Scaling up biodiversity ecosystem functioning relationships: the role of environmental variability in space and time

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Abstract

The biodiversity and ecosystem functioning (BEF) relationship is expected to depend on the spatial or temporal scale at which it is measured. Environmental variation is hypothesized to explain this scale dependence because it influences how quickly biodiversity accumulates with scale. However, this link has yet to be demonstrated in a formal model. Here we use a Lotka-Volterra competition model to simulate community dynamics when environmental conditions vary across either space or time. Species differ in their optimal environmental conditions, which results in turnover in community composition. We vary biodiversity by modelling communities with different sized regional species pools and ask how the amount of biomass per unit area depends on the number of species present, and the spatial or temporal scale at which it is measured. We find that more biodiversity is required to maintain functioning at larger temporal and spatial scales. The number of species required increases quickly when environmental autocorrelation is low, and slowly when autocorrelation is high. Both spatial and temporal environmental variation led to scale dependence in BEF, but autocorrelation had larger impacts when environmental change was temporal. These findings show how the biodiversity required to maintain functioning is expected to increase over time and space.

Keywords: environmental autocorrelation, biodiversity ecosystem functioning, beta diversity, competition, complementarity

Introduction

Biodiversity change arising from the loss and gain of species is now understood to affect many ecosystem processes, such as primary and secondary production, that together define how ecosystems function [1]. To date, our understanding of how biodiversity change affects ecosystem functioning (i.e. the so-called Biodiversity Ecosystem Functioning relationship, or BEF) is founded on tests of theory with controlled experiments and field observations conducted at relatively small scales of space and time [2]. However, recent research has found that the effects of biodiversity change on ecosystem functioning are scale dependent [3–5]. As a consequence, the slope of the BEF relationship (i.e. the rate at which function changes with biodiversity) will depend on the spatial and temporal scales over which it is measured. This scale dependence is important to consider for understanding the effects of biodiversity change on the functioning of ecosystems and on the services they provide to society [6].

Early research focused on small spatial scales to test theoretical predictions that species diversity influences ecosystem functioning at the scales at which species directly compete for resources [7]. Two ways in which biodiversity affects ecosystem functioning have been identified, complementarity effects and selection effects [8]. Complementarity effects emerge from niche differentiation and facilitation among species and lead to improved performance of species assemblages, compared to what would be expected based on the performance of monocultures of the component species. Selection effects arise when the species that perform well in monoculture also come to dominate (i.e. have high abundance) mixed species assemblages. These two effects are known to drive ecosystem functioning, such as primary production, to have a positive but decelerating relationship with increasing diversity within assemblages [9,10]. An important open question is whether other mechanisms support the emergence of BEF relationships across many assemblages spanning much larger spatial and temporal scales [2].

Long-term experiments are revealing that the slope of the BEF relationship, can vary with environmental context and variability, across sites and through time [5,11–15]. Indeed, the longer the length of the interval of time or space, the more likely we are to find new species contributing to ecosystem processes in different environments. This effect is accentuated when there is environmental heterogeneity among sites, or between time points, which sets the scale of species turnover (i.e. beta diversity) [16–18]. Compositional turnover in response to environmental heterogeneity can be considered a form of complementarity, when different species contribute to ecosystem functioning in different conditions [19]. Turnover in species composition across space, or over time, due to environmental variability is predicted to lead to BEF relationships at large spatial scales or long temporal scales that differ from the BEF relationships that are observed at small and short scales [3]. Factors mediating the rate of community turnover in the distribution of species are therefore predicted to determine how the BEF relationship will change with scale.

Despite the importance of environmental variability in determining community turnover, to date, relatively little theory has assessed whether environmental variability can explain scale dependence in the BEF relationship [2,20]. We address this important gap herein. Previous theory identified how community turnover could make the BEF relationship scale dependent [3], but did not provide a mechanistic link between community turnover and environmental variation. Spatial turnover arises because species' distributions are restricted and patchy. Factors explaining the patchiness of species distributions and biomass include dispersal limitation and environmental heterogeneity [21–23]. In turn, patchiness in species' occupancy and productivity will govern where and when different species contribute to ecosystem functioning.

Environmental autocorrelation describes the rate of decay in environmental similarity in time or space [19]. Low (high) autocorrelation defines high (low) rates of change in environmental conditions over short durations or distances resulting in rapid (slow) decay in environmental similarity. Environmental autocorrelation affects many properties of communities and ecosystems: Vasseur and Yodzis [19] found environmental time series to be autocorrelated, with aquatic environments more so than terrestrial environments. Theory and experiments have demonstrated that population extinction probabilities [24,25] as well as many aspects of population [26–29] and community structure [30] and dynamics [18,31–33] are strongly modulated by environmental autocorrelation. Similarly, the effects of biodiversity on the mean and temporal variability of ecosystem functioning (e.g. biomass production) depend markedly on the degree of autocorrelation of environmental variability because it sets the rate of species turnover [18,34,35]. However, this research did not address how environmental autocorrelation affects BEF relationships at different spatial and temporal scales.

Here we ask how environmental autocorrelation in space and time generate variation in BEF relationships at different scales, where scale is altered by aggregating local sites in time or space to increase the grain. We tested three hypotheses: H1 - the number of species required to maintain ecosystem functioning will increase with spatial scale because species vary in the conditions in which they are productive. H2 - the degree of scale dependence in BEF will depend on the degree to which environmental autocorrelation (i.e., high vs. low autocorrelation) mediates turnover in species composition. H3 - the degree of scale dependence in BEF will depend on whether environmental autocorrelation is temporal or spatial. This is because, in the absence of strong dispersal, the composition of a community is more likely to depend on the previous conditions experienced rather than on the conditions in adjacent habitats [36]. We addressed these hypotheses by simulating landscapes of many communities with Lotka-Volterra dynamics driven by environmental variability in space and time, and where autocorrelation is controlled.

Methods

We used numerical simulations of Lotka-Volterra competitive communities to explore how the relationship between biodiversity (as species richness) and ecosystem functioning (as total community biomass), hereafter the BEF relationship, depends on the spatial or temporal scale at which it is measured (Fig. 1).

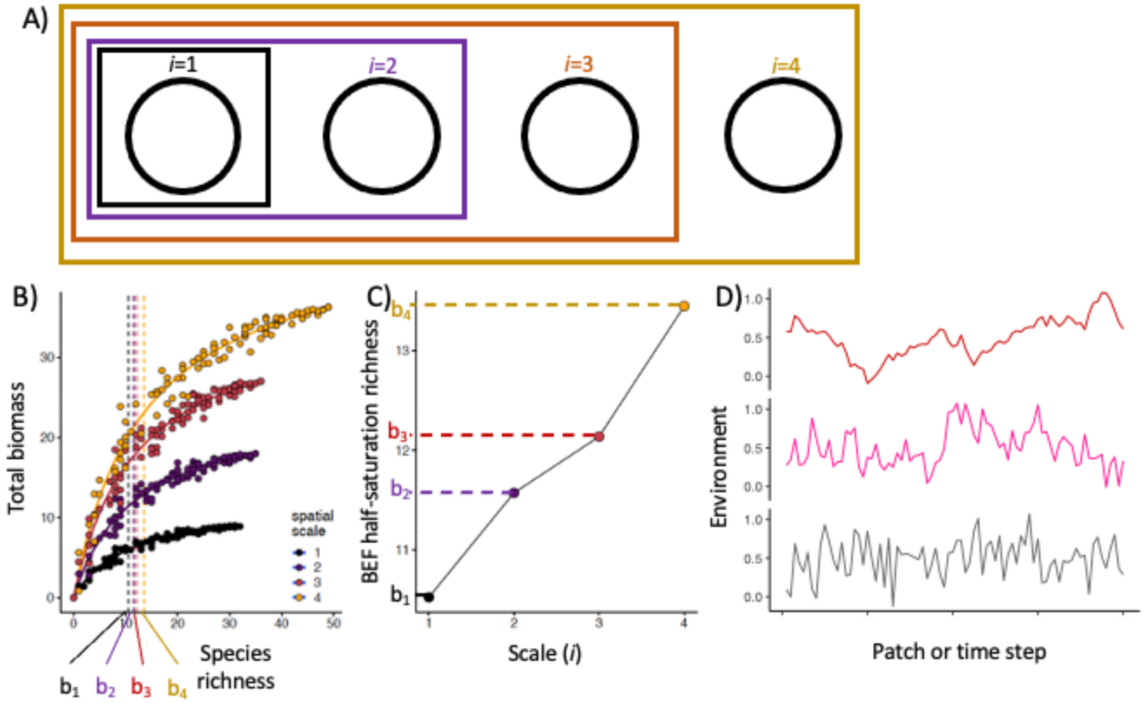

Figure 1. We investigated how the form of the BEF relationship (i.e., slope and asymptote) changes depending on the spatial and temporal scale at which it is measured. We used a model governed by Lotka-Volterra dynamics. In panel A, each black circle represents a community (or 'patch'), at different spatial locations or moments in time. For each community, we fit a Michaelis-Menten function to the relation between average biomass and species richness to estimate the half saturation constant (B), i.e. the number of species required to produce 50% of the biomass (parameter b_i). The four curves represent BEF relationships at different scales. The black curve is the BEF obtained in a single patch at a single moment (i.e. scale = 1). The other curves are obtained by aggregating data from *N* neighbouring communities (or time points for temporal scenarios). In panel C, we then plot the change in b_i—the half saturation of the BEF relationship— as a function of scale. We repeated this procedure for three different levels of environmental autocorrelation (see examples in panel D; γ = 0, 1, 2 respectively), which we hypothesized to govern the rate of turnover of species richness through time or across communities. This procedure allowed us to assess how the slope and asymptote of the scaling relationship changed with environmental autocorrelation.

We used two different scenarios to explore BEF scaling in time and space:

1) a *spatially variable scenario* of 80 patches arranged along a spatial environmental gradient, with no temporal change in environmental conditions.
2) a *temporally variable scenario* of one patch that experiences temporal fluctuations in environmental conditions over 160 time steps (80 burn-in and 80 sampled).

We chose 80 as our maximum spatial or temporal scale of interest because it is large enough to incorporate substantial environmental heterogeneity while remaining computationally tractable. Changing this maximal scale has little impact on our results (Figure S1, S2) as long as this scale is sufficient to allow for environmental variation to result in variation in community composition.

Environmental variation

In each scenario, we contrasted three levels of autocorrelation in environmental variation, low medium, and high. We define these levels of autocorrelation based on the inverse power law $1/f^{\gamma}$ [37] where γ corresponds to the level of autocorrelation (low = 0, medium = 1, and high = 2; Fig. 1D). Sequences of environmental variation corresponding to these three levels of autocorrelation were generated using the *phase.partnered* function in the *synchrony R* package [38]. These sequences defined how environmental conditions varied across space in the spatial scenarios and across time in the temporal scenarios. All three levels of autocorrelation had a mean value of 0.5 and a standard deviation of 0.25, so that local conditions, as defined by $env_x(t)$, are approximately in the range of 0 to 1.

Species responses to environmental variation

We considered a global pool of 100 species which differed in their environmental optima z_i. These optima were evenly distributed between -0.2 and 1.2, which covers the range of optima where species could have positive growth for any environmental condition included in our environmental sequences. The match between this environmental optimum and local conditions, $env_x(t)$, of the patch x in which species i is present, determines its density-independent rate of growth, $r_{ix}(t)$:

$$1) \quad r_{ix}(t) = r_{max} e^{-\left(\frac{z_i - env_x(t)}{2\sigma}\right)^2},$$

Where σ is equal to 0.25, and r_{max} = 5 is the maximum density-independent growth rate, which occurs when the local environmental conditions match the species environmental optimum, i.e. $z_i = env_x(t)$.

Community dynamics

The temporal dynamics of the abundance of each species depend on both the density-independent rate of growth (eq. 1) and density-dependent competition between species [following 36]:

$$2) \quad N_{ix}(t+1) = N_{ix}(t) \frac{r_{ix}(t)}{1 + \sum_{j=1}^{S} N_{jx}(t)\alpha_{ij}},$$

Where $N_{ix}(t)$ is the biomass of species i in patch x at time t. The per capita competition coefficients, α_{ij}, determine the strength of intraspecific α_{ii} and interspecific α_{ij} density-dependent competition. We set all values of intraspecific competition α_{ii} to 1 and draw values of α_{ij} from a uniform distribution between 0 and 0.25. An important assumption is that intraspecific competition is stronger than interspecific competition. Without this assumption, a positive local BEF relationship would not emerge [7,36]. We assume that there is no dispersal between patches, but that there is dispersal from an external species pool (see *Rationale for decisions in simulation* below).

Environmental sequences

We used the exact same 80 step environmental sequences for both our spatial and temporal scenarios. We ran the spatial simulations for 150 time steps, in order to allow the communities to reach equilibrium and then based our analysis on the community composition in the final time step. For the temporal simulations, we preceded the sampled environmental sequences with an 80 time step burn-in sequence with the same level of autocorrelation (see Supplementary methods for details). A shorter burn-in was used of the temporal sequences because there was no need give the community time to reach equilibrium (equilibrium is only reached when the environment is held constant).

Simulations

We considered three different levels of environmental autocorrelation for each of the spatially and temporally varying scenarios. This resulted in a total of six environmental sequence types.

For each environmental sequence type, 100 different randomizations of the environmental variability *R** (defined by equation 1) and species interactions α_{ij} were considered. For each instance of *R* and* α_{ij}, we ran the simulation with 100 different levels of potential biodiversity. We did this by selecting *S** species at random from the 100 potential species. Each patch was initialized with all *S** species, each with a biomass of 1. This allowed us to contrast different levels of species richness, under the same exact environmental conditions [*sensu* 39,40]. After initialization, we ran the simulation for *T* time steps, where *T=150* (*T=160*) for spatial (temporal), performing the following actions in each time step:

1. For each patch x and species i, update the biomass according to equation 2 (given the environment *R** at time t).
2. If in any patch a species from the initial pool of *S** species has a biomass value lower than 0.05, we consider it to be lost from that patch and set its biomass to zero.
3. Record the identity of all species that are present in each patch as well as their summed biomass.
4. Reintroduce all lost species in all patches, by setting their biomass values to 0.035 (below our extinction threshold).

   Update the time ($t = t + 1$), and go back to step 1; continue until the final time step is reached.

Rationale for decisions in simulation

The extinction threshold of 0.05 is necessary to ensure that species can be lost from the communities. Otherwise, biomass levels would decrease to extremely small values but never reach zero. The reintroduction step allows species to colonize the community following environmental change and ensures that we obtain temporal turnover in composition rather than just an erosion of diversity when the environment changes. This is equivalent to a low rate of dispersal from an external species pool. Because the reseeded biomass is below the extinction threshold and occurs after we record the occurrences and biomass, species will not show up in the community unless they increase above the extinction threshold within a single time step. This recolonization is not needed in the spatial scenario because the environment is constant through time, but we include it to keep the scenarios comparable.

The specific parameter values used in our model were chosen to ensure that: 1) there is turnover in community composition in response to environmental variation (i.e. $\sigma = 0.25$); 2) that species are capable of a stable coexistence within a local patch if they are suited to the local environmental condition (i.e. interspecific competition is weaker than intraspecific competition; $\alpha_{ji} < \alpha_{ii}$); 3) when experiencing optimal environmental conditions, species have an equilibrium abundance that far exceeds the extinction threshold (i.e. $r_{max}/(1+\alpha_{ii}) > 0.25$); 4) that the initial biomass values are below this equilibrium value but above the extinction threshold. However, our results are robust to variation of all of these key parameters, provided these conditions are still met (see sensitivity analysis in Supplementary Materials S1).

Estimating the BEF relationship at multiple scales

We refer to scale as the number of time steps (in the temporally variable scenario) or the number of patches (in the spatially variable scenario) used to evaluate the BEF relationship. In each simulation, we calculated the cumulative biomass and species richness at all scales, from one patch to all 80 patches when examining scaling in space, or from one time step to 80 time steps when exploring scaling in time. We did this by aggregating patches in space or across time steps sequentially to increase the grain, or 'scale'. We, for example, aggregate five sequential time steps or patches to evaluate the BEF at a scale of 5 and calculate species richness and the cumulative biomass (see Fig. 1). The sequential aggregation ensured that we maintained the spatial structure of the environment as we combined patches or time points. In all cases, we start at the final time step or patch and aggregate previous or adjacent time steps and patches. We performed this aggregation at all spatial and temporal scales from one to 30 patches (times), every two scale grains from 32 to 40, and then every 5 scale grains from 45 to 80. Then, at each spatial or temporal scale, we contrasted values of biomass and species richness from simulations with different species pool sizes but using the same sequence of environmental variation. We then used a Michaelis-Menten function [39] to estimate the relationship between species richness and average cumulative biomass (Fig. 1B): $B_i = \frac{S_i * a_i}{S_i + b_i}$, where B_i is the total biomass at scale i, S_i is the species richness, a_i is saturation level for biomass at scale i, and b_i is the number of species required to sustain half that asymptotic level of biomass (see dotted lines on Fig. 1B). Higher levels of *b* indicate that a greater number of species are required to maintain a given amount of biomass (e.g. yellow curve on Fig. 1B). To make it possible to determine whether biomass is accumulating linearly across space and time, we used the average biomass across all patches or time points considered. This averaging changed the magnitude of the BEF relationship that we observed but did not change the estimated number of species required to maintain biodiversity. Note that this is different from Thompson et al. [3]

who estimated the slope of the BEF relationship (the rate at which log biomass increases per log species) instead of the half saturation richness. All simulations and analyses were performed in *R* v.3.6.1 [40] (available at - https://doi.org/10.5281/zenodo.4174454).

The critical tests of our hypotheses are thus: H1 – that the half saturation constant *b* of the BEF relationship increases with spatial or temporal scale. H2 – that the degree to which *b* changes with scale depends on the autocorrelation of the environment. H3 – that *b* changes increases with scale at a different rate when environmental change is temporal vs. spatial.

Results

Compositional turnover and species richness

The degree of environmental autocorrelation in either space or time determines the rate of compositional turnover. Compositional turnover, between neighbouring patches or time points, is high when environmental variation is uncorrelated ($\gamma = 0$) and decreases as the environmental autocorrelation increases (Fig. 2A-C for space; Fig. 2D-F for time). This compositional turnover leads to an increasing but saturating relationship between species richness and scale (Fig. 3A,B). Species richness increases and saturates fastest with scale when environmental variation is uncorrelated ($\gamma = 0$) because the full range of environmental conditions is encountered over short scales of space or time. These increases in species richness with scale are slower in autocorrelated environments ($\gamma > 0$) because short scales tend to only include a subset of environmental conditions. Species richness saturates at a slightly lower level when autocorrelation is high ($\gamma = 2$), because these environmental sequences tend to include

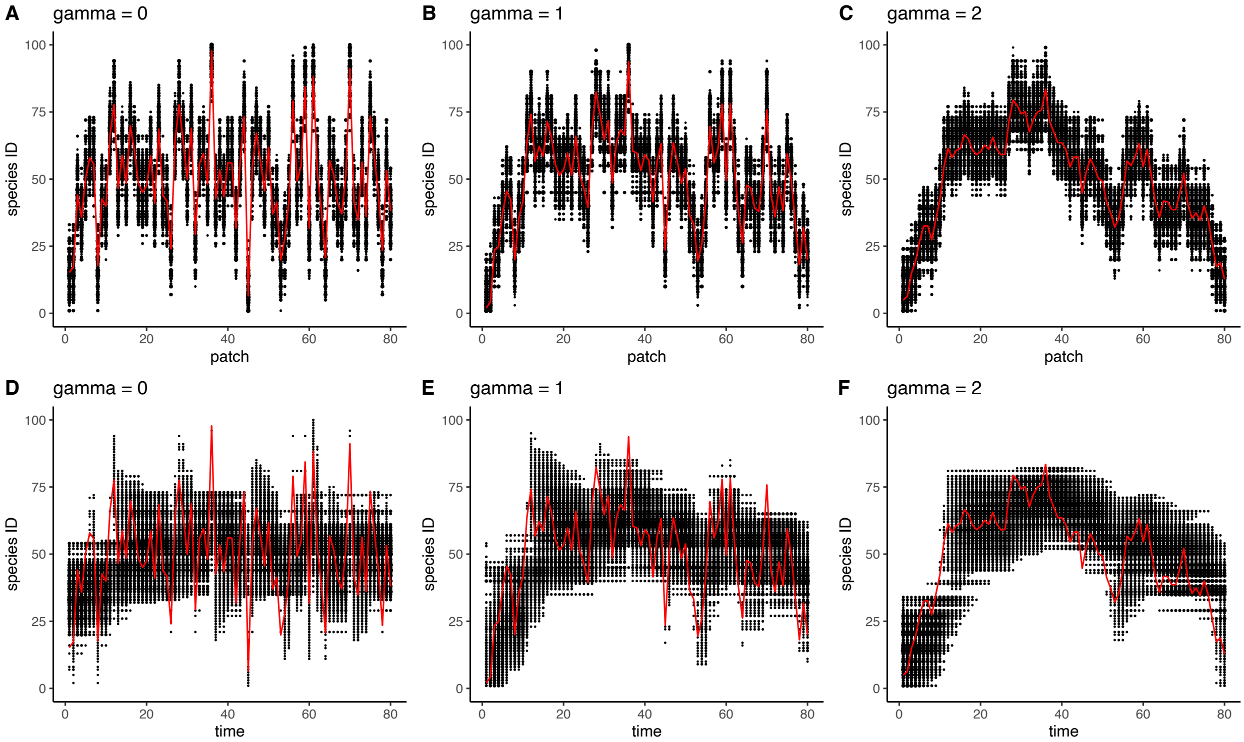

Figure 2: Spatial (A-C) and temporal (d-f) turnover in community composition as a function of environmental autocorrelation (A, D, $\gamma = 0$; B, E, $\gamma = 1$; C, F, $\gamma = 2$). The red line shows the environmental values, standardized to match the environmental optima of the species. Each species is represented by a single position on the y-axis, with the points showing presence in each patch in a temporally constant environment (A-C) or in a single patch in a temporally varying environment time (D-F). Species are ordered by their environmental optima z_i. Results from a single representative run of the model, with 100 potential species, for our spatially variable scenario (a-c) and time-varying scenario (d-f).

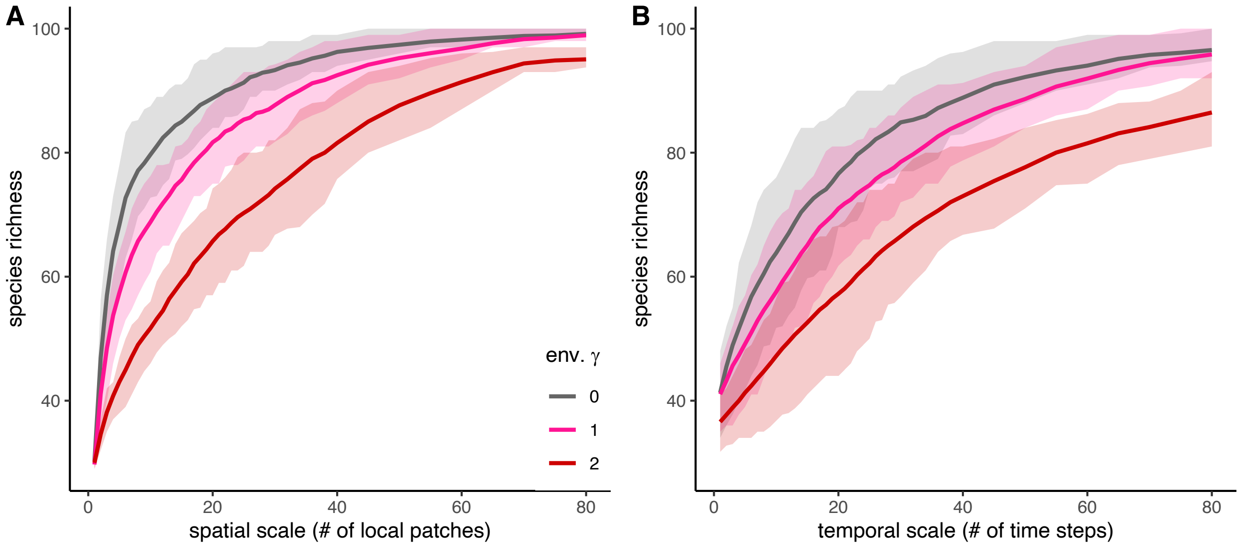

Figure 3. Species richness versus spatial scale (A), and temporal scale (B). Colour indicates the γ value of the degree of autocorrelation of environmental variability. Lines represent the mean and bands represent the interquartile range across 100 replicate simulations with the full species pool.

fewer extreme values compared to when autocorrelation is lower. Species richness increases faster with spatial scale (Fig. 3A) compared to temporal scale (Fig. 3B) because communities are at equilibrium with respect to the environment in the spatial scenario but not in the temporal environment. This non-equilibrium state in temporally changing environments results in a lag in how quickly species richness accumulates.

Cumulative biomass by scale

Biomass accumulates with scale additively and so the average biomass per patch or time point does not depend on the number of patches or time points considered. Because communities are independent in space, the average biomass does not depend on how environmental conditions are autocorrelated across space (Fig. 4A-C). However, the degree of temporal

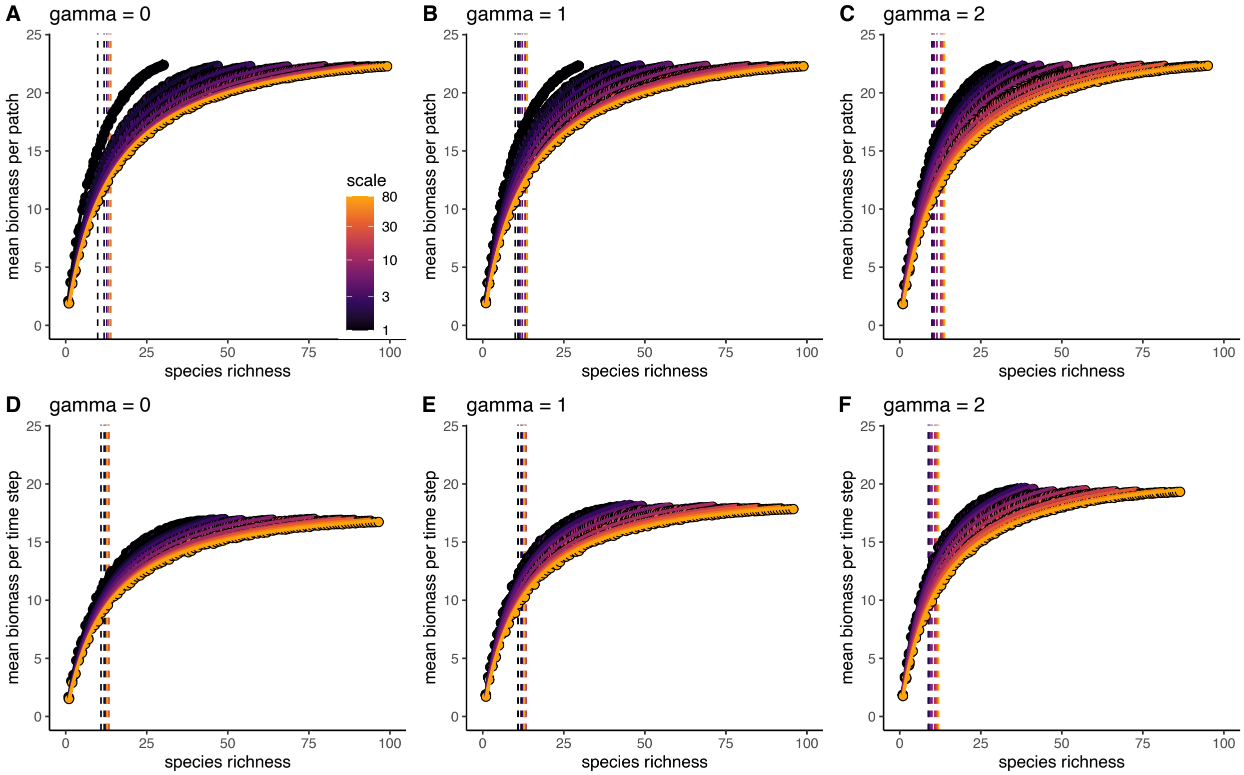

Figure 4. The relationship between species richness and mean biomass across space (A-C) or time (D-F) at multiple scales (colours) with different levels of environmental autocorrelation. To make the BEF curves visually comparable we use biomass per unit area (or unit of time). Environmental autocorrelation is different between panels (A, D, low (γ = 0); B, E, medium (γ = 1); C, F, high (γ = 2)). Colour indicates the scale at which the BEF relationship is observed at (darker = smaller or shorter, brighter = larger or longer). Variation in observed species richness and average biomass within a spatial scale results from different numbers of species used in the simulations (i.e. each data point is the value from a single simulation run with a different number of initial species *S**). Vertical lines show the mean value of the half saturation constant, estimated separately at each scale of observation. Data based on 100 replicate simulation runs.

autocorrelation does influence the average biomass that is produced (Fig. 4D-F). Biomass is higher when environmental conditions are temporally autocorrelated because species sequential environmental conditions allow species to establish and increase in abundance.

The biodiversity–ecosystem functioning relationship and scale

The half BEF saturation richness b_i increases with both spatial and temporal scales (Fig. 4, 5). This means that more species are required to sustain the same amount of biomass per unit area or time over larger scales compared to smaller scales.

When environmental conditions vary across space, the degree of autocorrelation has no effect on community composition or biomass at local scales, and so b_1 (at the single patch scale) has nearly the same value (approx. 8.5; see Fig. 5A) in all cases. But the rate at which b_i increases with scale depends on the degree of environmental autocorrelation, with the fastest increases when environmental autocorrelation is low (i.e. fastest when $\gamma = 0$, slowest when $\gamma = 2$). This is because more species are required to maintain productivity under the high variation in environmental conditions encountered over small spatial scales when the environment varies randomly. But over larger spatial scales, a greater range of environmental conditions is encountered, regardless of the degree of environmental autocorrelation, and so b_i saturates at roughly the same level (approx. 13.5; see Fig. 5A) in all cases. This result is highly dependent on our assumption that a similar range of environmental conditions experienced over large or long scales is the same, regardless of the degree of autocorrelation.

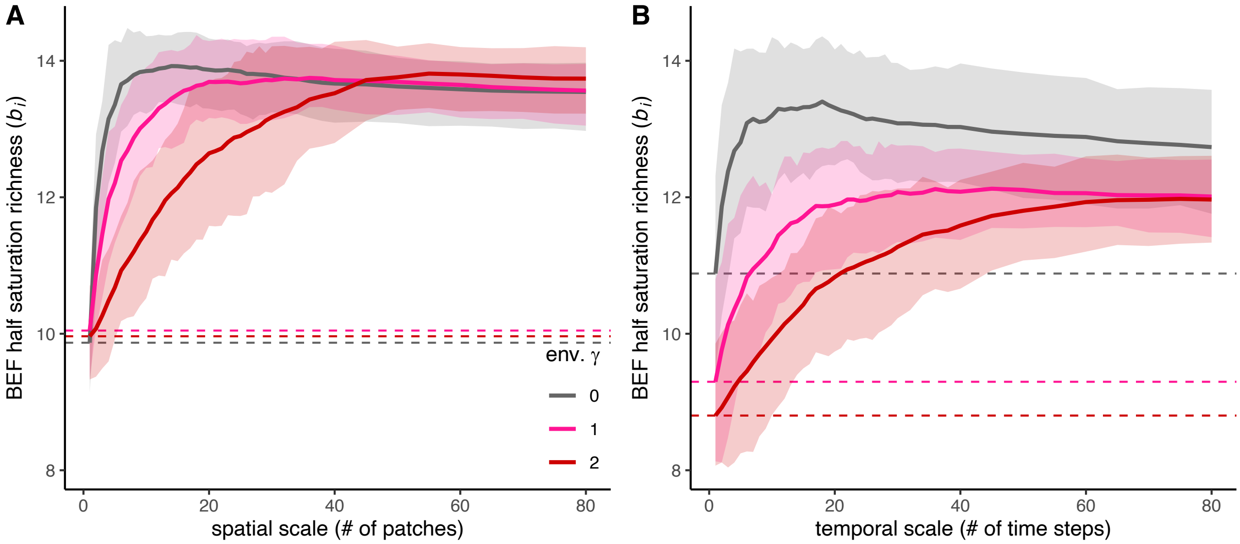

Figure 5. The relationship between the half saturation species richness of the BEF relationship and the spatial (A) or temporal (B) scale of observation. Colour indicates the γ value of the degree of autocorrelation of environmental variability. Dashed lines show the half saturation species richness at a scale of 1. Lines represent the mean and bands represent the interquartile range across 100 replicate simulations.

When environmental variation occurs across time, it impacts communities at short time scales. The local scale b_i is greatest in randomly varying environments (b_1 = 9.3 when γ = 0) and lowest in environments with high autocorrelation (b_1 = 8.1 when γ = 2; Fig. 5). This is because overall biomass is reduced by random temporal environmental variation (Fig. 4) since species never experience sustained environmental conditions and so cannot build up abundance. Therefore, more species are required in order to buffer the wide range of environmental conditions experienced through time. As with spatial variation, the rate at which b_i increases depends on the degree of temporal environmental autocorrelation, with the fastest increases when environmental autocorrelation is low (i.e. fastest when γ = 0, slowest when γ = 2). However, for temporal variation, b_i saturates at higher levels when the environment is random compared to when it is autocorrelated. This is due to the same effect of temporal variation in species performance that impacts the local scale b_i.

Discussion

We have found that the relationship between biodiversity (here the number of species) and ecosystem functioning (here total community biomass) persists at large spatial scales, but that the strength of the relationship changes with spatial and temporal scale when the environment varies. We have shown that the autocorrelation of environmental variation defines the strength of scale dependence in the biodiversity ecosystem functioning relationship (BEF). Simply put, a greater number of species is required to reach the same level of ecosystem functioning over larger spatial and temporal scales if there is more environmental variation at those larger scales. [2] Indeed, the degree of autocorrelation in environmental conditions determines how quickly this species turnover occurs and thus how quickly the number of species required to maintain ecosystem functioning increases with scale. Thus, the scale dependence in the BEF relationship is driven by the rate of species turnover that is required to maintain functioning across locations that differ in environment conditions [2]. Further, the number of species required to maintain function increases fastest with scale when environments have low autocorrelation because a wide range of conditions are encountered over relatively short spatial or temporal scales.

In our model, complementarity and selection effects both contribute to the positive BEF relationship, but their relative contribution shifts with scale. At the small or short scales where species interactions play out, complementarity occurs because intraspecific competition is stronger than interspecific competition (i.e. resource complementarity) [7]. At these scales, selection effects occur because species that are well suited to the abiotic environment produce more biomass than those that are poorly suited. Over larger or longer scales, when environmental conditions vary, these selection effects switch to being spatial or temporal complementarity effects as different species are needed to maintain functioning in different environments [41].

The degree of environmental autocorrelation is a key determinant of species turnover and thus how quickly the number and composition of species varies with spatial or temporal scale [30]. When environmental conditions are autocorrelated, conditions are similar over small spatial or temporal scales, so that the full range of environmental conditions are only found over large spatial scales. Thus, compositional turnover is low and the number of species required to maintain ecosystem functioning increases relatively slowly with scale. In contrast low autocorrelation results in fast environmental change, and so compositional turnover is fast. In general, we expect the scale of compositional turnover to be set by distance and environmental autocorrelation [21,30,42,43]. Differences in composition turnover between plant and animal communities is likely linked to the scales over which they move and experience environmental autocorrelation in the conditions that affect fitness [44]. These general qualitative findings are consistent when considering scaling across space or time, but some quantitative differences emerge for space versus time. Differences between results for time versus space are due to the fact that spatial and temporal environmental variability affects whether communities are at equilibrium, which we discuss in more detail below.

Comparing BEF scaling arising from variability in space versus time

Although spatial and temporal environmental variation both result in similar changes in the BEF relationship with scale, they have different impacts on community turnover, which has implications for how we can detect the contributions of space and time to the scaling of BEF. This is most evident over small and short scales (Fig. 3). These differences between space and time arise because of the way that spatial versus environmental changes affect whether communities are at equilibrium with respect to environmental conditions.

The composition of a community at a given time depends greatly on its previous composition, and so communities are unlikely to be at equilibrium with respect to a temporally varying environment. When environmental change is fast (i.e. autocorrelation is low; Fig. 2E) communities tend to track the averaged conditions. Thus, communities contain species at lower abundances because the environment is rarely ideal for them (Fig. 3D), and the species that do persist are those that are suited to average environmental conditions. When conditions change more slowly (i.e. autocorrelation is high; Fig. 2F), the community composition tracks environmental conditions but 'lags' behind because there is compositional inertia [18]. In contrast, when the environment is constant through time, but varies across space, each site is at equilibrium with respect to its local environment, regardless of the degree of autocorrelation (Fig. 2A-C).

In addition to driving different rates of biodiversity turnover, spatial and temporal environmental variation also impact the BEF relationship in different ways because they affect the levels of ecosystem functioning that are maintained at a given level of species diversity. By holding communities away from equilibrium, temporal variation decreases the average biomass that is maintained in the communities compared to when variation is across space (Fig. 4). Previous research noted this and found that temporally autocorrelated environments generate low-frequency and time-lagged fluctuations in biomass that reduce the contribution of diversity to biomass production at least over short temporal scales [18].

The outcome of these differential patterns of diversity and functioning mean that the degree of environmental autocorrelation has larger impacts in temporally varying environments as compared to the spatial scenarios (Fig. 5). Whereas the level of biodiversity required to maintain functioning—at either the smallest or largest scales—is similar across all types of spatial environmental variation (Fig. 5A), this is not the case for temporal variation. With temporal environmental variation, the number of species required to maintain functioning decreases as autocorrelation increases (Fig. 5B). This is because more species are required to maintain functioning (i.e. biological insurance) [45,46] in our simulations when environmental conditions change rapidly.

Our findings differ from expectations from previous simulations that compositional turnover should lead to a steepening of the BEF relationship with the spatial scale at which it is observed [3]. This is because the increased slope of the BEF relationship in Thompson *et al*. [3] is not the same as the increased half saturation species richness value found here. In fact, an increase in half saturation constant with scale actually corresponds to a decrease in BEF slope with scale if the saturation level of functioning remains constant. The reason for this difference is that here, spatial turnover in community composition occurs because species are not equally productive in all environments, whereas in Thompson *et al*. [3] species contributed equally to ecosystem functioning in all locations, and compositional variation arose through stochasticity. Taken together, these two approaches highlight the general expectation that compositional turnover should lead to a scale dependent BEF relationship, and whether this compositional turnover is driven by environmental factors or stochastic processes should determine if the BEF slope increases or decreases with scale.

Testing this theory

This work provides theoretical predictions that can be tested empirically, in the lab with microcosm experiments, or in controlled surveys and experiments in the field where environmental gradients can be modified or controlled over extended spatial and temporal scales. For example, our findings are consistent with the observation that pollination across sites over landscapes requires much greater diversity compared to that required to maintain pollination in local sites [47]. However, manipulation of environmental autocorrelation is required to perform a strong test of our theoretical expectations. To our knowledge, such an experiment has not been done [2].

In the lab, testing this theory could involve the assembly of many replicate communities varying in diversity and composition and responding to controlled patterns of spatial and temporal autocorrelation in the environment. The methods to do this are available [e.g. 34,48–51]. In the field, tests would require networked experiments over latitudinal gradients, much like BioDepth achieved [52], where species diversity and composition can be modified locally to estimate the slope of the BEF at different locations [51]. At each site, temporal and spatial autocorrelation in one or multiple key environmental variables (e.g. temperature or rainfall) could be manipulated across experimental plots while controlling for the mean and variance of environmental conditions [e.g. 53]. At still larger scales, remote sensing data can be used to link processes, such as primary production (on land and in the oceans), to turnover in taxonomic and functional diversity caused by shifting spatial and temporal environmental gradients obtained from global weather networks. Paleodata may also present an opportunity to assess BEF scaling over thousands of years of historical change in community composition [54]. Each of these approaches offers a different way to test our theoretical predictions, either by exploiting existing environmental gradients or manipulating them to change the scales over which environments are experienced by different assemblages.

Model assumptions and caveats

We expect that our main conclusion—that environmental variation should lead to a greater number of species being required to maintain a given level of ecosystem functioning at larger and longer scales— is most dependent on our assumption that species differ in the environmental conditions in which they are most productive. As discussed above, beta diversity that results from demographic stochasticity rather than environmental heterogeneity may actually have the opposite effect. A valuable next step would be to compare the scale dependence of the BEF in a single model while varying species sensitivity to environmental heterogeneity [sensu 36,55]. Because the scale dependence of the BEF relationship that we find here is driven by environmental heterogeneity, we do not expect our findings to depend strongly on our assumptions about the strength of competition between species. Although positive BEF relationships at small/short scales depend on the assumption that intraspecific competition is stronger than interspecific competition, this is not the case at larger/longer scales, where complementarity can arise through differential responses to spatial environmental heterogeneity [16].

We have assumed that ecosystem functioning is proportional to the abundance of species in our communities. This is likely to be a reasonable assumption when individuals of different species are of comparable size, and when considering ecosystem properties such as biomass. However, in cases when rare species contribute disproportionately to functioning [56,57], our findings may be less relevant. However, as long as environmental heterogeneity results in spatial and temporal variation in species performance, our conclusion that more species are required to maintain functioning over longer and larger scales should still hold.

Finally, we do not expect our main conclusion to be greatly influenced by our assumptions about dispersal. But we do expect that dispersal should affect the degree to which spatial and temporal environmental heterogeneity differ in how they cause the BEF relationship to change with scale. High rates of dispersal between nearby sites would produce mass effects and would cause communities to homogenize [58]. With extremely high rates of dispersal, the spatial and temporal patterns should converge, but this would require dispersal of more than half of the individuals at each time step, after which the temporal inertia of the communities would be overwhelmed. In addition, we expect that such spatial homogenization would reduce the differences between levels of spatial environmental autocorrelation.

Conclusions

Overall, this research contributes to our understanding of how changes in biodiversity at larger scales of space and time will affect the functioning of ecosystems. Our results suggest that at small scales, relatively low levels of biodiversity can sustain ecosystem functioning, but that we need to preserve biodiversity because high levels are necessary to maintain functioning over larger and longer scales where environmental variation is greater. Because environmental variation drives the BEF relationship, our results also demonstrate that the relationship between BEF and scale depends on the degree of autocorrelation of environmental conditions. Given that anthropogenic climate change is altering the autocorrelation of ecologically relevant climate variation in space and time [59,60], our predictions can help inform how changing climate variability may alter relationships between biodiversity and ecosystem functioning at different space and time scales. It is clear that we are just beginning to appreciate the importance of scale in BEF research [2], but this knowledge is needed for understanding the links between biodiversity, ecosystems and people from local to global scales [6].

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