

Linking intrinsic scales of ecological processes to characteristic scales of biodiversity and functioning patterns

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Keywords: ~~biomass production~~ [spatial patterns](#), landscape structure, local vs. regional scales, species-area relationships, ~~trophic interactions~~ [dispersal](#)

Abstract

Ecology is a science of scale, which guides our description of both ecological processes and patterns, but we lack a systematic understanding of how process scale and pattern scale are connected. Recent calls for a synthesis between population ecology, community ecology, and ecosystem ecology motivate the integration of phenomena at multiple levels of organization. Furthermore, many studies leave out the scaling of a critical process: species interactions, which may be non-local through ~~mobility or vectors (resources or species) movement or foraging~~ and must be distinguished from dispersal scales. Here, we use simulations to explore the consequences of [three](#) different process scales (~~i.e.~~ species interactions, dispersal, and the environment) on emergent patterns of biodiversity, ecosystem functioning, and their relationship, in a spatially-explicit landscape [and stable equilibrium setting](#). A major result of our study is that the spatial scales of dispersal and species interactions have opposite effects: a larger dispersal scale homogenizes spatial biomass patterns, while a larger interaction scale amplifies their heterogeneity. ~~We find that an interesting interplay between process scales occurs when the spatial distribution of species is heterogeneous at large scales, i.e., when the environment is not too uniform and dispersal not very strong.~~ Interestingly, the specific scale at which ~~scales of dispersal and interactions~~ [dispersal and interaction scales](#) begin to influence landscape patterns depends on the ~~environmental heterogeneity of the landscape scale of environmental heterogeneity~~ – in other words, the scale of one process allows important scales to emerge in other processes. [This interplay between process scales, i.e., a situation where no single process dominates, can only occur when the environment is heterogeneous and the scale of dispersal small.](#) Finally, contrary to our expectations, we observe that the spatial scale of ecological processes is more clearly reflected in landscape patterns (~~i.e.~~ distribution of local outcomes) than in global patterns such as Species-Area Relationships or large-scale biodiversity-functioning relationships. [Overall we conclude that long-range interactions often act differently and even in opposite ways to dispersal, and that the landscape patterns that emerge from the interplay of long-ranged interactions, dispersal and environmental heterogeneity are not well captured by often-used metrics like the Species-Area Relationship.](#)

Introduction

Scale is fundamental to ecology, from the spatial and temporal scales at which we observe and manage ecosystems [1, 2, 3] to the intrinsic scales at which processes occur within and across ecosystems [4]. Much of current research efforts describe ecological patterns across scales, such as ~~species-area or biodiversity-ecosystem functioning~~ [Species-Area or Biodiversity-Ecosystem Functioning](#) relationships [5, 3]. However, the scaling of ecological patterns is largely phenomenological – we can describe how patterns scale but not why [6, 5]. Although links between scales of patterns and processes have been explored in recent years [7, 8, 9], as we will discuss, a systematic and unified treatment of scale in ecology is incomplete. ~~Thus, a~~ [A](#) critical question remains: how is the scaling of ecological patterns,

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58 such as patterns of biodiversity and ecosystem functioning, ~~related to~~ generated by scales
59 of specific processes, and why?

60 In answering this question, a crucial process is often overlooked: the spatial scale of
61 species interactions. While dispersal and environmental variation are often understood to
62 operate at various spatial scales, existing research generally assumes that species only inter-
63 act locally [10, 11, 12] ~~—(although exceptions exist, e.g., studies using multi-layer networks~~
64 ~~to link interaction networks at local scales to their realization at the global scale [13, 14]).~~
65 Yet many species move, forage, or otherwise interact with each other at a range of spatial
66 scales ~~[15][16, 17]~~, even in the absence of ~~population fluxes (dispersal)~~ dispersal. A simple
67 distinction is that dispersing species establish new “home” ranges when they move across
68 the environment, while mobile species always return to their “home” range. Many move
69 daily across multiple habitat types ~~(e.g., such as seabirds connecting marine and terrestrial~~
70 ~~ecosystems), for some species even at scales which exceed dispersal (e.g., salmon returning~~
71 ~~to their natal streams)~~ — [16], or predatory insects moving between different habitats in
72 the landscape [17]. Non-local competition ~~arises can therefore arise~~ from foraging across
73 multiple localities ~~[15]~~. Additionally, species interact indirectly across long distances via
74 intermediary species, (e.g., plants interacting indirectly via pollinators or herbivores), and
75 many such intermediary interactions are not explicitly studied, thus being best represented
76 by long range interactions. As a result, scales of species interactions, such as compe-
77 tition, likely have consequences for population persistence, affecting the spatial distribu-
78 tion of biodiversity and ecosystem functioning in ways that are distinct from other process
79 scales [18, 19].

80 How do the spatial scales of dispersal, environmental heterogeneity, and species inter-
81 actions interactively influence ecological patterns? Answering this question is unlikely to
82 be achieved via observational studies, as different combinations of ecological processes may
83 generate identical patterns, but computational models can explore patterns that emerge as
84 processes interact across scales. Indeed, the scale of dispersal relative to the environment
85 has been studied most extensively, in particular within a metacommunity context [20, 7, 21].
86 These studies generally find that high rates of dispersal blur differences between local com-
87 munities, leading to losses of biodiversity and ecosystem functioning. Although there are
88 reasons to expect increased scales of dispersal and species interactions to have similar conse-
89 quences, as both processes are influenced by ~~some~~ many of the same variables (e.g., animal
90 mobility) and serve to spread out the effects of species interactions, there are also reasons
91 to expect the opposite [22]. A key difference is that large dispersal scales can allow popu-
92 lations to permeate through whole landscapes over a few generations, whereas individuals
93 with large interaction scales are still bound to specific localities. As a result, increasing
94 scales of interactions may amplify spatial heterogeneity in an ecological system [23], counter
95 to the blurring effect of larger dispersal scales.

96 In addition to scales of species interactions, we will address an additional major gap
97 which ~~is preventing prevents~~ a complete knowledge of scaling in ecology: consideration
98 of a wider range of ecological patterns within a single study than has been examined
99 previously. Two well-recognized ecological patterns are ~~species-area~~ Species-Area (SAR)
100 and ~~biodiversity-ecosystem functioning~~ Biodiversity-Ecosystem Functioning (BEF) relation-
101 ships. The ~~species-area~~ Species-Area relationship is the earliest and most widely-examined
102 ecological pattern to explicitly consider scale [5, 24]. Although SARs have been described
103 as one of “ecology’s few universal regularities” [25], accumulating evidence reveals consid-
104 erable variation within and among biological systems [26, 5, 27]. Likewise, BEF theory has
105 revealed consistent patterns, typically a saturating relationship between community diver-
106 sity and biomass production [28], but most work has focused on BEFs at local scales, with
107 only recent work highlighting the importance of scale [3]. Previous studies have examined
108 how one pattern or the other are affected by process scales [29, 27, 30], but no study has
109 examined how SAR and BEF relationships change in tandem and if effects that are masked
110 through one pattern are apparent ~~through in~~ the other. As a consequence, it is unclear
111 how both SAR and BEF relationships are affected by the interplay of processes acting at
112 different scales, making it difficult to assess how process scales affect the overall behavior of
113 ecosystems as different measures highlight different aspects of ecosystems. These Resolving
114 these issues will be useful ~~to resolve, as they link for both~~ basic and applied biodiversity
115 problems, for ~~the preservation of productive, biodiverse landscapes instance allowing us to~~
116 scale up to landscape scales our predictions of biodiversity loss and its effect of ecosystem
117 productivity, that are often based on local scales [31].

118 Here, we use a modified Lotka-Volterra metacommunity model to explore the conse-
119 quences of the scaling of ecological processes for biodiversity, ecosystem functioning, and
120 their relationship across spatial scales. Our simulations consist of species interacting in a
121 spatially-explicit landscape, with “patches” emerging from the environmental structure
122 of the landscape. Although metacommunities tend to be modelled as systems of discrete
123 patches embedded within an inhospitable matrix, Chase and Leibold [32] describe this

124 approach as useful (easing computation and interpretation) but limited – they foreshadow a
 125 “coming” in ecology in favour of models that allow “patches” to emerge from the structure
 126 of the environment, which our model achieves. We first study the heterogeneity of local
 127 outcomes across the landscape: patterns of patch biodiversity, patch functioning, and rela-
 128 tionships between them (local BEF). We can then scale up to the whole landscape scale and
 129 every scale in between. By varying the spatial scales over which metacommunity processes
 130 (abiotic environment, competitive interactions, and dispersal) play out, we test the hypoth-
 131 esis that ecological patterns depend on how processes interact across scales, including scales
 132 of species interactions, and lead to different patterns from those generated by commonly-
 133 assumed hierarchical process scales (i.e., scales of interactions < environment < dispersal;
 134 Fig. 1).

135 Species-Area relationships depend on spatial turnover in species composition, and com-
 136 positional turnover is driven by ecological processes [33]. Thus, we would expect that
 137 ecological processes should strengthen SARs in scenarios where they increase compositional
 138 turnover. We predict that the strongest slopes of the SAR will occur when scales of dis-
 139 persal < environment < species interactions, because (i) interactions are not constrained to
 140 abiotically suitable patches, and (ii) weaker dispersal prevents the homogenization of species
 141 composition across the landscape. Additionally, we predict that the consequences for BEF
 142 relationships will differ between local and regional scales. On local scales, we expect BEFs
 143 to weaken as interaction scales increase relative to the others, given that species that are
 144 locally absent but present in nearby areas can affect local functionfunctioning. On regional
 145 scales, we expect BEFs to strengthen as interaction scales increase, since regional competi-
 146 tion would only-keep-keep only the most suitable species at a given location, and hence,
 147 Hence, more species would mean that multiple species are productive within a given region.

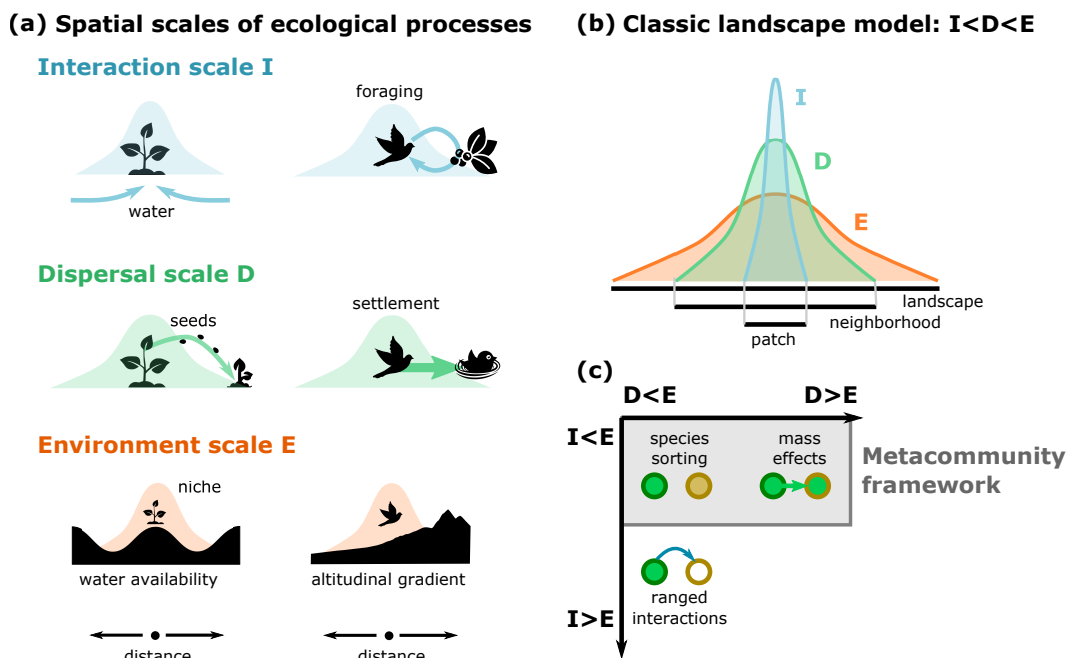


Figure 1: **Conceptual diagram of spatial scales of ecological processes.** (a) Illustration of the spatial scale of species interactions I , dispersal D and environmental heterogeneity E relative to the total size of the landscape (i.e., width of curves). (b) In the classic scenario, interactions take place within a patch, while dispersal is thought to act within a neighborhood and environmental factors vary broadly over the landscape. (c) Comparison of ecological scenarios along scales of I , D and E . Yellow and green represent two different species, with circle and its rim representing the resident species and the favoured species, respectively. Metacommunity theory has explored different scenarios for the relative scales of dispersal and environment (i.e., the ratio D/E), notably distinguishing “species sorting” (local environmental factors determine species distribution at the landscape scale) and “mass effects” (population fluxes homogenize the landscape). Our work adds highlights the relative importance of species interactions scale (e.g., expressed through the ratio I/E , which was previously considered only in particular ecological settings (e.g., vegetation patterns or territoriality). Ranged interactions may for instance induce exclusion of weaker competitors in a neighboring patch, even without a population flux of a stronger competitor into that patch.

148 Methods

149 Model

150 We use a modified Lotka-Volterra metacommunity model to explore the consequences of the
151 spatial scaling of three ecological processes – abiotic environment, species interactions, and
152 dispersal – for biodiversity and ecosystem functioning. Our specific assumptions and param-
153 eters are motivated by two important choices. First, we focus on a classic setting of ecological
154 assembly, i.e., the patterns that arise when many species, originating from a regional pool,
155 come together and reach an equilibrium state, with some species going locally or regionally
156 extinct. Furthermore, we take species interactions in the pool to be disordered, that is, het-
157 erogeneous but without a particular functional group or trophic level structure [34]. We do
158 not exclude that different patterns could emerge for more ordered interactions (e.g., a realis-
159 tic food web), or for parameter values that lead to a more complex dynamical regime regimes
160 (e.g., population cycles or chaos, driven by stronger species interactions or environmental
161 perturbations). We note that our communities, in the chosen parameter regime of moderate
162 competition, contain many species in a stable equilibrium (i.e., due to the assembly process).
163 Our methodology thus differs from the extensive literature that has considered models with
164 random interactions in order to study stability-complexity relationships [35], including more
165 recent works in a spatial context [36, 37], as we rather focus on the abundance and diversity
166 patterns arising from community assembly.

167 Second, we consider the possibility of species interacting over large spatial scales. Con-
168 ventional metacommunity models describe discrete local communities of habitat patches
169 connected by dispersal, within which species interact [38]. In doing so, they implicitly
170 assume that the spatial range of species interaction is smaller than the scale of dispersal
171 and contained within a patch, for all species and types of interactions [18]. To relax these
172 assumptions, we construct a metacommunity model where populations of species can dis-
173 perse and interact at different spatial scales, without specifying the a mechanism underlying
174 these ecological processes. Species interactions that manifest beyond local scales are ab-
175 stracted from mechanisms such as individual foraging, vector species (e.g., pathogens) [39],
176 and spatial resource fluxes [40, 18].

177 The model details the dynamics of S different species in a community distributed across a
178 spatially-explicit lattice landscape of 320x320 cells. The dynamical equation for the biomass
179 N_i of species i at position \vec{x} in the landscape at time t is given by a generalized Lotka-Volterra
180 equation of the form

$$\frac{\partial}{\partial t} N_i(\vec{x}, t) = N_i(\vec{x}, t) \left(r_i(\vec{x}) + \sum_j^S \int d\vec{y} A_{ij}(\vec{x}, \vec{y}) N_j(\vec{y}, t) \right) + \delta_i \Delta N_i(\vec{x}, t) \quad (1)$$

181 where \vec{x} and \vec{y} represent vectors of spatial (x, y) coordinates in the landscape. Equation
182 (1) models the effects of three ecological processes on the abundance-biomass of species i :
183 its intrinsic growth rate $r_i(\vec{x})$, which is influenced by abiotic environmental conditions at
184 location \vec{x} , dispersal to and from location \vec{x} , which is controlled by the diffusion coefficient
185 δ_i , and interactions with all other species j , including when they are located elsewhere
186 in the landscape, $A_{ij}(\vec{x}, \vec{y})$. Although at face value cells in our model resemble patches in
187 traditional metacommunity models, given that discrete populations are necessary to simulate
188 Lotka-Volterra dynamics, here it is best to interpret cells as neighborhoods on a landscape.
189 Each neighborhood may take on a unique environmental value and hold unique densities of
190 individuals of different species. Viewed in this way, landscape dynamics can be simulated
191 more continuously, with the numerical limitation of needing to discretize dynamics at their
192 finest resolution. While “patches” can emerge in autocorrelated environments (i.e., a spatial
193 clustering of cells that are suitable to a given species), our model is also generalizable to
194 landscapes with a diversity of environmental structures.

195 Environment

196 Abiotic conditions in each location are encoded by an environmental variable $V(\vec{x})$. This
197 variable is continuous and varies smoothly over space, with parameters allowing one to tune
198 the typical spatial scale of this variation [41]. For more details on the construction of the
199 environment, see the Appendix section A2.

200 Each species has a Gaussian fundamental niche that determines its abiotic fitness in each
201 location, with an optimal environmental value H_i and abiotic niche width ω_i

$$f_i(\vec{x}) = \exp \left[-\frac{(V(\vec{x}) - H_i)^2}{2\omega_i^2} \right] \quad (2)$$

202 Each fitness value is bound between 0 and 1 and reaches its maximum at an optimal envi-
203 ronmental condition (i.e., when $V(\vec{x}) = H_i$). We take the growth rate as $r_i(\vec{x}) = f_i(\vec{x})$. In

204 other words, $V(\vec{x})$ sets the actual structure of environmental conditions across the landscape,
 205 whereas $r_i(\vec{x})$ is how species experience the environment and its structure.

206 Interactions

207 We choose to limit ourselves to competitive interactions, defined by the matrix C_{ij} , which
 208 represents the per-capita competitive effect of species j on species i . The diagonal of the
 209 matrix (the impact of a species on itself) is set to 1, whereas all other interactions are
 210 taken independently from a random uniform distribution between 0 and \tilde{c} . We choose $\tilde{c} = 1$
 211 to allow for moderate interactions between different species (inter-specific competition is
 212 always weaker than intra-specific), suggesting that pairwise coexistence is often possible
 213 for species with different growth rates r_i , but the total impact of many competitors is
 214 still strong enough to allow for extinctions. Previous work has shown that, in disordered
 215 communities, the outcomes of ecological assembly are robust to many details such as the
 216 nature of interactions (e.g., mutualism, predation), and depend only on a few statistical
 217 properties such as the mean and variance of interaction effects [34].

218 Furthermore, interactions are assumed to occur over a characteristic spatial scale encoded
 219 by a spatial kernel K . This scale may represent the distance an animal forages from its nest
 220 (without establishing a new nest), the scale at which trees gather resources with their roots,
 221 or the effective distance an immobile species interacts with its neighbors via an intermediary
 222 species (where the intermediary is not explicitly modeled). We use a Gaussian kernel whose
 223 standard deviation defines the interaction range such that

$$K(\vec{x}, \vec{y}|\gamma) = k_0 \exp\left[-\frac{\|\vec{x} - \vec{y}\|^2}{2\gamma^2}\right] \quad (3)$$

224 where $\|\vec{x} - \vec{y}\|$ indicates the norm of (distance between) the vectors \vec{x} and \vec{y} , and γ is the
 225 spatial range (scale) of the interactions. We note that while this modeling strategy is not
 226 physical as it implies that interactions occur instantaneously across distances, this is not
 227 expected to bias our results since we are focusing on the equilibrium state of the system,
 228 where hypothetical lag effects should be minimal.

229 We normalize the interactions by k_0 such that the overall effect of the kernel is always
 230 the same (i.e., the integral over K always equals 1). This normalization means that for large-
 231 scale interactions, local competition becomes weaker. However, some amount of (especially
 232 intra-specific) competition must remain locally strong to prevent species densities from
 233 growing exponentially and exploding. Therefore, we define interactions as partially local
 234 and partially regional, with β governing the fraction of interactions that are regional:

$$A_{ij}(\vec{x}, \vec{y}) = -\beta C_{ij} K(\vec{x}, \vec{y}|\gamma) - (1 - \beta) C_{ij}. \quad (4)$$

235 We choose β to ensure that the effect of interactions changes with ~~their spatial scale (see~~
 236 ~~scales subsection below)~~, but local competition is never negligible ~~(see more details in the~~
 237 ~~Appendix, Fig. S12).~~

238 Dispersal

239 Finally, dispersal is modeled by the diffusion (Laplace) operator,

$$\delta_i \Delta N_i(\vec{x}, t), \quad (5)$$

240 where δ_i is the diffusion or dispersal coefficient of the species. For simplicity, we set the
 241 dispersal coefficient to be the same for all species.

242 Contrary to interactions, we do not use an explicit spatial kernel here, because intensity
 243 and spatial scale are unavoidably entangled in the case of dispersal (see **Discussion**). ~~Thus,~~
 244 ~~as will be seen, the Appendix section A1).~~ The coefficient δ_i sets the spatial scale over
 245 which dispersal impacts ecological dynamics. ~~We note~~ Note that two aspects of our modeling
 246 choices mean that our choice of dispersal by diffusion ~~will not be~~ is not qualitatively different
 247 from applying a large dispersal kernel: our focus on the equilibrium state, and having initial
 248 conditions where all species are introduced to every point in the landscape. The former
 249 aspect of equilibrium means that any potential non-equilibrium dynamics driven by species
 250 moving quickly across space due to a large dispersal kernels ~~do not apply~~ are not applicable.
 251 The latter aspect means that there is no ~~dispersal limitation~~ limit to dispersal, i.e., a short
 252 or long-ranged dispersal kernel does not affect which parts of the landscape can be reached
 253 by a species.

254 Scales

255 In this study we are concerned with spatial scales of three ecological processes:

- 256 1. E : environmental heterogeneity
- 257 2. D : dispersal
- 258 3. I : species interactions

259 To properly compare the interplay of different process scales, we must first compute
 260 their values for a given set of model parameters (Table 1). The scale of the environment
 261 ~~(spatial autocorrelation) is controlled by two parameters~~ combines two features often used in
 262 ~~the literature to generate realistic, spatially-autocorrelated landscapes [42]:~~ spectral color
 263 ~~ρ and~~, which indicates the relative importance of long-range and short-range variations
 264 ~~in the environment, and spectral cutoff k_c ,~~ which indicates the finest grain of variation
 265 ~~(Appendix section A2). The effective environmental scale E is controlled by these two~~
 266 ~~parameters.~~

267 In the main text, we focus on a single value for the environment scale $E = 32$, and vary
 268 the other two scales on a logarithmic scale, with values of 1, 3.2, 10, 32 and 100, where the
 269 system itself has the scale (length) of 320 ~~cells. Our distribution of I and D are equally~~
 270 ~~spaced along a log scale and allow us to have a clear separation between the scales of each~~
 271 ~~ecological process, while also being substantially smaller than the system size (320 cells)~~
 272 ~~and larger than the smallest scale in the system (1 cell). Details on the construction of the~~
 273 ~~environment are given in the Appendix section A2. We choose a value of $E = 32$ specifically~~
 274 ~~as it is the most straightforward to demonstrate our results (see Appendix section A3 for~~
 275 ~~other values). See the Appendix for calculations and discussion of other values of E .~~ The
 276 scale of interactions is set by, and coincides with, the width of the Gaussian kernel γ , such
 277 that $I = \gamma$. The scale of dispersal is mainly determined by the diffusion coefficient δ_i ,
 278 and it is expected to scale as $D \sim \sqrt{\delta_i}$ (see, e.g., [43]). The normalization constant is,
 279 however, not trivial, and as we show in the Appendix [section A1](#), it is approximately 10.
 280 We therefore use: $D = 10\sqrt{\delta_i}$. ~~Fixing the environmental scale and varying the scale of~~
 281 ~~interactions and dispersal allows us to isolate the effects of interaction and dispersal scale~~
 282 ~~without confounding the effects of different landscape structures or differences between~~
 283 ~~species.~~

284 Parameterization and simulations

285 To initialize our simulations, we first add environmental structure to a two-dimensional
 286 landscape of size 320x320 ~~cells~~ (see the Appendix [section A2](#) for details). We do not define
 287 patches explicitly, but rather allow them to emerge from the spatial structure of the envi-
 288 ronment. ~~We then seed $S = 20$ species are initially seeded~~ onto the landscape, with initial
 289 ~~abundances-biomass~~ at each location drawn from a uniform distribution between 0 and 1,
 290 resulting in roughly equal ~~abundances-biomasses~~ at the landscape scale. For simplicity, we
 291 use periodic boundary conditions for the two-dimensional system (i.e., a torus topology),
 292 for both dispersal and interactions. We do not expect this choice to impact the results, due
 293 to the large size of the system considered.

294 We use 20 replicate landscapes, allowing environmental structure to vary among repli-
 295 cates while keeping the environmental scale constant (~~$E = 32$, see Appendix for other values~~
 296 ~~).~~ ~~Each replicate.~~ ~~Replicates with other values of environmental scale are presented in~~
 297 ~~the Appendix section A3. Each landscape replicate uses a different set of species and their~~
 298 ~~interactions, chosen at random. Each replicate~~ landscape was used to systematically vary
 299 the spatial scale of interactions I and dispersal coefficient D . ~~Doing so allows us to isolate the~~
 300 ~~effects of interaction and dispersal scales within any one replicate without the confounding~~
 301 ~~effects of different landscape structures. The~~, with 25 different combinations (5 values of D
 302 and 5 values of I , as given in Fig. 2), giving a total of 500 simulations. We ascertain the
 303 generality of our findings ~~are ascertained~~ by comparing across replicates.

304 We run each simulation, where a simulation is defined as a model run with a unique
 305 combination of process scales and replicate landscape, to a maximum time of $T = 1000$, or
 306 until equilibrium is reached. For practical purposes, we define an equilibrium as when the
 307 maximal change in biomass of any species in any location over a time-span of $T = 1$ is less
 308 than 10^{-5} . A full list of parameter values can be found in Table 1. ~~The value of δ_i was~~
 309 ~~changed to control the dispersal scale D , the values of ρ and k_c were changed to control~~
 310 ~~the environment scale E , and the value of γ was changed to control the interaction scale I .~~
 311 ~~Values of I and D were chosen along a logarithmic scale.~~ All simulations were performed
 312 using MatLab 2019a.

313 Measurements

314 For each simulation we measure individual and total community biomass, species richness,
 315 and sample the landscape to calculate ~~species-area relationships~~ [Species-Area Relationships](#)

Parameter	Interpretation	Baseline value [Range]
General		
S	species number	20
L	landscape size (pixels cells) ($area = L^2$)	320
δ_i	dispersal coefficient	[0.01, 100]
Environment		
H_i	optimal environment value	\sim uniform(20, 80)
ω_i	abiotic niche width	\sim normal(10, 2)
ρ	spectral color	0.95
k_c	spectral cutoff	0.04
$K(\vec{x})$	local abiotic conditions	[0, 100]
k_0	normalization constant	-
Interactions		
\tilde{c}	max interaction strength	1.0
β	fraction of regional interactions	0.9
γ	spatial scale of interactions	[1, 100]
C_{ij}	interaction matrix	\sim uniform(0, \tilde{c})

Table 1: Parameters, default values and ranges.

(SAR curves) as well as ~~biodiversity-ecosystem functioning~~ [Biodiversity-Ecosystem Functioning](#) relationships (BEF curves). For species richness, SARs, and BEFs, we define a species to be extinct at a given location if its biomass is below than a threshold of 10^{-3} .

To calculate SAR curves, we ~~use sample at~~ 40 different spatial scales from 1x1 (single ~~pixels~~cells) to 320x320 (the entire landscape) on a logarithmic scale, and computed the species richness at each. For a given scale, we randomly choose 100 locations in the landscape, and sampled a region centered around the location chosen. We averaged over the ~~100 estimates of the species richness~~ [locations](#) to obtain the mean richness value for a given scale.

We calculate both local and regional BEF curves, based on random sampling of the ~~system, on average measuring each pixel one~~ [landscape](#). We do this in a similar way to the SAR curves, ~~but also measure~~ [measuring species richness but also](#) total community biomass. For the local BEF, we use a 1x1 ~~pixel~~ cell area with 102,400 random locations chosen, while for the regional BEF we use an intermediate area of size 10x10 with 1024 locations sampled. ~~Thus, on average, we measure every location in the system once, for~~ [In this way the BEF measurement is done consistently for different region sizes. For](#) both local and regional BEF ~~curves, we measure every cell on average once.~~

A striking ~~pattern we observe~~ [outcome observed](#) in our results ~~are is that~~ spatial patterns of biodiversity and functioning in landscapes ~~that~~ are not well captured by ~~summary variables~~ [landscape summary measures](#), such as SARs. To ~~capture~~ [explain](#) these patterns, we calculate how correlated the biomass is of a given species as distance between sampling locations increases (i.e., ~~'spatial correlation'~~ [spatial correlation](#)), which can be used to quantify the properties of spatial patterns we observe. To calculate species' spatial correlations, we do the following: 1) ~~We we~~ normalize the species' distribution by subtracting its average biomass (taken over the whole system).; 2) ~~We we~~ obtain a correlation map by calculating the convolution of a spatial distribution with itself, using a two-dimensional Fast Fourier Transform.; 3) ~~We we~~ normalize the correlation map by dividing the resulting two-dimensional map by its maximum value (i.e., we set a correlation value of 1 at the origin).; ~~and~~ 4) ~~We we~~ define the one-dimensional correlation function as the average between a vertical and horizontal transects through the correlation map. To define the scale of correlation for a given species, we locate the distance at which the correlation function reaches half its height, i.e., the distance from the origin where its value is the average of the maximum value (which is always 1) and its minimal value (typically around 0). ~~A step-by-step illustration of calculating the spatial correlation is provided in the Appendix. Fig. S13.~~

Results

Local outcomes: functioning and diversity across localities

Our first major result is that, although they can arise from similar biological mechanisms (e.g., individual mobility), dispersal and interaction scales have opposite impacts on biodiversity and functioning patterns across the landscape (Fig. 2 and S9). We start from the

355 case of weakly-connected communities with local interactions where all landscape patterns
 356 result from environmental variation (top-left panel, Fig. 2). Increasing the spatial scale of
 357 dispersal leads to a blurring of total community biomass over the landscape (from left to
 358 right, Fig. 2). In contrast, increasing the scale of species interactions leads to a sharpening
 359 of spatial patterns, amplifying underlying environmental heterogeneity (top to bottom, Fig.
 360 2). The antagonism between these two effects can be seen by the fact that they counteract
 361 each other when increasing both scales at once, leading to similar-looking outcomes (along
 362 the diagonal, Fig. 2), but dispersal eventually wins out – the states along the right column
 363 are virtually identical, whereas the same is not true across the bottom row. Critically, it
 364 is not until the scales of dispersal or interactions exceed the scale of environmental hetero-
 365 geneity (i.e., outside the dashed-lined boundary in Fig. 2) that the scale of either process
 366 significantly alters spatial patterns in biomass (see also Fig. S4). Larger emergent scales
 367 of total community biomass due to high D , and the opposite due to high I , can also be
 368 seen in Fig. 5, which shows how quickly patterns among locations become dissimilar as the
 369 distances between them increase.

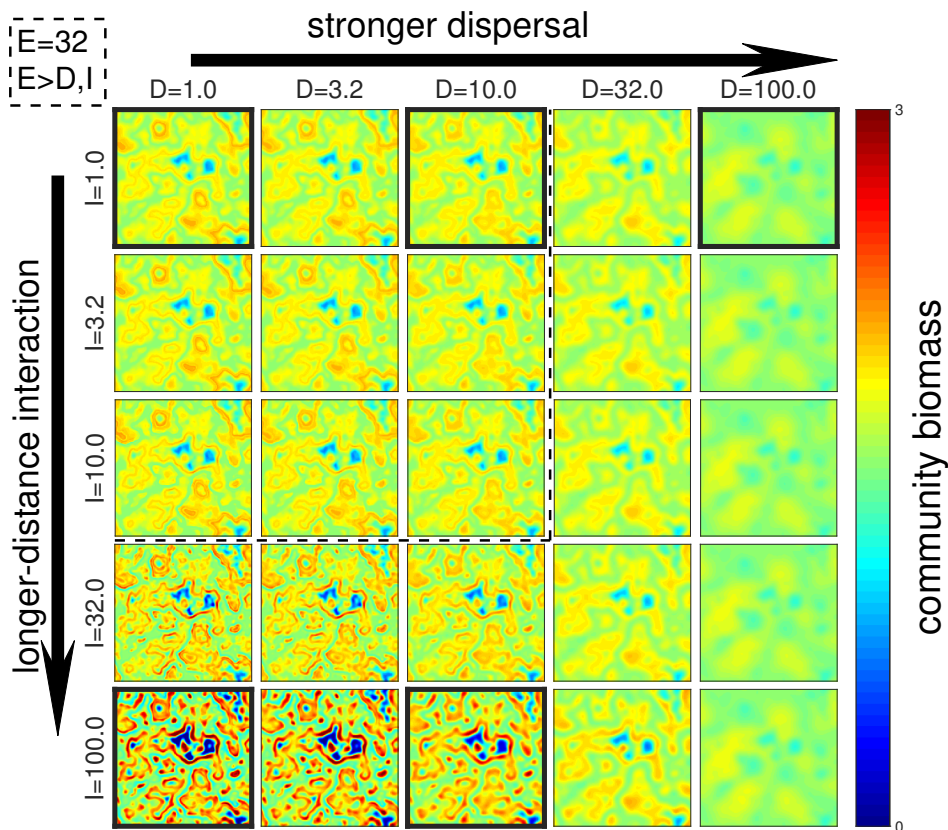


Figure 2: **Distribution of total community biomass** across the landscape as we change dispersal D (columns) and interaction I (rows) scales. Dashed black line shows where the environment scale $E = 32$ is larger than both D and I . Black frames around panels designate parameter values that we further examine in other figures. For better legibility, biomass levels above 3 are not shown.

370 We then focus on a subset of our scenarios above to show how process scales impact not
 371 only total biomass but also individual species distributions (Fig. 3). We observe that in-
 372 creasing dispersal scale predictably makes larger, more coherent domains (i.e., fairly defined
 373 areas with similar characteristics) with typically higher local diversity. Increasing interaction
 374 scale creates a more granular landscape with a broader range of diversities, including many
 375 low-diversity patches and a few high-diversity ones. Indeed, large interaction scales lead to
 376 more spotty species distributions, with rare species persisting in some locations where they
 377 would not in other scenarios (Fig. 3 bottom row). Two notable examples include species 1
 378 (red patches, individually green, but here cyan due to its coexistence with species 3,
 379 blue) taking on a more clumped distribution with large interaction scales.

381 Regional outcomes: functioning and diversity at the landscape scale

382 The outcomes described above allow us to identify spatial patterns in local outcomes in
 383 the landscape, but what are outcomes for the landscape as a whole? Given the additive
 384 nature of biomass across localities, two regions could have identical biomass at the land-
 385 scape scale even if one region has high variation among localities that span extremes of
 386 high and low values, whereas another varies little with biomass values that are intermedi-

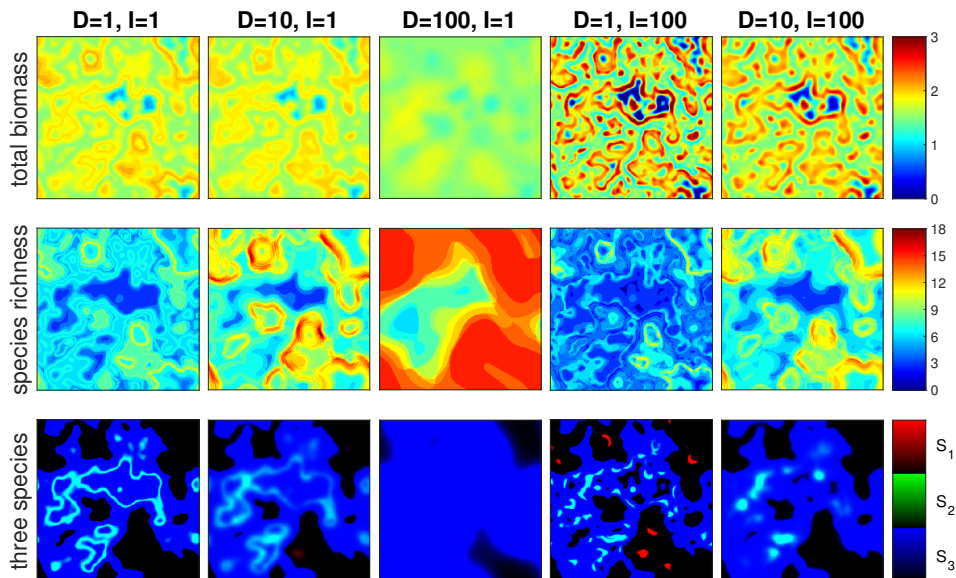


Figure 3: **Species distribution patterns for five selected parameter sets**, representing different scales of dispersal (D) and interaction (I), as designated in Fig. 2. **Top row**: total community biomass. **Middle row**: local species richness. **Bottom row**: distribution of three of the 20 species in original species pool (their *abundances*-biomass are encoded in the red, green and blue color channels, respectively; thus, cyan regions corresponds to coexistence of species 2 and 3). For better legibility, biomass levels above 3 are not shown.

387 ate. Here, we see that biomass is highest when interaction scales are large (Fig. S10), an
 388 effect that is quickly eroded as dispersal scales increase. Interestingly, these high-biomass
 389 landscapes had extreme variation in biomass among localities, including areas of extremely
 390 low biomass (dark blue in Fig. 2) and extremely high biomass (red in Fig. 2). Therefore,
 391 high biomass is driven by a disproportionate subset of local communities in a landscape.
 392 Furthermore, these high biomass landscapes were unremarkable in regional species richness
 393 in the landscape \bar{r} , and actually had fewer species per locality on average than other scenar-
 394 ios (Fig. S4a)–S11). For those who may be interested in comparing our findings to those
 395 typically reported in traditional metacommunity models more explicitly (e.g., [44], we note
 396 that the left and right plots in Fig. S11 essentially show local (i.e., alpha) and regional (i.e.,
 397 gamma) diversity, respectively, whereas compositional turnover among localities (i.e., beta
 398 diversity) is essentially differences between them.

399 Cross-scale outcomes: BEF and SAR

400 Next, we turn to two types of cross-scale outcomes (Fig. 4). First, we consider the rela-
 401 tionship in BEF curves (i.e., total biomass vs. species diversity) \bar{r} , which we compute at
 402 local and regional scales. At the regional scale, we are unable to distinguish between the
 403 scenarios investigated in at neighborhood (i.e., single cell) scales. In doing so, we find that
 404 BEF curves (Fig. 3. By contrast, local BEF relationships better reflect the 4, left panel)
 405 reflect underlying process scales. In particular, they exhibit a hump-shaped relationship for
 406 large interaction scales, suggesting that patches with the largest total biomass are not the
 407 most diverse, but rather have a few high-performance high-performing species. This result
 408 ties into our previous observation that the interaction scale tends to amplify environmental
 409 heterogeneity, and may thus put more weight on selection effects, where abiotic conditions
 410 select the best-performing species at the exclusion of others. We also examined BEF curves
 411 measured at larger scales, i.e., when spatially aggregating 100-cell neighborhoods, and found
 412 qualitatively identical patterns (Fig. 4, middle panel).

413 We also look at a pattern aggregated over continuously increasing spatial scales – the
 414 SAR (Fig. 4, right panel). We would expect that changes in the slope or shape of the SAR
 415 as the aggregation scale (x-axis) exceeds the spatial scales of our ecological processes, as has
 416 been demonstrated for the Stability-Area Relationships [8]. However, we do not observe a
 417 clear link between process and pattern scales, beyond the fact that the inflection point (in
 418 particular, for low D and I) corresponds to the environmental scale E (vertical gray line in
 419 Fig. 3). The main impact of process scale is that, by amplifying landscape heterogeneity, a
 420 large interaction scale I leads to a stronger SAR when large interaction scales are coupled
 421 with short dispersal scales. Specifically, as predicted, at the smallest scale the $D < E < I$
 422 scenario (magenta curve) yields the lowest species richness compared to all other scenarios,
 423 whereas at the scale of the entire landscape, its richness is very high.

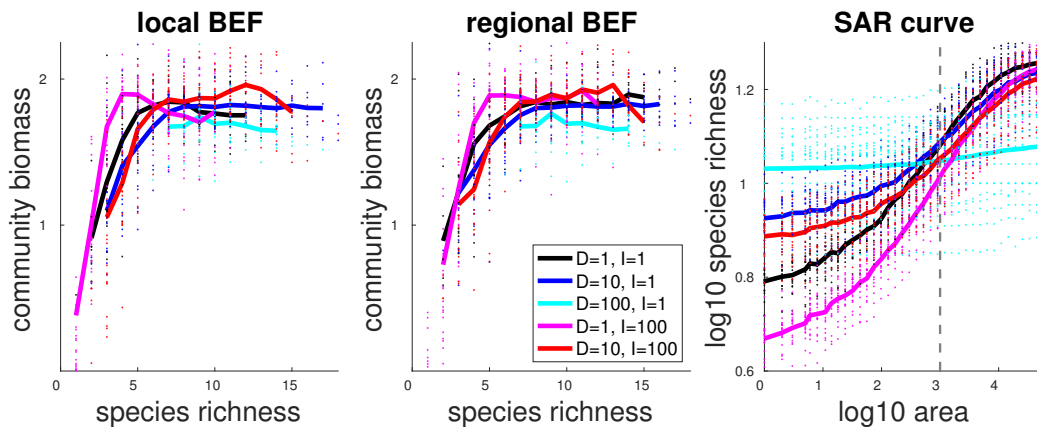


Figure 4: **BEF and SAR relationships.** Solid lines show average values over 20 replicates, ~~dotted lines-small circles~~ show ~~curves-values~~ for individual replicates. Colors correspond to five selected parameter sets, representing different scales of dispersal (D) and interaction (I), as designated in Fig. 2. Local and regional BEF curves are measured at regions of size 1 and 100, respectively. Vertical gray line shows the area corresponding to the environmental scale $E = 32$. Although our model is deterministic (i.e., each replicate has only one possible outcome, given a specific set of parameter values and initial conditions), differences among replicates reflect differences in parameter values caused by sampling those values from distributions (Table 1).

424 ~~However, aggregated~~ Aggregated measures of biodiversity and functioning at regional
 425 scales miss much of the information captured by local measures, such as the distribution
 426 and turnover in biomass (Fig. 2 and Fig. 3). Yet these local patterns can be quantified.
 427 Figure 5 presents the results of the spatial correlation of species biomass distributions,
 428 which measures how the biomass of a species correlates over the distance between sampling.
 429 We observe clear trends in scale, with consistent patterns of growing (shrinking) correlation
 430 with higher dispersal (interaction) scales.

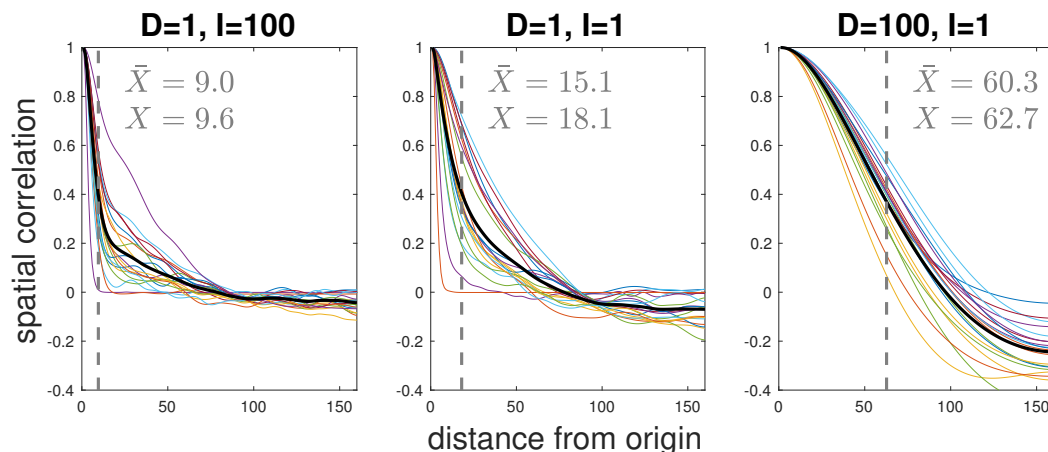


Figure 5: **Spatial correlation of each species's biomass distribution**, for three scenarios. **Left:** $I = 100, D = 1$; **Middle:** $I = 1, D = 1$; **Right:** $I = 1, D = 100$. Recall that $E = 32$. Each of the 20 species is represented by a different color, with black showing the average correlation function, all for a single replicate. For this simulation run, the scale of correlation X is given, and is shown by gray vertical lines. The correlation scale averaged over the 20 replicates, \bar{X} , is also noted.

431 Discussion

432 This study focuses on a critical question: how is the scaling of ecological patterns, such as
 433 patterns of biodiversity and ecosystem functioning, related to scales of specific processes,
 434 and why? We have modelled how intrinsic scales of ecological processes align with the
 435 emergence of ecological patterns in a metacommunity, where we control the spatial scale of
 436 environmental heterogeneity, dispersal, and species interactions. ~~We further focused on the~~
 437 ~~regime where many species may coexist in a stable equilibrium. Under these assumptions,~~
 438 ~~we have arrived at the following answer: In doing so, below, we highlight the following three~~
 439 ~~take-home messages of our results:~~

- 440 • the scale of one process (here, environment) can cause the emergence of character-
 441 istic scales of ~~biodiversity and functioning, as summarized by the inflection point of~~

~~species-area relationships, are set by scales of environmental heterogeneity. Scales of dispersal and species interactions do not affect those inflection points. Rather, they have opposing effects on the magnitude of differences between small-scale and large-scale patterns—other processes (dispersal, interactions)~~

- two interlinked ecological patterns (biodiversity and ecosystem function) and their relationship to each other are oppositely affected by two forms of organismal movement
- averaging ecological patterns at any one scale misses a rich patterning of spatial variance that is closely tied to process scales

Below, we expand upon ~~and place our findings~~ each finding and place them within existing knowledge, examine the mechanisms that underlie our findings, contrast results among ecological variables, and end by placing our results within a context of ecosystem preservation.

A main finding of our study is that the spatial scale of interactions amplifies environmental heterogeneity, sharpening observed spatial patterns, in contrast to dispersal scales. Importantly, observed spatial patterns did not reflect the absolute value of the spatial scale of each ecological process, but rather, their values relative to the environment; decreasing the spatial scale of the environment shifts the boundary of blurring/sharpening effects of dispersal and species interactions (Fig. S4). We find this effect because environmental conditions are quite literally the template upon which dispersal and species interactions mold species distribution. Large-scale (i.e., at scales above the template) processes are more important than small-scale ones in determining overall patterns, meaning that only when dispersal or interactions have large scales can they impact large-scale patterns.

We examined the impacts of process scales on two classes of patterns: first, on the spatial scaling of patterns (SAR and BEF), and second, on the spatial structure of species ~~abundances~~ biomass in the landscape. Unexpectedly, the latter class of patterns appears to better reflect the scale of ecological processes, such as the distribution and turnover of biomass and biodiversity across the landscape. These patterns would be lost by examining mean biodiversity and function at specific aggregation scales (e.g., local vs. regional; Fig. S4), but were well captured via spatial autocorrelation (Fig. 5). From these analyses, one take-home message is that increasing the scale of species interactions actually amplifies variation on small scales. In other words, large-scale processes do not necessarily beget large-scale patterns.

The question of how process scales affect observed patterns can also be spun around: what information about process scales can be inferred from the various patterns we see? Considering the opposing effects that dispersal and interaction scales have on pattern scales (Fig. 2), it is not clear that such an inference is possible. However, given that patterns scales change differently (compare Fig. 2 with Fig. S3, for instance), combining several measures together may provide an answer, for instance by finding when changes in spatial correlations of biodiversity and biomass no longer behave similarly. In this context, it is perhaps to be expected that no clear connection was found between well known patterns such as BEF and SARs, and process scales. Over the past few decades, ecologists have been cautioned from inferring processes from patterns [45]. Our results demonstrate exactly why this is important: a lack of a 1:1 mapping between a pattern and any one specific process.

Indeed, our finding that the SAR curves did not exhibit transitions at particular spatial scales, that would allow us to identify the typical scales of the underlying processes (other than the environment), runs counter to other contexts, such as the invariability-area relationship [8]. In particular, we do not find a triphasic SAR curve that is often reported [46, 8]; This is the case since our model does not consider individual sampling and dispersal limitation, which typically lead to stronger SAR slopes at small and large scales, respectively. We thus see the strongest slopes at intermediate spatial scales, consistent with results under similar settings [47], and hinting that we are largely seeing community dynamics typical of species-sorting [38]. Centering on the average SAR slope itself, on the one hand, we found that large interaction scales may enhance the SAR by amplifying landscape heterogeneity and creating low-diversity strips along the edges of species ranges. On the other hand, this spatial heterogeneity could also promote coexistence as a weaker competitor might thrive in the margins [48][49]. This suggests that edge effects may play a prevalent role in the case of long-range interactions, and deserves more extensive investigation. Overall, the scales of biotic processes (interaction and dispersal) are mainly reflected inasmuch as they change overall community properties, such as total diversity across the landscape.

~~In line with our expectations, dispersal tends to homogenize spatial patterns and can thus hinder our ability to infer the properties of smaller-scale processes. However, it is important to note that this generic blurring effect may disappear in some specific ecological settings, such as the well-known Turing instability arising from interactions between two~~

506 reactants dispersing at different rates, an “activator” and an “inhibitor”. In this study we
507 focused on many interacting species, so that finding these two very distinct behaviours of
508 activator and inhibitor is not typical, and hence dispersal always leads to a smoothing effect.
509 We can therefore reconcile this apparent discrepancy by noting that, within our framework,
510 such Turing patterns [50] where regular spatial scales emerge due to dispersal and local
511 interactions alone, appear when a fast-diffusing species induces an effective long-range
512 self-competition for a slow-diffusing species. This has been discussed in the context of
513 vegetation patterns, where plants compete at a range through fast-diffusing water [51, 52].
514 Thus, it may be that dispersal in one species effectively creates a type of ranged interaction
515 in another species, leading to the formation of heterogeneous spatial patterns that do not
516 reflect the underlying environmental conditions.

517 An interesting problem we encountered, which is worth expounding upon to aid future
518 research in this area, is how to place dispersal on comparable scales to other processes.
519 For both environmental factors and species interactions, we could separate the intensity of
520 variation and the scale over which it takes place, for instance, by modelling interactions
521 with a spatial kernel which defines the range of these interactions. For dispersal, however,
522 this distinction does not hold in the continuum limit nor in the stable equilibrium regime
523 that we consider in this study. This can be understood intuitively in a single dimension:
524 organisms who disperse from site x to site $x + 1$ at time t will be counted in those that
525 disperse from site $x + 1$ to site $x + 2$ at a later moment in time. Therefore, dispersing
526 twice as fast between neighboring sites can be equivalent to dispersing twice as far. This
527 equivalence breaks down when the details of individual dispersal events matter, e.g. for very
528 rare and long-ranged dispersal events [53]. But even then, the strength of each dispersal
529 event would still play into the spatial scale over which dispersal impacts the dynamics over
530 longer times. As a consequence, defining dispersal scale from a spatial kernel alone might
531 seem more intuitive, but would actually hide the importance of intensity, and we prefer
532 to simply model nearest-neighbor dispersal and acknowledge that intensity and scale are
533 entangled. We detail in the Appendix how we ensure that our metrics of spatial scale are
534 dynamically meaningful and comparable for all three processes.

535 Knowledge of the spatial scale of ecological processes is critical to understanding the
536 maintenance of ecosystems. To illustrate this argument, one can imagine a landscape man-
537 ager interested in preserving some baseline level of functioning in a landscape at a specific
538 spatial extent, for example, primary production. If the spatial scale of interest does not en-
539 compass the intrinsic scales of processes that govern functioning, then landscape alteration
540 beyond that scale might impact functioning in an unanticipated and undesirable manner;
541 these scales will differ among ecosystems based on how species’ traits and the physical
542 landscape affect how organisms experience scales of E, D, and I. In other words, the scales
543 important to the maintenance of ecosystem function may be mismatched from the (typi-
544 cally small) spatial scales at which ecosystem functioning is observed and managed, but
545 the degree to which this is true depends on process scaling. Predictions of our model could
546 be best tested empirically in microcosm or mesocosm setups or using data syntheses, for
547 example, by examining the spatial structure of species richness and biomass depending on
548 process scales of focal taxa (e.g., small vs large-bodied animals using remotely sensed data,
549 experiments with insects where mobility is restricted).

550 Our results suggest that it will be difficult to manage landscapes to preserve biodiver-
551 sity and ecosystem functioning simultaneously, despite their causative relationship, for two
552 related reasons. First, the fact that increasing dispersal and interaction scales had opposing
553 effects on either ecosystem property presents a unique management challenge, given that
554 both scales are tied to organismal movement, albeit on distinct timescales (i.e., daily vs.
555 once-per-generation). Second, ecosystems attained the highest biomass in scenarios which
556 also led to the lowest levels of biodiversity, specifically, when interaction scales were large
557 and dispersal scales were small. We note that this second issue may only be relevant when
558 interactions are largely competitive, since our modeling, and thus results, did not consider
559 mutualistic interactions which would likely change the observed trade-off between biodiver-
560 sity and biomass. How would a manager plan a landscape to enhance interaction scales
561 (preserving function) while simultaneously minimizing scales of dispersal (preserving biodi-
562 versity)? This can, for instance, be relevant for managing predation of pest herbivores in
563 agricultural landscapes [17]. This type of intervention might be most successful in species
564 with body plans for long-distance movement, but that can remain philopatric for behavioural
565 reasons (which can be environmentally determined; i.e., territorial hunters).

566 Our metacommunity model differs from traditional metacommunity models in several
567 important ways. Traditional metacommunity models tend to include discrete local patches
568 embedded within an implicit inhospitable matrix, interconnected by rates of dispersal, often
569 from a spatially-implicit regional pool of dispersers. By contrast, “patches” in our model
570 emerge from the environmental template (Fig. 3), the structure of which may be viewed
571 differently by different species according to their fundamental niche. Further, these patches

572 may have fuzzy boundaries, within-patch heterogeneity, as well as different shapes and sizes.
 573 Individuals may be lost to the matrix (i.e., habitat falling outside of the fundamental niche)
 574 if they disperse there or may form stepping stone populations to reach new patches. In
 575 doing so, dispersal limitation is more likely to emerge as the spatial grain of the environment
 576 exceeds the scales at which species disperse, a major result of our study. These features align
 577 with the recent calls [54, 32] to develop more realistic metacommunity models applicable
 578 to a wider range of systems, beyond discrete, patchy, island-like systems. Given these
 579 strengths, the next step is to extend a model like ours to multi-trophic systems, beyond
 580 “horizontal” (sensu Vellend [55]) competitive communities. Our model is naturally amenable
 581 to multi-trophic systems, as predators often perceive the landscape at a different scale
 582 than their prey (i.e., a different interaction scale) and would perceive the scale of the
 583 environment via spatial distributions of their prey—additionally, there is an opportunity
 584 to move beyond Lotka-Volterra dynamics for modelling species interactions, towards more
 585 mechanistic consumer-resource approaches [56]. Most metacommunity models have been
 586 applied to competing species [18], with multi-trophic extensions becoming more common in
 587 recent years [57].

588 Our conclusions are twofold. First, we bring forward an important spatial scale – the
 589 range of species interactions – that has been largely neglected in previous analyses (e.g.,
 590 metacommunity theory). This interaction range can ~~derive~~ be derived from many of the
 591 same ecological mechanisms as dispersal, ~~for instance such as~~ individual mobility, yet these
 592 two ~~scales~~ processes lead to opposite ecological effects. This suggests that we must care-
 593 fully distinguish whether mobility actually leads to population dispersal or to large-range
 594 interactions, and re-evaluate possible consequences of evolution or environmental change in
 595 these processes. Finally, we saw that the spatial scale of ecological processes might not ap-
 596 pear clearly in the scale of resulting patterns such as Species-Area or Biodiversity-Ecosystem
 597 Functioning relationships, though they may sometimes be reflected in local outcomes. While
 598 we focused on a few important biodiversity and functioning patterns, our study paves the
 599 way for future work investigating systematically under which conditions various ecological
 600 pattern scales may or may not reflect the spatial scale of underlying processes.

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744 networks under environmental change,” *Nature Ecology & Evolution*, vol. 1, no. 6,
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746 **Acknowledgements**

747 YRZ, MB, DWS and ML were supported by the TULIP Laboratory of Excellence (ANR-
748 10-LABX-41), and by the BIOTASES Advanced Grant, funded by the European Research
749 Council under the European Union’s Horizon 2020 research and innovation programme
750 (grant agreement no. 666971). We thank all members of the BEF Scale working group for
751 valuable discussions and feedback.

752 **Conflict of interest disclosure**

753 The authors declare they have no conflict of interest relating to the content of this article.

754 **Data accessibility**

755 Script files for simulations and analysis of results shown in the manuscript are available at
756 the open-access repository: <https://doi.org/10.5281/zenodo.5543190>.

757 Appendix

758 Measurement of scales

759 ~~As mentioned~~ This appendix is made of four sections. A1: Measurement of scales; A2:
760 ~~Generating the landscape; A3: Different environmental scales; A4: Additional plots.~~

761 A1 Measurement of scales

762 ~~As explained~~ in the main Methods section, we explicitly measure and compare three spatial
763 scales: environmental conditions (E), dispersal (D) and species interaction (I). ~~We now~~
764 ~~detail the definition of these three scales, and finally note the peculiarity of dispersal scale.~~

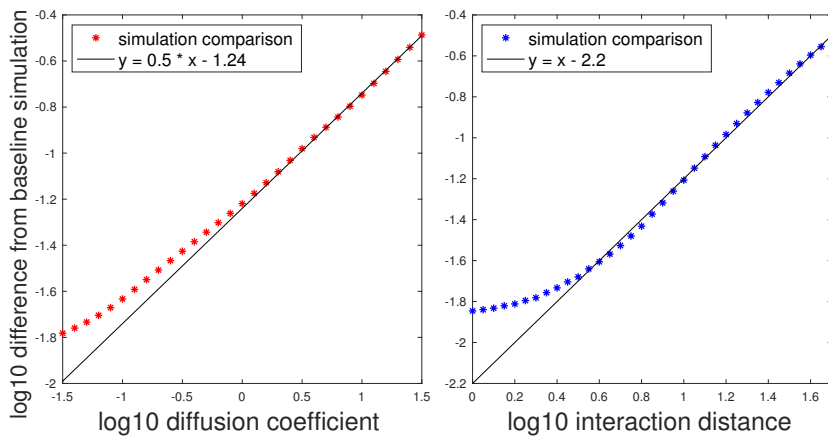
765 ~~In our model, Environmental scale E:~~ The environment itself is generated using a
766 ~~combination of a spectral color and cutoff wavenumber (see next section), but this does not~~
767 ~~explicitly define the scale. To measure the species interactions are explicitly defined with~~
768 ~~a distance over which they occur—via the Gaussian kernel function. This naturally gives~~
769 ~~us the scale of interactions I , as the width of the Gaussian function, such that $I = \gamma$.~~ ~~the~~
770 ~~environment, we follow the same approach as for the correlation function and measure the~~
771 ~~scale for a species biomass distribution (using a convolution based on FFT), except that we~~
772 ~~do this for the value of intrinsic growth rate $r_i(\vec{x})$, as it is directly set by the environment.~~
773 ~~For each of the 20 species, we can calculate a correlation function (in the same manner~~
774 ~~as explained in the methods), and from this we calculate the correlation scale (the point~~
775 ~~of middle height for the correlation function). We average this value over all 20 species,~~
776 ~~to calculate the environment's scale for a given system. Since this result depend on the~~
777 ~~randomization of the environment, we repeat this for many replicates, and choose values of~~
778 ~~ρ and k_c that will on average give a value of E we want to have.~~

779 ~~Dispersal scale D:~~ To estimate the dispersal scale D , we compare the effect of changing
780 the dispersal coefficient δ with changing γ . In Fig. S1 we show how changing δ and γ (and
781 thereby D and I) affects the community biomass distribution. As seen in the left panel, with
782 low δ and γ the difference from a null scenario of no dispersal and no interaction distance
783 is very small, but increasing either δ or γ changes the community biomass distribution
784 considerably. In the middle and right panels we see these differences, as we change only
785 δ (middle) or only γ (right). This clearly shows three things: 1) The effect of interaction
786 distance scales linearly with γ , as expected by its definition. 2) The effect of dispersal
787 coefficient scales with $\sqrt{\delta}$, as expected from dimensional considerations (e.g., [43]). 3) More
788 specifically, to make these two effects comparable, the dispersal scale is missing a factor of
789 10, i.e., $D = 10\sqrt{\delta}$. This can be seen by the fact that for both $\delta = 1$ in the middle panel
790 and $\gamma = 10$ in the right panel, the y-axis values are roughly the same ($10^{-1.2}$).

791 ~~The environment itself is generated using a combination of a spectral color and cutoff~~
792 ~~wavenumber (see subsection below), but this does not explicitly define the scale. To measure~~
793 ~~Interaction scale I:~~ In our model, the species interactions are explicitly defined with a
794 ~~distance over which they occur—via the Gaussian kernel function. This naturally gives us~~
795 ~~the scale of the environment, we follow the same approach as for the correlation function and~~
796 ~~measure the scale for a species biomass distribution (using a convolution based on FFT),~~
797 ~~except that we do this for the value of intrinsic growth rate $r_i(\vec{x})$, as it is directly set by~~
798 ~~the environment. For each of the 20 species, we can calculate a correlation function (in the~~
799 ~~same manner as explained in the methods), and from this we calculate the correlation scale~~
800 ~~(the point of middle height for the correlation function). We average this value over all 20~~
801 ~~species, to calculate the environment's scale for a given system. Since this result depend~~
802 ~~on the randomization of the environment, we repeat this for many replicates, and choose~~
803 ~~values of ρ and k_c that will on average give a value of E we want to have~~ interactions I , as
804 ~~the width of the Gaussian function, such that $I = \gamma$.~~

805 Generating the landscape

806 ~~Peculiarity of dispersal scale:~~ An interesting problem we encountered, which is worth
807 ~~expounding upon to aid future research in this area, is how to place dispersal on comparable~~
808 ~~scales and strength to other processes. For both environmental factors and species interactions,~~
809 ~~we could separate the intensity of variation and the scale over which it takes place. We~~
810 ~~could do this, for instance, by modelling interactions with a spatial kernel which defines~~
811 ~~the range of these interactions. For dispersal, however, this distinction does not hold in the~~
812 ~~continuum limit nor in the stable equilibrium regime that we consider in this study. This~~
813 ~~can be understood intuitively in a single dimension: organisms who disperse from site x to~~
814 ~~site $x + 1$ at time t will be counted in those that disperse from site $x + 1$ to site $x + 2$ at~~
815 ~~a later moment in time. Therefore, dispersing twice as fast between neighboring sites can~~
816 ~~be equivalent to dispersing twice as far. This equivalence breaks down when the details of~~



Comparison of different diffusion coefficient and interaction distance scenarios to the case of no dispersal and local interactions alone. Differences are squared, summed over all species, and averaged over domain. This is done along the diffusion coefficient (interaction distance) axis in the left (right) panel. Comparison shows that diffusion scales like a square root, and that a normalization factor of 10 should be applied to make it comparable to interaction distance (i.e. $d = 1$ is comparable to an interaction distance of 10).

Figure S1: Comparison of different diffusion coefficient and interaction distance scenarios to the case of no dispersal and local interactions alone. Differences are squared, summed over all species, and averaged over domain. This is done along the diffusion coefficient (interaction distance) axis in the left (right) panel. Comparison shows that diffusion scales like a square root, and that a normalization factor of 10 should be applied to make it comparable to interaction distance (i.e., $d = 1$ is comparable to an interaction distance of 10).

817 individual dispersal events matter, e.g., for very rare and long-ranged dispersal events [53].
 818 But even then, the strength of each dispersal event would still play into the spatial scale
 819 over which dispersal impacts the dynamics over longer times. As a consequence, defining
 820 dispersal scale from a spatial kernel alone might seem more intuitive, but would actually
 821 hide the importance of intensity, and we prefer to simply model nearest-neighbor dispersal
 822 and acknowledge that intensity and scale are entangled.

823 **A2** Generating the landscape

824 The landscape profile is defined by a spectral color (ρ) and cutoff (k_c). A spectral color
 825 close to 0 corresponds to “white” noise, i.e., noise that exhibits little or no spatial au-
 826 tocorrelation; a spectral color close to 1 indicates “red” noise – noise with high spatial
 827 autocorrelation [41]. The spectral cutoff creates a point of truncation in the frequency pro-
 828 file that prevents high variation between adjacent **pixels/cells**, in effect smoothing the noise
 829 across the landscape. Together, color and cutoff control the degree of structural fragmen-
 830 tation of the landscape – (see Fig. S3). More weight on higher frequencies (low ρ , high k_c)
 831 entails smaller and less-connected fragments of similar environmental conditions. Weight on
 832 lower frequencies (high ρ , low k_c) creates long bands of constant environmental conditions
 833 which can act as corridors for species favoring this value.

To generate the environmental landscape $K(\vec{x})$, we prescribe a frequency profile for the noise:

$$F(k \neq 0) = \frac{1}{k^\rho} e^{-k/k_w}, \quad F(0) = 1$$

834 which is a power-law with color ρ ($\rho = 1$ corresponds to red noise) and an exponential
 835 cutoff with wavenumber $k_w = k_c L/2$ which removes high spatial frequencies, smoothing the
 836 landscape and avoiding strong variations between adjacent **pixels-cells**. The construction
 837 process is demonstrated in Fig. S2. Note that the cutoff wavenumber is simply the nor-
 838 malization of the spectral cutoff by the number of different frequencies represented by the
 839 chosen resolution of the domain, $L/2$, with L the number of **pixels-cells** along the x and y
 840 axes, such that in the spectral domain it represents the resolution of the landscape.

Practically speaking, for a two-dimensional landscape, we generate a $L \times L$ matrix R_{ij} of uniform random numbers over $[-1, 1]$ corresponding to amplitudes for each wave vector (k_x, k_y) . We then multiply these random numbers by the profile above

$$M_{ij} = R_{ij} F(\sqrt{k_i^2 + k_j^2})$$

841 with $k_i = i - \frac{L}{2}$ where index i is a natural number running over $[1, L]$. We set the element

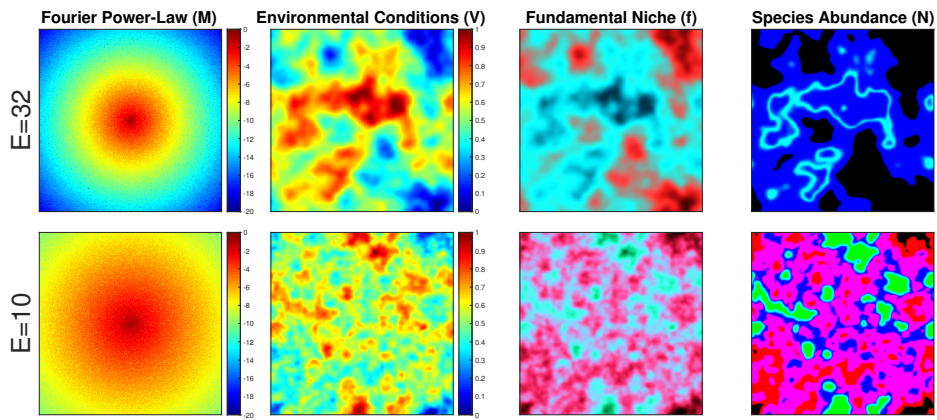


Figure S2: Demonstration of landscape construction. The steps of landscape construction are shown in the different columns, with the top (bottom) row corresponding to a landscape with $E = 32$ ($E = 10$). From left to right, the four columns correspond to: 1) The function M , which is a power-law function with exponential cutoff, on a two-dimensional spectral map (i.e., where each cell corresponds to a different spatial frequency), with the addition of random noise. 2) The environmental conditions V , which result from applying the Fourier transform on the previous step, and normalizing the values to range between 0 and 1. 3) The fundamental niches f_i of 3 species, where the value of f_i of each species are encoded in the red, green and blue color channels. 4) The spatial distribution of species biomass N_i at equilibrium, of the same 3 species and with the same color coding, as the previous column. Note that the top-right panel corresponds to the bottom-left column of Fig. 3.

842 $M_{L/2,L/2}$ corresponding to the uniform trend ($k_i = k_j = 0$) to 5. Finally, we apply a Fast
 843 Fourier Transform on the matrix M_{ij} to obtain the landscape matrix $-V$. As explained in
 844 the main text, this landscape matrix V is used to define the growth rate r_i using a Gaussian
 845 function (see eq. 2), which in turn determines the species biomass distribution N_i (see eq. 1).
 846 We show in Fig. S3 the environment as a function of different values of ρ and k_c , to better
 847 visualize their effect.

848 **Additional plots**

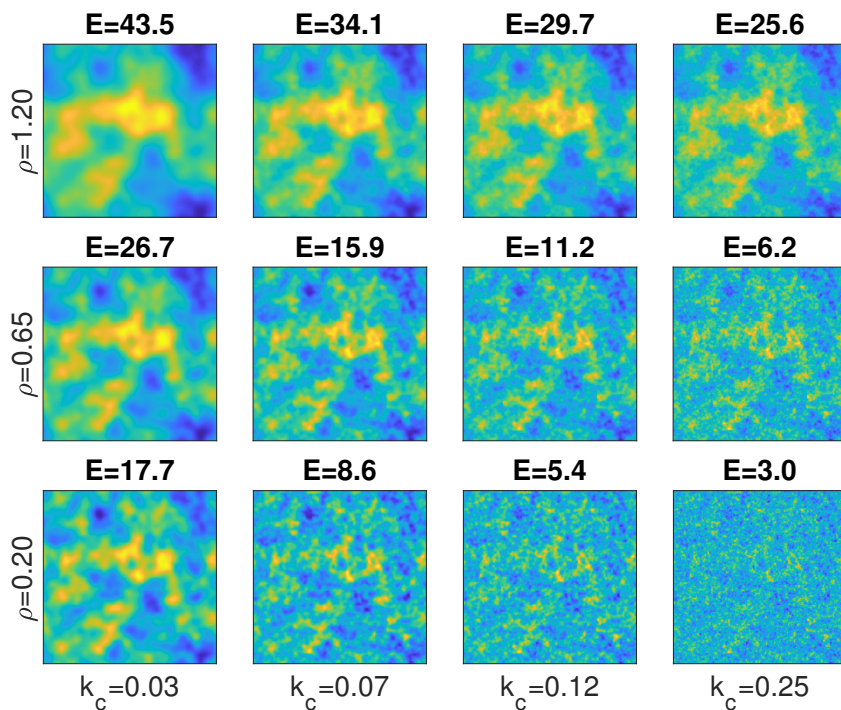


Figure S3: How ρ and k_c shape the landscape structure, shown by maps of the environmental conditions V . We show an example of how a landscape is affected by different values of ρ (rows) and k_c (columns). On top of each panel we also note the environmental scale E that corresponds to the combination of ρ and k_c . We can see that smaller k_c values lead to a landscape with less sharp transitions (i.e., smoother), whereas ρ has a more significant effect on the overall scale. In other figures and in the main text we choose ρ and k_c concordantly, with large ρ values together with small k_c values for a large E , and small ρ values together with large k_c values for a small E .

849 A3 Different environmental scales

850 We show below a few additional plots, ~~to clarify issues discussed in the main text~~ which
 851 explore the impact of different values of environmental scale E . In Fig. S4 we show the
 852 overall difference in community state, between different sets of values of D and I to the case
 853 of no dispersal and local interactions, for two values of E .

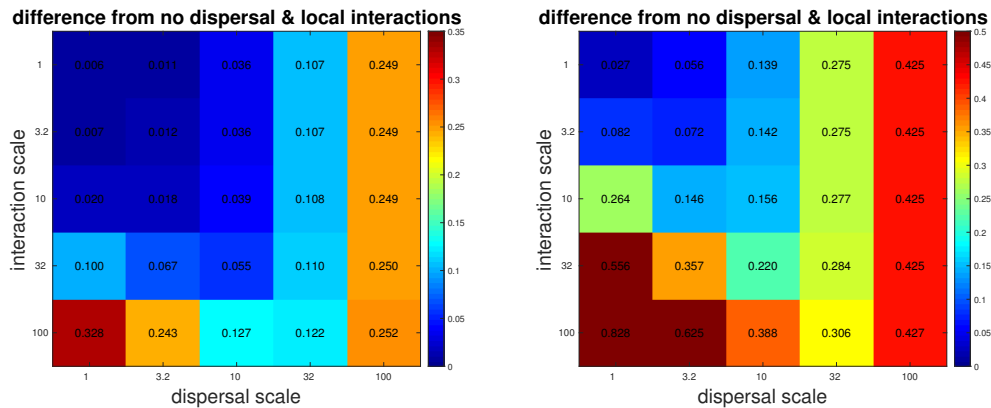


Figure S4: Comparison of various scenarios to the case of no dispersal and local interactions alone. Difference is measured by averaging over the squared sum of each cell for a given value of I and D , against the baseline of $D = I = 0$. This is done for for 5x5 different parameter sets with different values of D and I , for two different values of E , 32 and 10, in the left and right panels, respectively.

854 In Fig. S5 we consider different E values, and see how changing either I or D affects
 855 the overall change in system state (compared with the baseline of no dispersal and local
 856 interactions). In both figures we can see that big differences in the state of the system due
 857 to higher I or D (seen as dark blue region in Fig. S4, and region below the dotted line in
 858 Fig. S5) occur for lower values for I and D , and only when E is sufficiently high. This
 859 demonstrates that the environmental scale E determines the threshold scale of I and D in
 860 which they can have a substantial effect on the community.

861 We also test how the inflection point of SAR (measured in the same way as in the main
 862 text), changes along a range of E values (Fig. S6). We can see that as long as dispersal is not
 863 too high (i.e., the three cases where $D = 1$), the inflection point follows the environmental
 864 scale E (seen by the roughly parallel lines to the 1:1 line).

865 In Fig. S7 and Fig. S8 we show the spatial distributions of biomass and species richness,
 866 for a different landscape, one that has an environmental scale of $E = 10$.

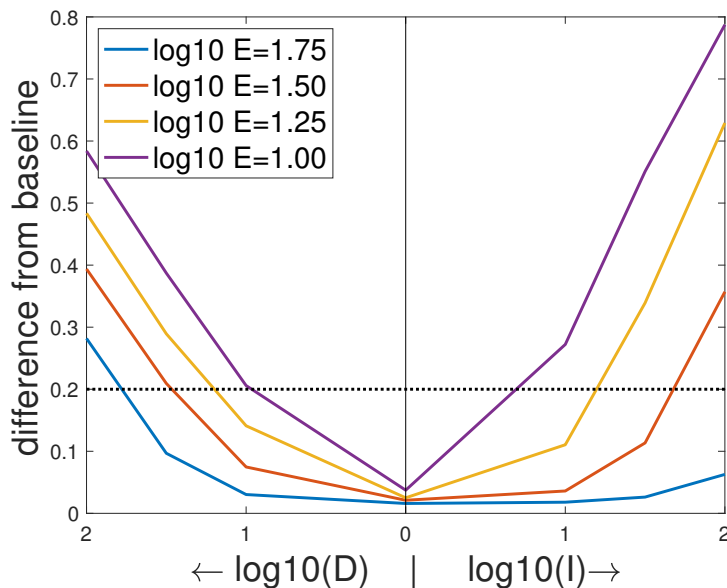


Figure S5: Average difference from a community with no dispersal and local interactions only. Difference is measured by averaging over the squared sum of each cell for a given value of I and D , against the baseline of $D = I = 0$. Left half shows the effect of D alone, while right half shows the effect of I alone.

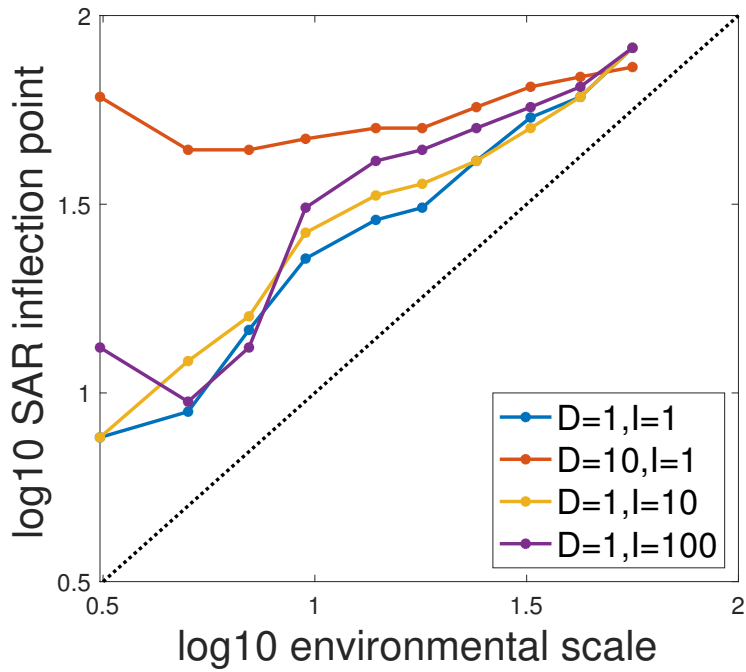


Figure S6: Inflection point of SAR for different combination of scales. For four sets of values of l and D ($D=1, l=1$; $D=1, l=10$; $D=1, l=100$; $D=10, l=1$), we show how the inflection point of SAR changes along a range of 10 values of E (with values between 56 and 3).

FIG.S7 IS REMOVED SO AS TO MAKE THIS PDF SMALLER THAN 5MB. IT HAS NOT CHANGED FROM THE PREVIOUS VERSION.

Figure S7: Total community biomass, for the 5x5 scenarios, with $E=10$. For better legibility, biomass levels above 3.0 are not shown.

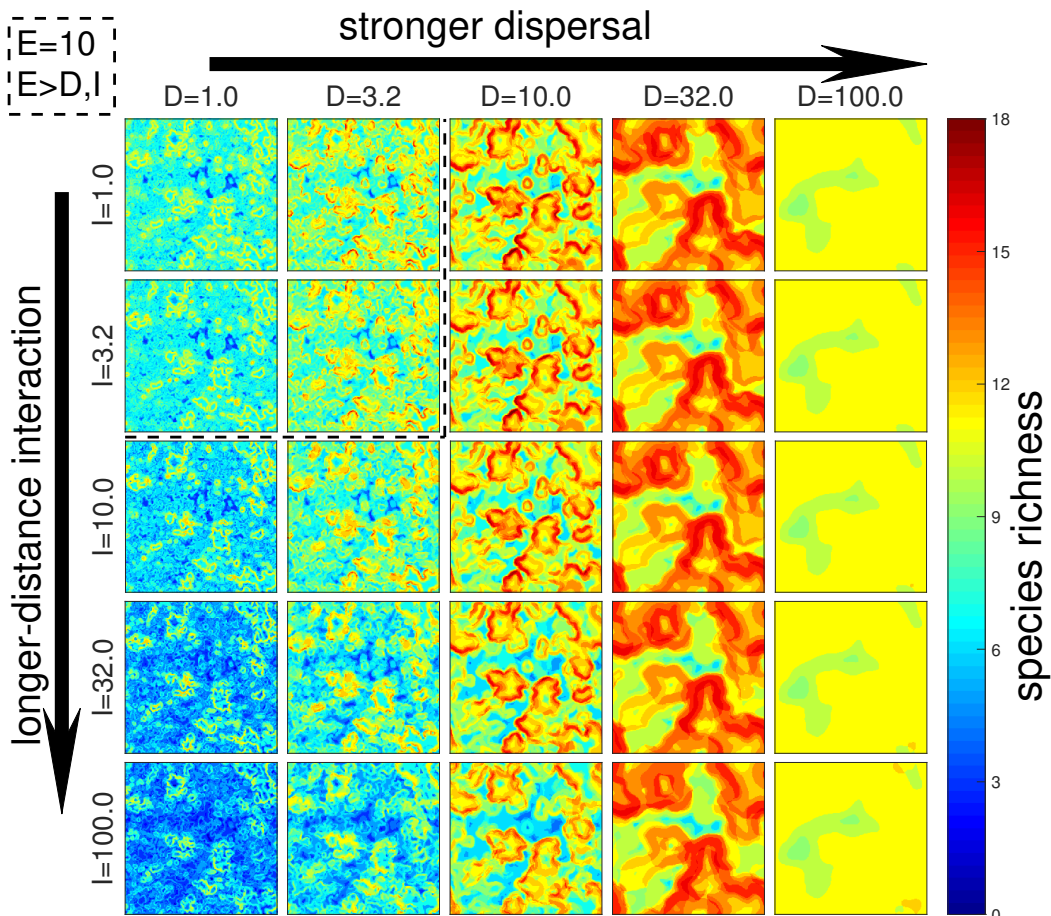


Figure S8: Local species richness, for the 5x5 scenarios, with $E=10$.

867 **A4** Additional plots

868 We show below a few additional plots.

869 In Fig. S9 we show the spatial distribution of species richness, for 5x5 different parameter
 870 sets with different values of D and I , corresponding to Fig. 2. In Fig. S10 and Fig. S11 we
 871 show summary statistics for each of these 5x5 parameter sets, of total community biomass,
 872 average local diversity, and total diversity. In

873 Finally, we explore in Fig. S7 and S12 the sensitivity of our results to the parameter β ,
 874 and demonstrate using Fig. S8 we show the spatial distributions of biomass and species richness,
 875 for a different landscape, one that has an environmental scale of $E = 10$ S13 the calculation
 876 of species' spatial correlations, which is used to estimate the environmental scale E .

877 **Comparison of various scenarios to the case of no dispersal and local interactions**
 878 **alone.** Differences are squared, summed over all species, and averaged over domain. This is
 879 done for for 5x5 different parameter sets with different values of D and I , for two different
 880 values of E , 32 and 10, in the left and right panels, respectively. Note the dark blue color
 881 representing scenarios where the combinations of D and I do not have a significant impact
 882 on pattern observed. In particular, for $E = 32$ (left) the top 3x3 area shows little effect,
 883 while for $E = 10$ (right) there is only a 2x2 area.

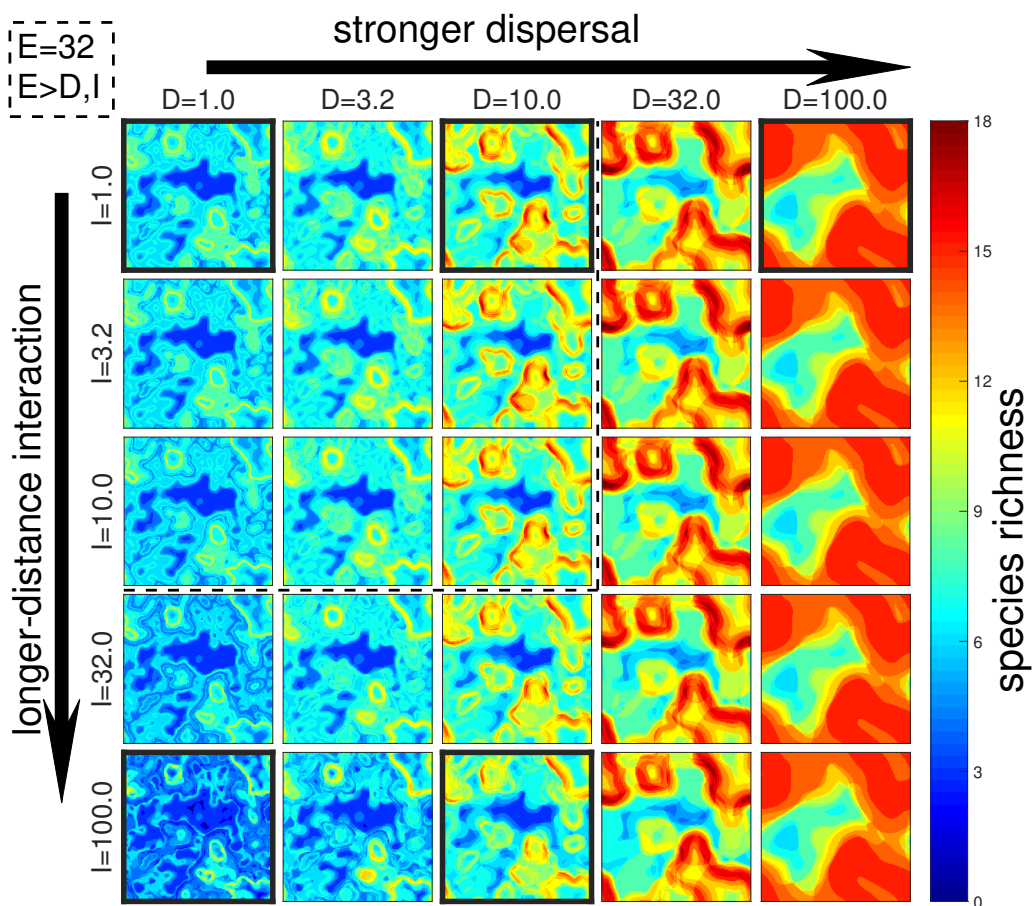


Figure S9: *Species richness plots*, corresponding to Fig.2, for the 5x5 scenarios ($E = 32$).

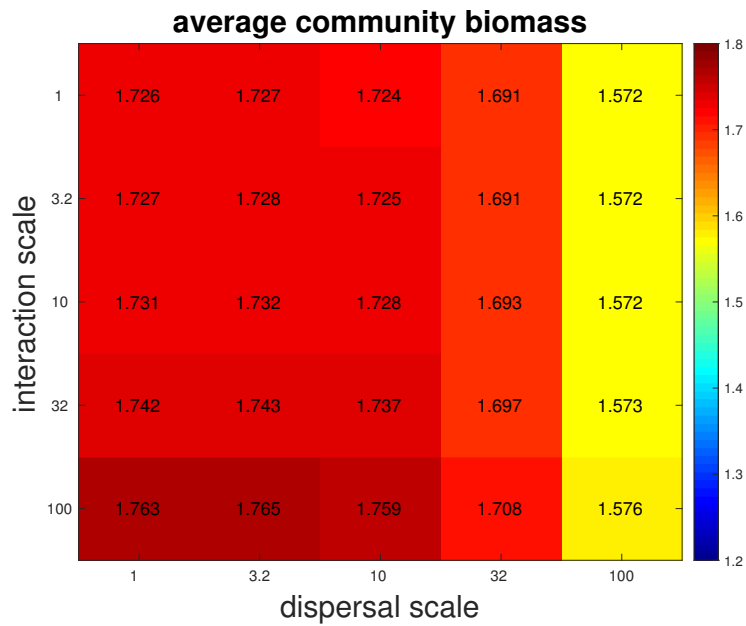


Figure S10: *Total community biomass*, averaged over domain, for the 5x5 scenarios ($E = 32$).

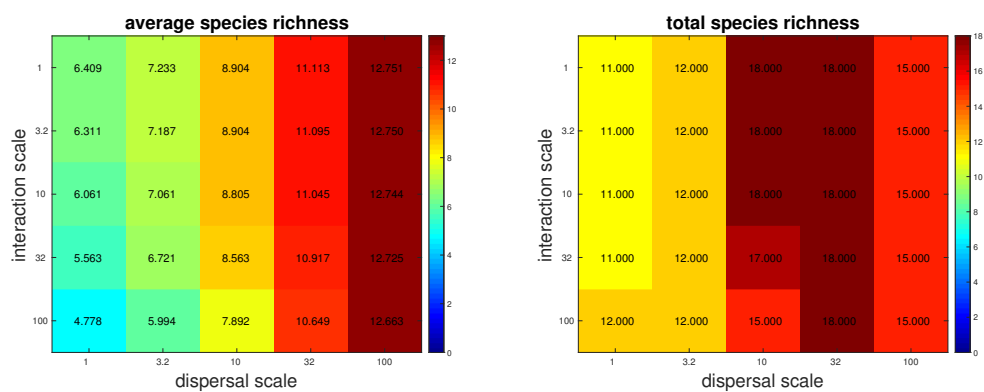


Figure S11: *Diversity plots*. Average local diversity of community (left) and total community diversity, (right) for the 5x5 scenarios ($E = 32$).

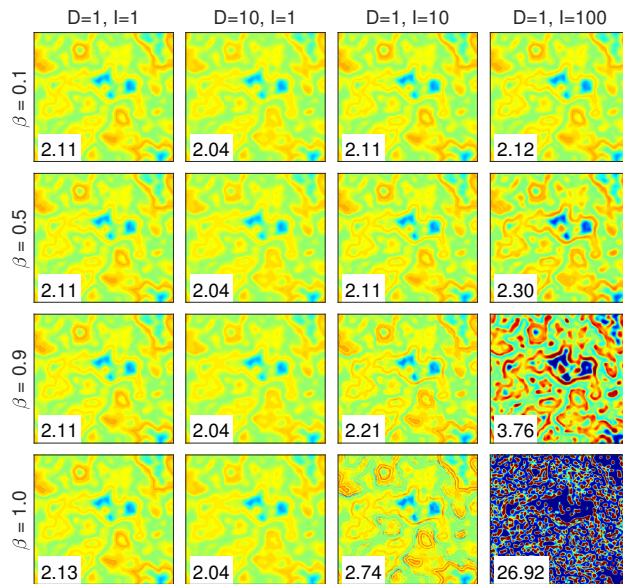


Figure S12: **Total community biomass** Effect of changing the value of the parameter β , for which determines the 5×5 scenario fraction of regional interactions. Each panel shows the spatial distribution of total biomass, with $E=10$ columns showing results for different values of I and D , while lower rows showing increasing values of β . For low values of β (top two rows) scale of interactions I has minimal effect (clearly seen by right column looking the similar to other columns). For values of β (bottom two rows) the effect of I becomes strong and clearly visible. However, for very high values of β (bottom row) the effect also includes very high densities of biomass levels above 3.0 are, which is not shown very realistic. We therefore choose a high value of β but not so high as to lead to very high densities (leading us to the middle ground of $\beta = 0.9$).

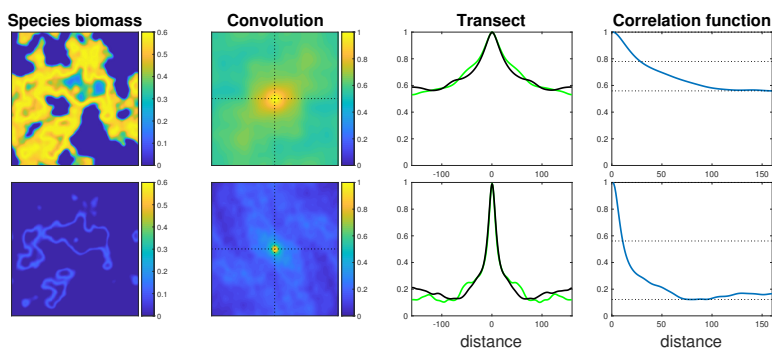


Figure S13: **Local species richness** Demonstration of calculation of correlation function. The steps of calculating the correlation function are shown in the different columns, for with the 5×5 scenario top (bottom) row corresponding to two different species in the same landscape used in Fig. 2. From left to right, the four columns correspond to: 1) The spatial distribution of biomass of a single species N_i . 2) Correlation map, which is the result of a convolution of this spatial distribution with $E=10$ itself. 3) Transects of the correlation map (horizontal and vertical, shown in green and black), also marked in previous column by dotted lines. 4) Averaging of transects resulting in the correlation function. Horizontal dotted lines show the highest and lowest values of the correlation function, along with the average of the two which is used as a threshold to determine the scale of correlation.