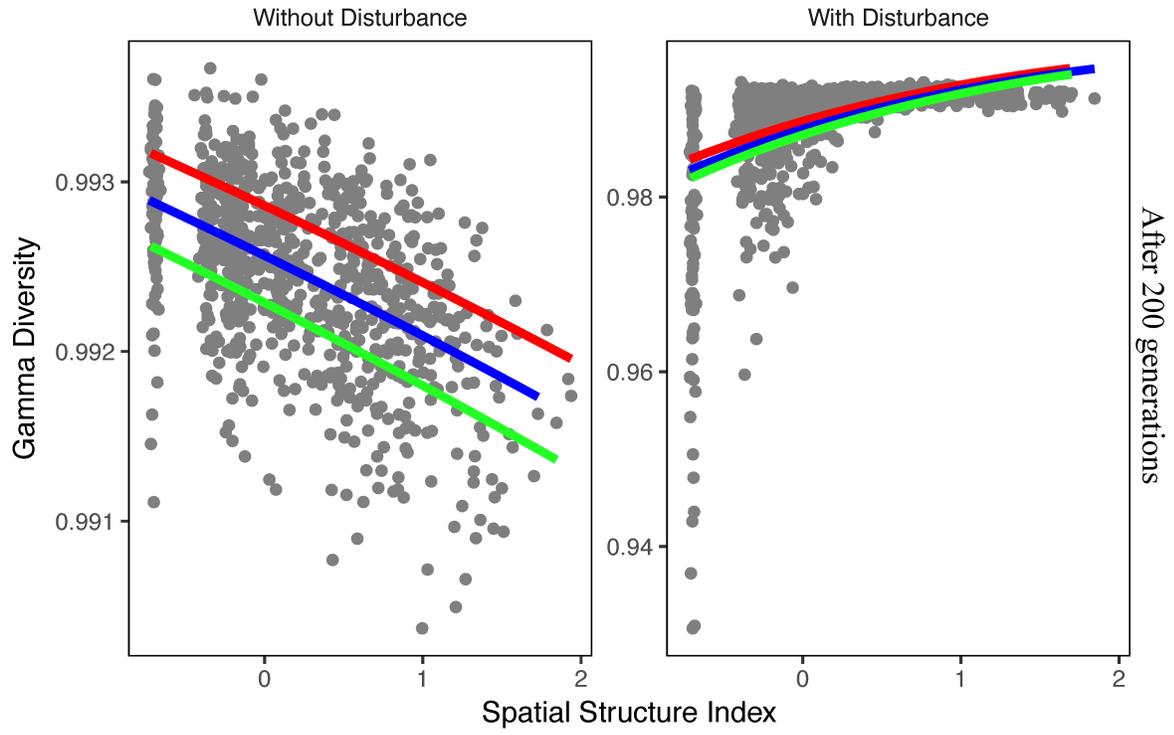
## Gamma diversity

Here we present the analog of Fig. 7 for 100<sup>th</sup>, 200<sup>th</sup>, 300<sup>th</sup>, and 400<sup>th</sup>. The following legend, which is a copy of Fig. 7's legend, applies equally to the subsequent figures.

**Figure S4a-d: Gamma diversity as a function of the spatial structure of the environment (SSI) with and without disturbance.** Note that the Y-axes are on different scale. Each point (in grey) represents the regional (metacommunity) gamma diversity of each simulation (900 per panel) as a function of the SSI of its landscape. Larger values of SSI are associated with stronger spatial structure (greater ranges and stronger autocorrelations). Large values of gamma diversity indicate greater regional species coexistence. The line represents the fitted model for each level of dispersal rate. Low, medium, and high dispersal rate ( $\delta = \{0.1, 0.25; 0.5\}$ ) are in red, blue, and green, respectively.



**Figure S4a**



**Figure S4b**

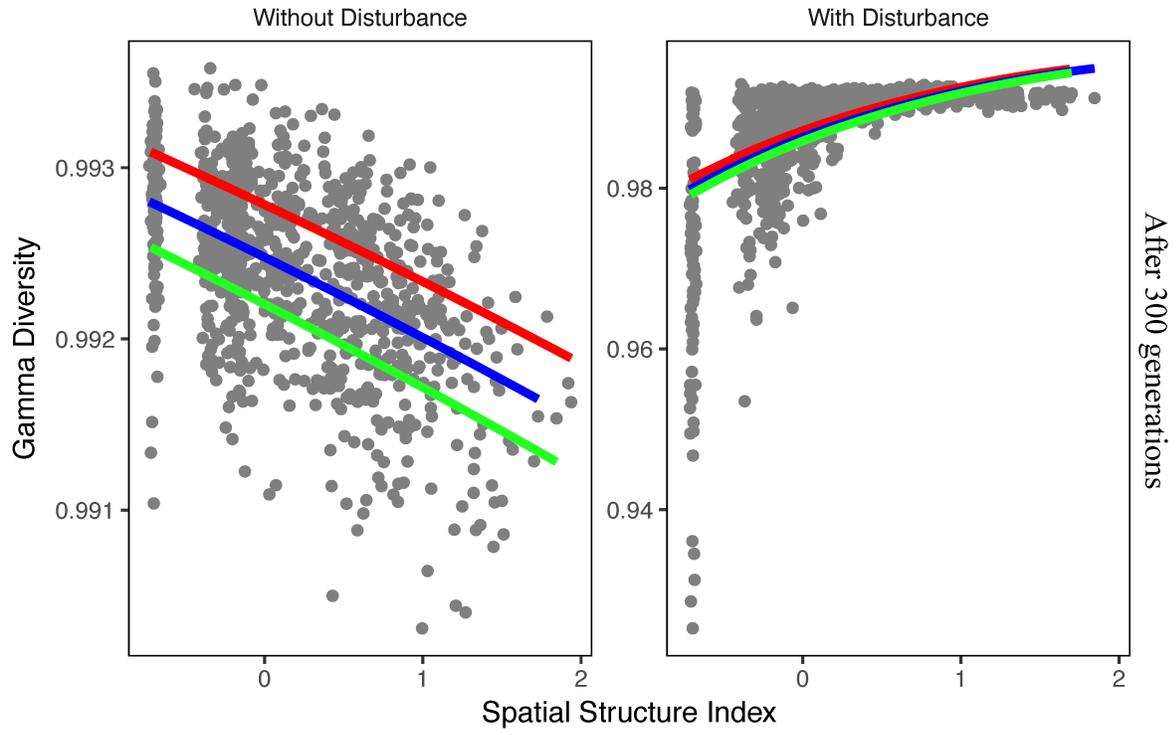
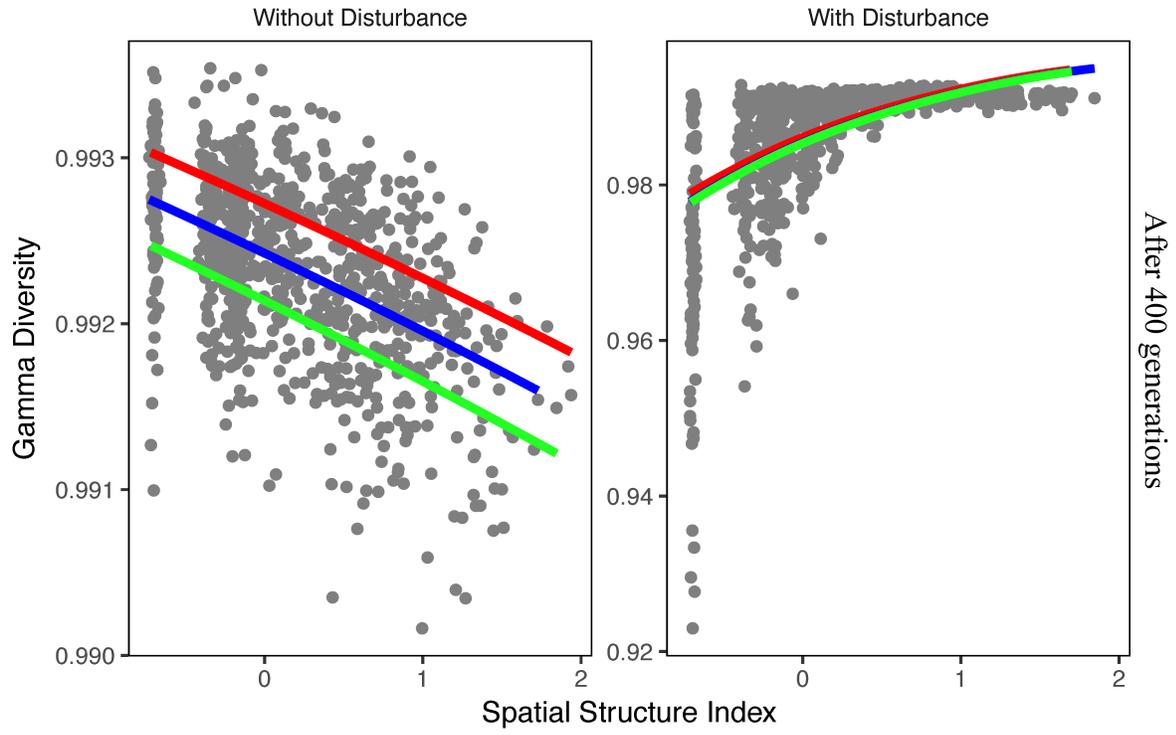


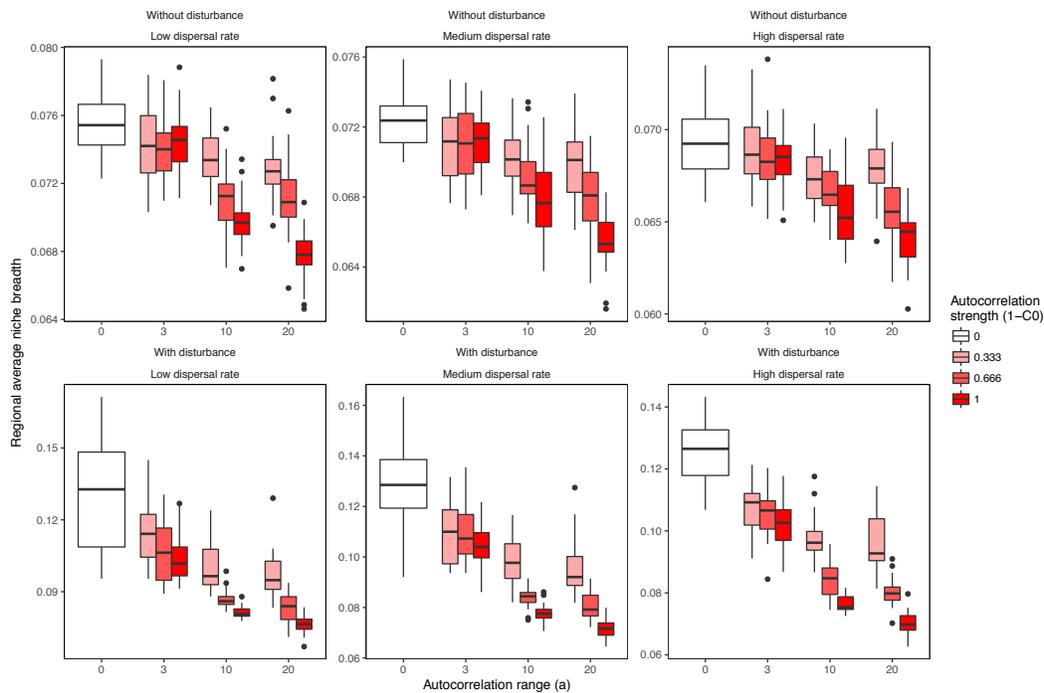
Figure S4c



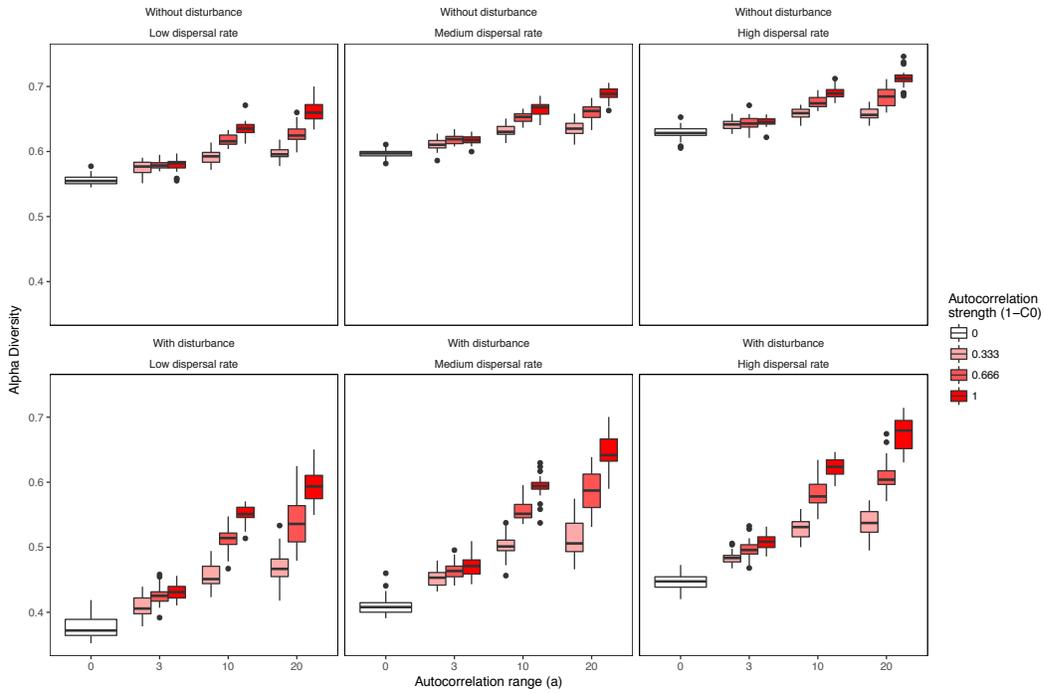
**Figure S4d**

## APPENDIX VI – RESULTS (BOXPLOT) AS A FUNCTION OF THE TEN DIFFERENT LANDSCAPES

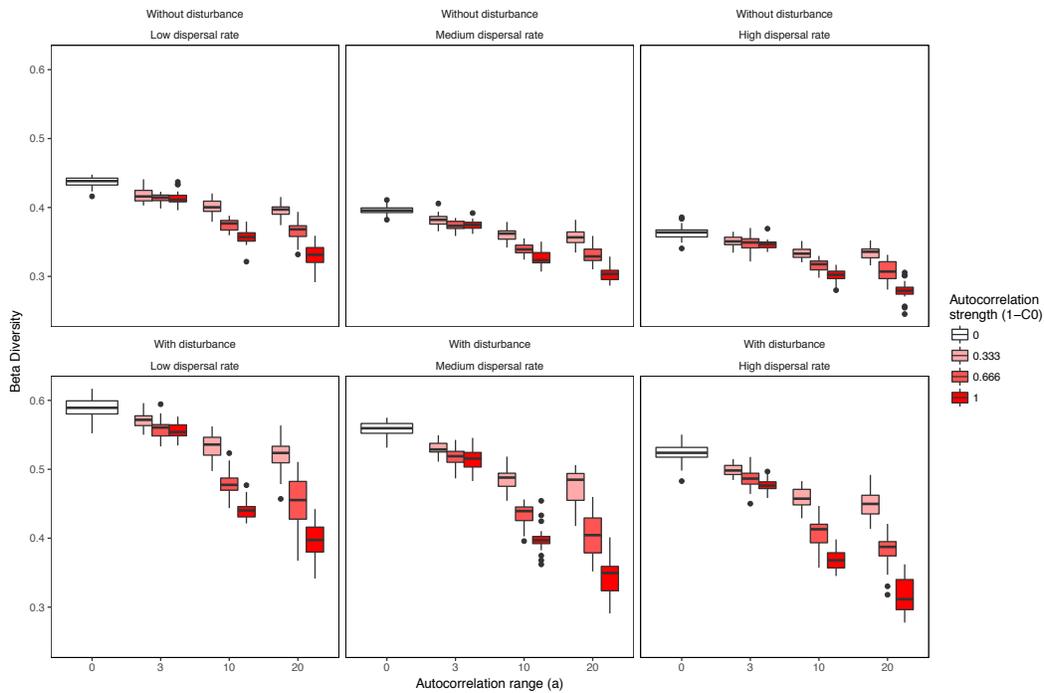
Here, we present the same results as in Figs. 4-7, but as a function of the ten different combinations of variogram parameters (i.e., spatial structure) instead of the spatial structure index (*SSI*). For each figure, the response variable is identified on the y-axis, while the scenario is identified over the panel. The range of autocorrelation ( $\alpha$ ) is on the x-axis, and levels of autocorrelation strengths ( $1 - C_0$ ) are nested within the levels of autocorrelation range. Note that for regional average niche breadth and for gamma diversity, the y-axis changes scale as it would otherwise be impossible to appreciate the differences.



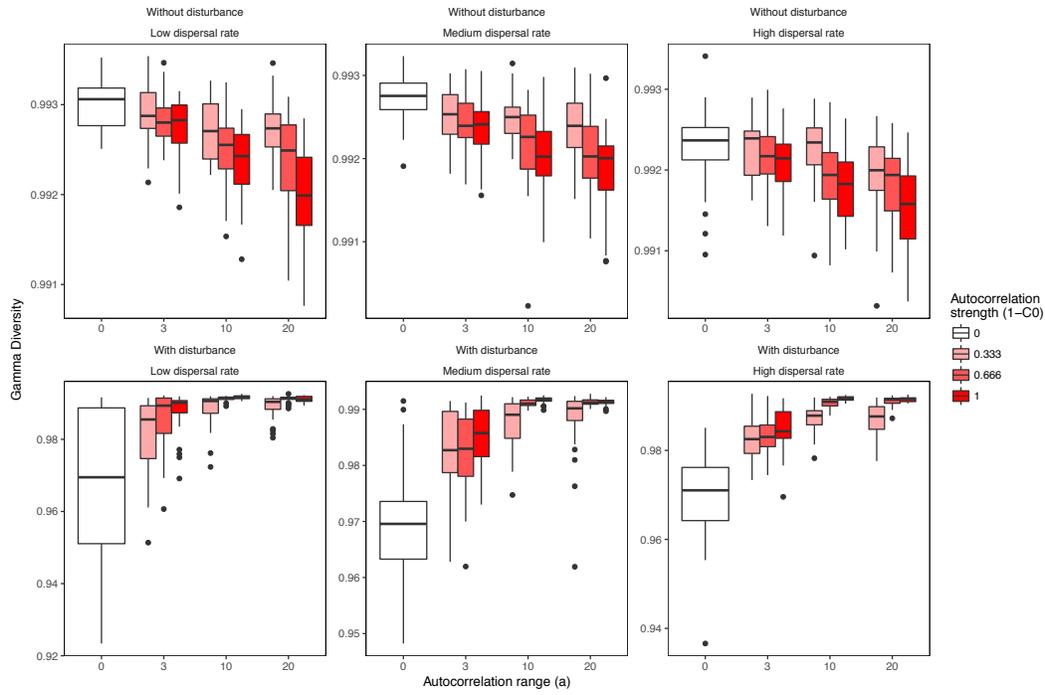
**Figure S5: Niche breadth (specialization) as a function of the spatial structure**



**Figure S6: Alpha diversity as a function of the spatial structure**



**Figure S7: Beta diversity as a function of the spatial structure**



**Figure S8: Gamma diversity as a function of the spatial structure**

## APPENDIX VII – COEFFICIENTS OF THE GLM

Here we present a table with the coefficients of each GLM. Note that the parameter for “Dispersal 0.1” is included in the intercept of the model.

**Table S1: Coefficients of the GLM**

<b>Response variable</b>	<b>Disturbance regime</b>	<b>Intercept</b>	<b><i>SSI</i></b>	<b>Dispersal 0.25</b>	<b>Dispersal 0.5</b>
Specialization	Undisturbed	-2.62	-0.05	-0.04	-0.07
	Disturbed	-2.28	-0.29	-0.02	-0.04
Alpha diversity	Undisturbed	-0.52	0.08	0.06	0.1
	Disturbed	-0.8	0.23	0.08	0.14
Beta diversity	Undisturbed	-0.92	-0.14	-0.1	-0.17
	Disturbed	-0.63	-0.24	-0.09	-0.16
Gamma diversity	Undisturbed	-4.92	0.06	0.04	0.08
	Disturbed	-4.25	-0.6	0.04	0.04