Research

The strength of the biodiversity–ecosystem function relationship depends on spatial scale

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Our understanding of the relationship between biodiversity and ecosystem functioning (BEF) applies mainly to fine spatial scales. New research is required if we are to extend this knowledge to broader spatial scales that are relevant for conservation decisions. Here, we use simulations to examine conditions that generate scale dependence of the BEF relationship. We study scale by assessing how the BEF relationship (slope and R^2) changes when habitat patches are spatially aggregated. We find three ways for the BEF relationship to be scale-dependent: (i) variation among local patches in local (α) diversity, (ii) spatial variation in the local BEF relationship and (iii) incomplete compositional turnover in species composition among patches. The first two cause the slope of the BEF relationship to increase moderately with spatial scale, reflecting nonlinear averaging of spatial variation in diversity or the BEF relationship. The third mechanism results in much stronger scale dependence, with the BEF relationship increasing in the rising portion of the species area relationship, but then decreasing as it saturates. An analysis of data from the Cedar Creek grassland BEF experiment revealed a positive but saturating slope of the relationship with scale. Overall, our findings suggest that the BEF relationship is likely to be scale dependent.

1. Introduction

Much of our understanding of how biodiversity affects ecosystem functioning stems from hundreds of experimental studies and field observations conducted at relatively small scales of space and time, often considered 'local scales' [1–3]. These experiments consider biodiversity effects to be local, because this is the scale at which species interact and compete for resources (e.g. less than 200 m²). At the local scale, selection and complementarity effects [4] generally cause ecosystem functioning to increase with species richness in a positive but decelerating fashion [1,5–7]. Do these findings, and the theory that explains them, apply to larger scales where resource complementarity may occur over regional environmental gradients [8,9]? This gap in our knowledge limits our ability to link biodiversity and ecosystem functioning (BEF) science to the larger spatial scales where conservation decisions are generally made, and which are relevant for the provisioning of many ecosystem services [10]. Extending local mechanisms to broader scales is possible; recent advances in theory now allow us to scale up our understanding of the biodiversity–ecosystem stability relationship [11,12]. Here, we address the similar challenge of providing scaling theory for the BEF relationship.

Scaling the BEF relationship to larger spatial extents is more complicated than simply applying the local BEF relationship to the greater number of species that are present in larger regions [8]. Spatial variation in environmental conditions, connectivity, biotic interactions and stochastic processes causes local communities

to differ in composition [13] and in the shape of their BEF relationships [2,14]. Recent studies have highlighted the importance of compositional turnover in space (β-diversity) in maintaining high rates of ecosystem functioning at landscape scales, because greater diversity is required to maintain ecosystem functioning across the range of environmental conditions present in larger regions [15–19]. Because of this, we might expect that the BEF relationship should become stronger at larger spatial scales [8,9]. This importance of regional biodiversity is further supported by metacommunity models comprising two spatial scales, where productivity is more strongly dependent on regional than local diversity, but the slope of the BEF relationship locally and regionally is mediated by dispersal, which affects the β-diversity present in the region [20–22]. However, Cardinale et al. [23] demonstrated that the slope of the BEF relationship can be constant across spatial scales (from small to large extents) if the local BEF relationship as well as the community composition is equal across all local patches. Thus, in this unlikely scenario of homogeneous conditions across space, changes in local diversity result in similar proportional changes to the biodiversity of the region. However, Cardinale et al. [23] and Chesson et al. [24] found that the processes driving the BEF relationship change with spatial scale, with selection effects becoming complementarity effects at broader spatial scales if species tend to dominate local habitat patches that match their niche requirements [22].

To develop theoretical expectations for scaling the BEF relationship, we can start with our understanding of the relationship at local scales for which there exists substantial theoretical understanding and empirical evidence. Theory suggests that the relationship between ecosystem functioning and local species richness (α-diversity) is driven by complementarity and selection effects [5,7,25]. This theory is supported by empirical evidence from hundreds of experiments that report a relationship that can be described as a power law, $Y = aS^b$, where Y is the level of ecosystem function, S is the number of species present, a is a constant, and b is the exponent of the BEF relationship (or the slope in log–log space), which indicates the strength of biodiversity effects (i.e. the proportional change in ecosystem functioning per change in richness [1,2,6,26]). The shape of this relationship, described by the value of b, can vary among locations and communities, and with attributes, such as trophic level and over time.

In reality, biodiversity generally only explains a fraction of the variation in the ecosystem functioning at local scales because other factors, such as soils or climate, are also important for functioning [27]. For example, in experiments designed to test for the BEF relationship, it is typical for less than half of the variance in ecosystem functioning to be explained by local diversity (e.g. [6]). If environmental factors change with spatial scale, then we may expect the explanatory power of the BEF relationship (i.e. the coefficient of determination, R^2) to also change with spatial scale. In scaling up, it is unclear whether biodiversity will still be an important predictor of ecosystem functioning. Therefore, in considering how the BEF relationship changes with spatial scale, we must consider both changes in the slope of the relationship as well as changes in the explanatory power of the relationship.

This power-law relationship $Y = aS^b$ allows us to consider what would be required for the BEF slope, b, to change with spatial scale. In previous applications of this relationship, S is equal to α-diversity, the diversity present at the local scale where species interact and compete for resources. Scaling

this up to larger regions, for example, landscapes comprised many local habitat patches, requires that we consider the relationship between γ-diversity, the diversity present across all patches at a given spatial scale, and the total ecosystem functioning at that scale. For b to remain constant across spatial scales, then proportional changes in α- and γ-diversities must result in the same proportional change in ecosystem functioning. Our question is therefore: what causes proportional changes in α- and γ-diversities to result in different proportional changes in ecosystem functioning, and when this occurs, does it result in an increase or decrease in the BEF slope? Furthermore, how does the predictive power of the BEF relationship change with spatial scale? And do effects of scale depend on whether the BEF relationship is strong, weak, positive or negative?

Here we develop basic theoretical expectations for how the slope of the biodiversity–ecosystem functioning relationship might change with spatial scale. For this, we use simulation models to explore how variation in different BEF parameters (a, S and b, of $Y = aS^b$), as well as different patterns of β-diversity, causes the BEF relationship to change with spatial scale. In taking this approach, we do not directly consider the ecological mechanisms driving this variation (e.g. environmental heterogeneity, connectivity and biotic interactions), which can also directly affect rates of ecosystem functioning. Rather, we simply ask how spatial variation in community composition and the shape of the local BEF relationship might be expected to cause the BEF relationship to change with spatial scale. We do this by simulating regions composed of local habitat patches where functioning in each local patch depends on the number of species in that patch, following $Y = aS^b$. We aggregate these local patches to estimate the BEF relationship over larger spatial scales. Regional ecosystem functioning is assumed to be the sum of functioning in all patches, while γ-diversity is assumed to be the number of species across all local patches in the region. Therefore, γ-diversity will be less than the sum of the α-diversity in all patches when there is compositional overlap among patches. We start with a control case study (case I), in which we demonstrate how the BEF relationship remains constant across spatial scales when (i) the BEF relationship is constant across all local patches and (ii) community composition is equal across all local patches, following Cardinale et al. [23]. We then explore four case studies, each deviating from these initial criteria in one way: case II, variation in local a; case III, variation in local S; case IV, variation in local b; case V, β-diversity among local patches. In cases II–V, we explore how the slope and explanatory power of the BEF relationship changes with spatial scale. Cases III–V, but not I or II, change the slope of the BEF relationship with spatial scale. Of these, case V (β-diversity) shows the largest scale dependence, whereas the changes in b with increasing spatial scale in cases III and IV are relatively minor in comparison. We then compare these theoretical expectations with empirical data from the Cedar Creek biodiversity experiment to show how our expectations hold in empirical communities where the local BEF relationship arises through biological interactions.

2. Simulation model

We simulate the BEF relationship at multiple spatial scales by modelling regions composed of local habitat patches governed by
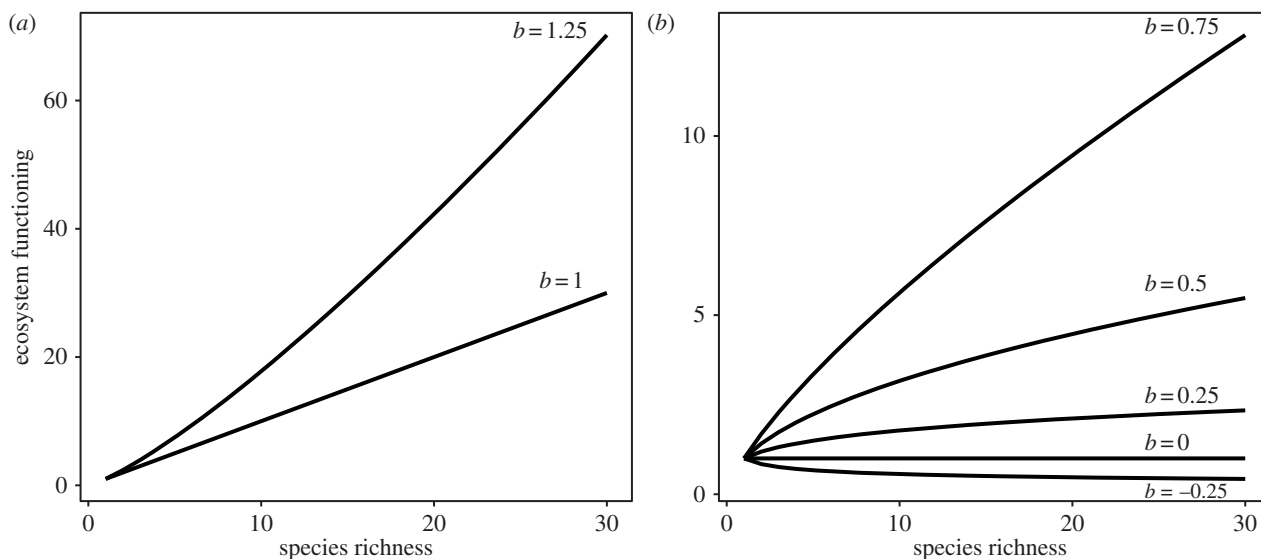
$$Y_i = a_i S_i^{b_i}, \tag{2.1}$$

Figure 1. Illustration of the shape of the BEF relationship with different values of b. Higher values of b are shown in panel (a), lower values of b are shown in panel (b). This separation was done for clarity to show the curvature of the BEF relationship for low values of b.

where Y_i is the level of ecosystem function in patch i, S_i is the number of species present, a_i is a coefficient that determines the magnitude of the BEF relationship in a patch, and b_i is the exponent of the BEF relationship in that patch. We scale ecosystem functioning to larger spatial areas by

$$Y_A = \sum_{i=1}^{A} Y_i, \tag{2.2}$$

where A is the number of local patches comprising the region. S_A is the number of species in the region. At each spatial scale, A, we estimate the slope of the linearized BEF relationship, b_A, given

$$Y_A = a_A S_A^{b_A}, \tag{2.3}$$

which we estimate using linear, least-squares, regression on a log–log scale across 2000 simulated replicate regions. We repeat this procedure 100 times to obtain replicate estimates of b_A to estimate variability across simulation runs. To test the sensitivity of results to different possible BEF relationships, we contrast seven different values of $\overline{b_i}$ ranging from -0.25 to 1.25. This incorporates the various shapes of the BEF curve observed in empirical data [1,2,28]: negative decelerating $(-1 < b_i < 0)$, no relationship $(b_i = 0)$, positive decelerating $(0 < b_i < 1)$, positive linear $(b_i = 1)$ and positive accelerating $(b_i > 1)$ (figure 1). In our simulations, we have assumed that the BEF relationship follows a power law. However, our conclusions should not depend on the specific functional form used, but rather whether the BEF relationship is linear or nonlinear, and whether the curve is concave up or down. All simulations were performed in R v. 3.4.2 [29].

3. Case I: control—no variation in a_i, α richness, b_i, and no (or maximum) β-diversity across patches

In case I, we assume that all patches in a region have equal a_i, S_i and b_i, and that β-diversity is either zero (all patches with the same composition) or maximal (all patches contain different species). We generate variation in diversity across replicate regions by drawing different values of S_i from a normal distribution centered on 10 with a standard deviation of 3,

rounded to the nearest integer and, excluding non-positive cases.

We find that b_A and the R^2 of the BEF relationship remain constant across spatial scales (figure 2; electronic supplementary material, figure S1). This is true regardless of whether we assume that all patches contain the same set of species or completely unique species (same relationship as figure 2).

4. Case II: variation in a_i across local habitat patches

In case II, we draw values of a_i from a normal distribution with a mean of 5 and a standard deviation of 2, excluding non-positive values. We assume that b_i is equal across all patches, and that all patches contain the same species.

We find that variation in a_i does not cause the mean BEF slope, b_A, to change with spatial scale (figure 2a). This is because a is a linear coefficient in the local BEF relationship and so there is no potential for nonlinear averaging to cause the BEF relationship to change with spatial scale. However, variation in a_i does reduce the explanatory power of the BEF relationship (figure 2b), but this explanatory power increases as spatial scale is increased. Aggregating patches at larger spatial scales reduces noise in the local BEF relationship associated with variation in a_i.

5. Case III: variation in α richness across local habitat patches

In case III, we draw values of S_i from a normal distribution with a mean of 10 species and a standard deviation of 3, rounded to the nearest integer and excluding non-positive values. We assume that b_i is equal across all patches, and that all patches contain unique species, to avoid incomplete compositional turnover. Note that it is not possible to have complete compositional overlap between patches when S_i varies across patches.

We find that the mean BEF slope, b_A, changes with spatial scale, and this variation across scales depends on the shape of the local BEF relationship (figure 2a). When the local relationship is positive and decelerating $(0 < b_i < 1)$, as is most often
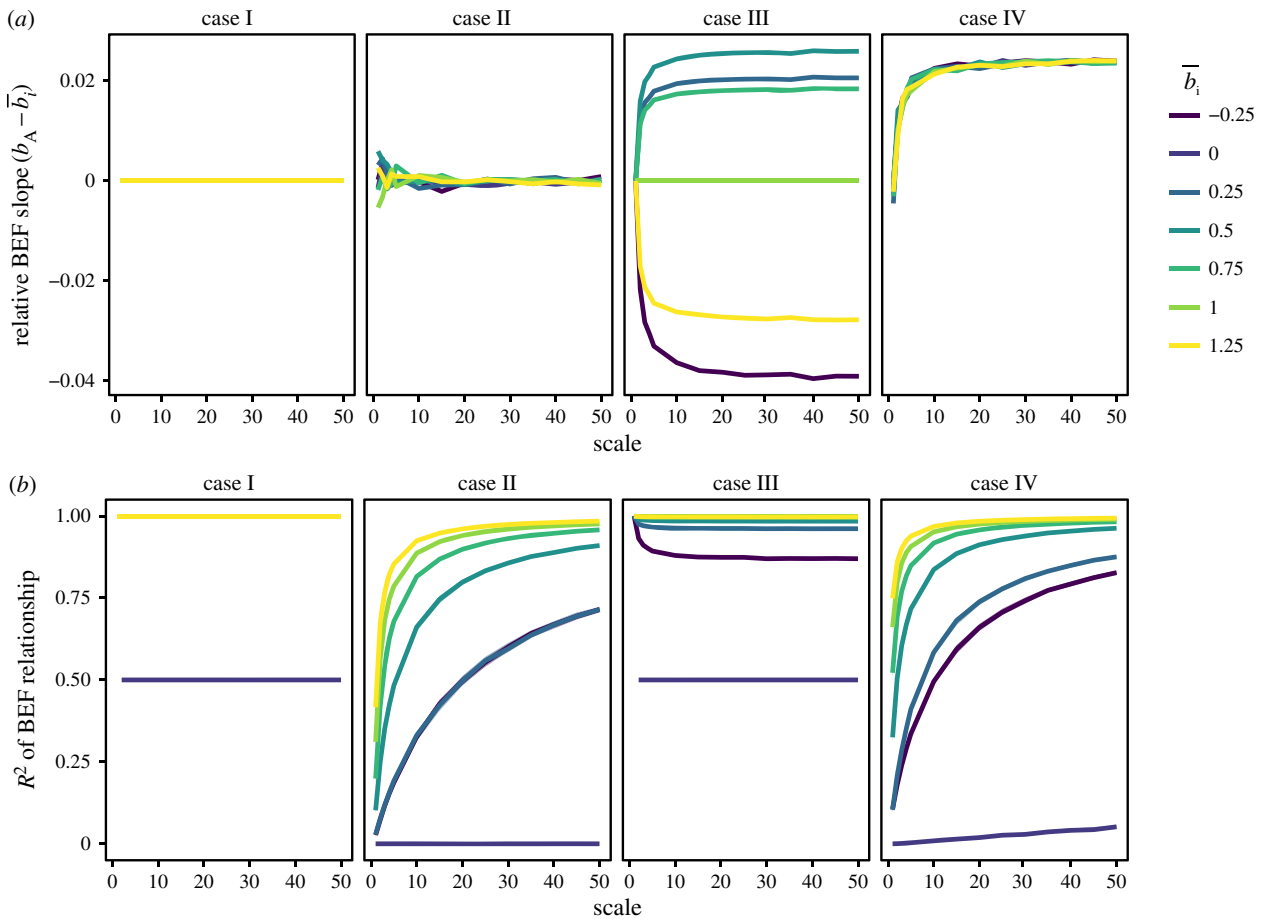
Figure 2. Illustration of how the BEF relationship changes with spatial scale in cases I–IV. Panel (*a*) shows how the BEF slope, b_A changes relative to the mean local slope $\overline{b_i}$, at different spatial scales (see electronic supplementary material, figure S1 for raw values of b_A). Panel (*b*) shows the R^2 of this relationship. The four cases are shown in the different panels—no variation in local species richness or local b_i (case I), variation in local a_i (case II), variation in local S (case III) or variation in local b_i (case IV). The solid line shows the median across 100 replicate simulations each consisting of 2000 replicate regions at each scale. Inter-run variability omitted for clarity in panel (*a*), but shown in electronic supplementary material, figure S1. In panel (*b*), the interquartile range is smaller than the width of the lines and so is not shown. (Online version in colour.)

the case in empirical data [2,28], b_A increases as a saturating function of increasing spatial scale. When the local relationship is linear, either due to no relationship ($b_i = 0$) or a linear relationship ($b_i = 1$) between species richness and function, b_A does not change with spatial scale (electronic supplementary material, figure S1). When the local relationship is negative and decelerating ($-1 < b_i < 0$) or positive and accelerating ($b_i > 1$), b_A decreases as a saturating functioning of increasing spatial scale. Across multiple local patches, the strength of biodiversity effects changes with spatial scale to a greater or lesser extent, as shown by the interquartile range around the mean trends in (electronic supplementary material, figure S1), due to variation in local species richness across replicate random draws of species richness within patches. Across all possible values of b_i, except when the local BEF relationship is linear ($b_i = 0$ or 1), there is a slight decrease in the R^2 of the BEF relationship with scale, with the greatest decrease occurring with the smallest values of b_i (figure 2*b*).

Variation in α richness across a region leads to a saturating change in b_A with increasing spatial scale because of nonlinear averaging (i.e. Jensen's inequality [30,31]) of the contribution of each local patch to the functioning of the region (electronic supplementary material, figure S2*a*). That is, because the local BEF relationship is nonlinear, changes in diversity result in greater changes in ecosystem functioning in low-diversity compared with high-diversity patches, although the opposite is true

when the BEF relationship is accelerating ($b_i > 1$). Consequently, whether b_A increases or decreases with spatial scale depends on local BEF relationships' shape. In summary, when the relationship is concave down (e.g. positive decelerating; figure 1), as is typical of local BEF relationships, b_A increases with spatial scale. When the relationship is concave up (e.g. positive accelerating or negative decelerating), b_A decreases with spatial scale.

6. Case IV: variation in b_i across local habitat patches

In case IV, we hold S_i equal across all patches in a region but now draw b_i for each patch from a normal distribution centred on $\overline{b_i}$, with a standard deviation of 0.15; this variance corresponds roughly to what has been observed in experimental grassland plant communities [2,14] and in local forest communities [28]. We generate variation in diversity across replicate regions as in case I. To avoid incomplete compositional turnover, we assume that all patches contain unique species, but our estimated values of b_A are the same if we assume that all patches share the same set of species, as this would also meet this requirement.

We find that the mean BEF slope, b_A, increases as a saturating function of increasing spatial scale, regardless of the value
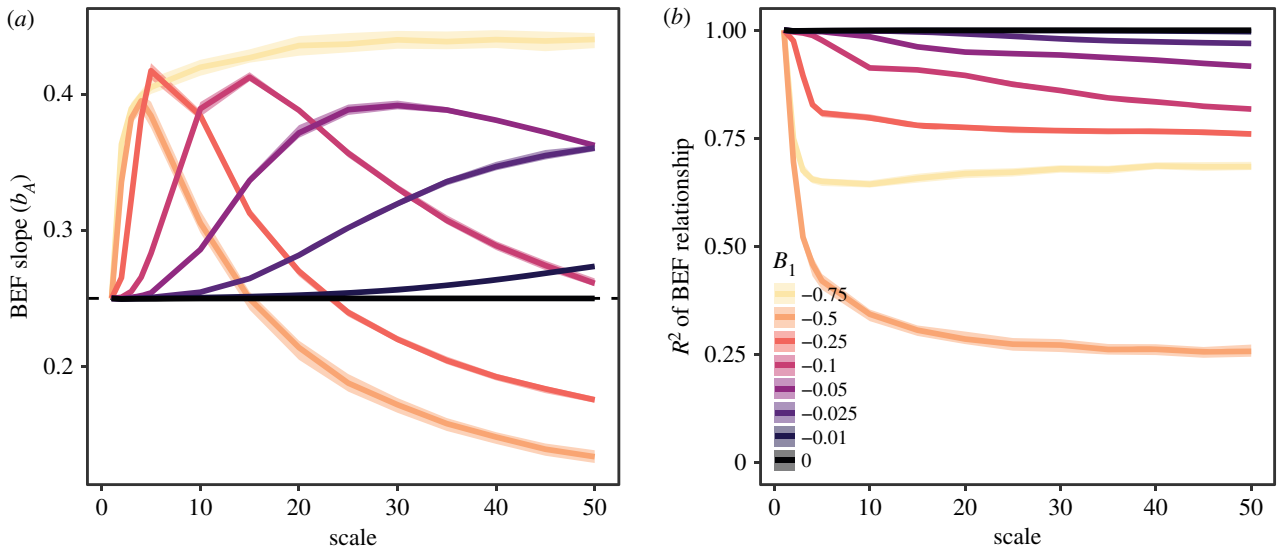
Figure 3. The strength of biodiversity effects, b_A (panel (a)) and R^2 (panel (b)), at different spatial scales when there is incomplete compositional turnover across local patches. Different degrees of compositional turnover are indicated by colour (low values of B_1 correspond to low turnover, $B_1 = 0$ indicates complete turnover). The solid line indicates the median across 100 replicate simulations each consisting of 2000 replicate regions at each scale. The bands show the interquartile range. (Online version in colour.)

of $\overline{b_i}$ (figure 2a). In this case, there is considerable variation in b_i across local patches (electronic supplementary material, figure S1), as dictated by our assumptions, but because this variation is averaged at larger spatial scales, we find that the disproportionate effect of biodiversity change on local function in communities with high b_i (electronic supplementary material, figure S2b) causes the average b_A to increase. This variation at local scales, and the averaging out at larger spatial scales causes the R^2 of the BEF relationship to increase in a saturating manner with spatial scale (figure 2b). This occurs because variation in b_i adds noise to the local BEF relationship, but this noise is reduced by aggregating patches at larger spatial scales.

In this case, variation in the slope of the BEF relationship across patches, b_i, leads to a positive saturating increase in b_A with spatial scale (figure 2), now, because of nonlinear averaging of the contribution of each patch to regional ecosystem functioning. A given change in α richness in patches with higher than average b_i will have a proportionally greater effect on regional ecosystem functioning than would the same change in α richness in patches with lower than average b_i (electronic supplementary material, figure S2b). Therefore, as we aggregate across larger and larger regions, we are more likely to capture a greater range of b_i, and so changes in γ richness result in a greater proportional change in ecosystem functioning than they would at small scales.

7. Case V: β-diversity across patches

In case V, we explore how different levels of β-diversity affect how the BEF relationship changes with spatial scale. We again assume equal S_i across all patches in a region, and an equal b_i. However, across replicate simulated regions, S_i is drawn from the same normal distribution as in the previous cases. We now determine the regional species richness S_A by combining the patches in the region, one at a time, and determining whether species are already present in the region by $p = e^{(\beta_0 + \beta_1 S_{\hat{A}})}/(1 + e^{(\beta_0 + \beta_1 S_{\hat{A}})})$, where p is the binomial probability that a new species is unique. β_0 and β_1 are the intercept and slope of the logit model that determines the rate at which this probability decreases with $S_{\hat{A}}$, the number of species in the

communities that have been combined. In our simulations, we set $\beta_0 = 5$, and we contrasted a range of β_1 (-0, -0.05, -0.1, -0.25, -0.5 and -0.75) to explore how the BEF scaling relationship depends on the species accumulation rate across space. The value of β_1 determines the shape of the species area relationship (SAR), with high and low values resulting in steep and shallow SARs, respectively (electronic supplementary material, figure S3).

We find that the BEF slope, b_A, increases with spatial scale, peaking at intermediate scales and then decreasing (figure 3a), while variation in ecosystem functioning explained by γ-diversity decreases as a saturating function with spatial scale (figure 3b). These effects are consistent across all values of $\overline{b_i}$, although the pattern flips when $\overline{b_i}$ is negative (electronic supplementary material, figure S4). The magnitude of the peak in b_A and the scale over which it occurs depends on the degree of compositional turnover. The peak is greatest, and occurs at the lowest spatial scales, when compositional turnover is low. It decreases in magnitude and shifts successively to higher spatial scales as compositional turnover increases. Likewise, the scale at which b_A falls below b_1 increases as compositional turnover increases. The magnitude and speed of the decline in R^2 of the BEF relationship with spatial scale also increase as functional turnover increases. When compositional turnover is high, b_A remains equal or greater than b_1 across the full range of scales considered. Consistent with case I above, with complete compositional turnover ($\beta_1 = 0$), there is no effect of scale on b_A.

In this case, the slope of the BEF relationship changes with spatial scale because changes in mean α richness do not result in the same proportional change in γ richness. Incomplete compositional turnover drives two mechanisms, which together determine how b changes with spatial scale: (1) proportional changes in γ richness are always less than proportional changes in α richness; and (2) the correlation between α and γ richness becomes weaker at larger spatial scales.

Mechanism 1 causes b_A to increase with spatial scale because it means that a proportional change in γ richness allows for a greater change in ecosystem functioning compared with the same proportional change in α richness. This mechanism is strongest when β-diversity is low. Mechanism 2 causes

b_A to decrease with spatial scale because it erodes the signal of the local BEF relationship, which is ultimately responsible for driving b_A at larger spatial scales. This is because as spatial scale increases, so does the range of possible α-richness values that can lead to the same γ-richness. For example, in a simulated region of 10 patches, a γ-richness of 10 can result from each patch containing a single unique species, from all patches containing the same 10 species, and every scenario in between these extremes. However, these two regions would have very different levels of biodiversity-driven ecosystem functioning, and so the relationship with γ-richness is weak. The strength of mechanism 2 increases with spatial scale as the number of possible values of α-richness for each level of γ-richness increases. However, it depends on the level of β-diversity in the region; greater β-diversity leads to a slower increase in the strength of the mechanism with spatial scale. Because of mechanism 2, the local signal of the local BEF relationship can be lost entirely at larger spatial scales and so b_A decreases to 0. Together these two mechanisms cause b_A to have a hump-shaped relationship, increasing at small spatial scales because the first mechanism dominates, but then decreasing at larger scales as the second mechanism increases in strength.

A variation on the pattern described above occurs when compositional turnover is extremely low ($p = 0.75$). In this case, the decline in b_A at large spatial scales is slower than it is when compositional turnover is higher (figure 3a) because only low-diversity plots have differences in composition and so γ richness increases in regions with low, but not high α-diversity. As in the other cases, this results in a steepening of the BEF relationship. However, this increase in slope persists at larger spatial scales as most of the changes in γ richness occur when the first few low-richness plots are aggregated.

8. Experimental comparison using the Cedar Creek biodiversity experiment

We analysed the Cedar Creek biodiversity experiment data for above-ground biomass to ask whether the BEF relationship across spatial extents observed in this empirical dataset is consistent with our theoretical predictions. The experiment included 18 species, drawn at random in combinations of 1, 2, 4, 8 and 16 species. To estimate the BEF relationship at spatial scales larger than a single plot ($81 \ m^2$) we simulated regions by randomly drawing individual plots. We excluded all plots with 16 species because γ-diversity in the experiment was 18 so these plots contained almost all species. Excluding these plots allowed for a greater range of species richness resulting from random draws of plots at each spatial scale. We also excluded all plots that were not sampled in all years of the experiment. We then summed the above-ground biomass and calculated the number of unique species that were planted in the plots in each simulated region. We did this at increasing spatial extents spanning the range from one plot to 30 plots. We were unable to extend our approach to larger spatial scales because the limited species pool in the experiment caused γ-diversity to converge on one or two values at all larger spatial scales, preventing us from accurately estimating b_A. We repeated this process 5000 times at each spatial scale for each of the 14 years in the dataset. For each random draw of plots, we estimated biomass and species richness in each year of the experiment. We then estimated the slope of the BEF

relationship, b_A, as we did in our simulations. We then estimated the median and interquartile range of b_A across all years. To isolate the mechanism causing the BEF relationship to change with spatial scale, we performed the same simulation, but ignored the species identities and assumed that all patches contained unique species. This eliminates incomplete compositional turnover (i.e. maximizes compositional turnover) and makes γ-diversity unbounded.

Consistent with our theoretical predictions from cases III–V, we find that b_A increases with spatial scale but appears to saturate at the largest spatial scale considered (figure 4a, dark grey). At the same time, the BEF relationship R^2 decreases asymptotically as scale increases, reaching close to zero by $2000 \ m^2$ (roughly 24 aggregated patches; figure 4b). Because the limited species pool in the experiment precludes us from estimating the BEF relationship at larger spatial scales, we cannot determine whether the saturation in the slope, b_A, and the R^2 of the BEF relationship is due to biological processes or constraints to do with the size of the species pool. From this test of the model predictions, we cannot identify which of the three mechanisms (cases III–V) may or may not be responsible. We hypothesize that the pattern is dominated by the effect of compositional turnover as the increase in b_A disappears when we assume that local patches have unique species (figure 4a, light grey). By assuming that patches have unique species, we remove any compositional overlap and so artificially elevate γ-diversity.

9. Discussion

Our work shows that the relationship between BEF is expected to change with the spatial scale at which it is observed. We have identified three mechanisms which can drive this scale dependence: (i) variation in species richness across local habitat patches in a region (case III), (ii) variation in the strength of the BEF relationship across local habitat patches in a region (case IV) and (iii) incomplete compositional turnover across local habitat patches in a region (case V). The first two mechanisms result from the effects of noninear averaging on the effects of diversity change in low- versus high-diversity patches or in patches with weak versus strong BEF relationships, respectively. The third mechanism, which results in the greatest changes in the BEF relationship with spatial scale, results from the fact that, with incomplete compositional turnover, proportional changes in mean γ-diversity are always less than proportional changes in mean α-diversity, and because the explanatory power of γ-diversity on changes in ecosystem functioning decreases with spatial scale. When the local BEF relationship is positive and decelerating, as has generally been found in experiments and often in field observations [1,2,28], the first two mechanisms cause the slope of the BEF relationship to increase with spatial scale, while the effect of the third mechanism is more variable and depends on the degree of compositional turnover present in a region. However, in general, the slope of the BEF relationship is expected to increase with spatial scale when species accumulate with space, but to decrease when this accumulation has saturated. Overall, our findings provide an expectation for a scale-dependent BEF relationship.

While all three mechanisms probably contribute to scale dependence of the BEF relationship, we expect that effects of incomplete compositional turnover should dominate the
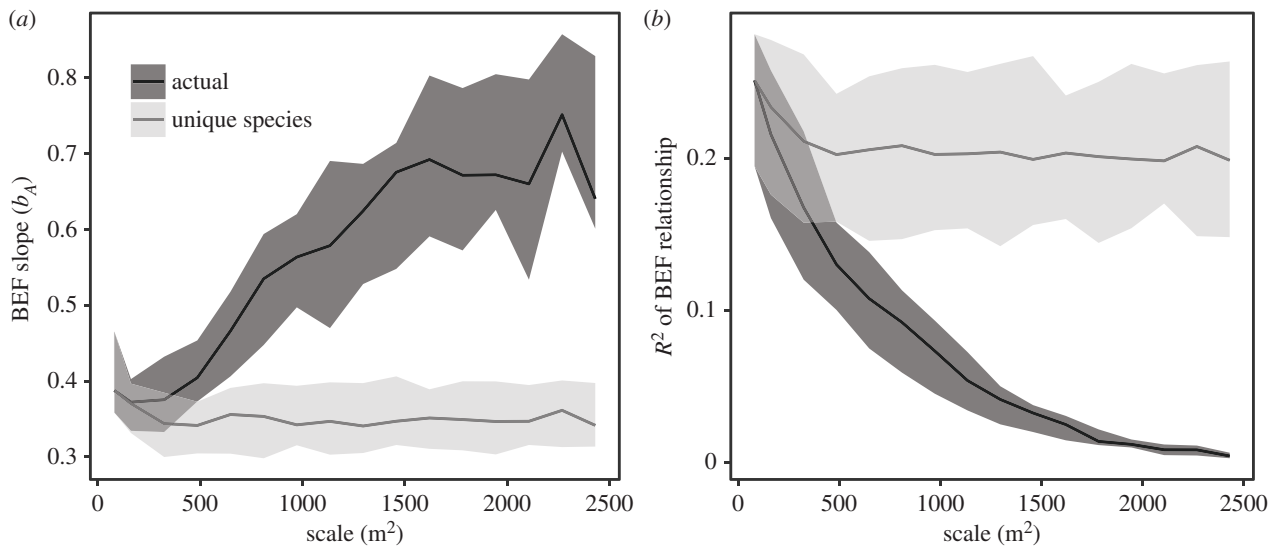
Figure 4. The strength of biodiversity effects, b_A (panel (a)) and R^2 (panel (b)), estimated for each year at each spatial scale in the Cedar Creek simulations. Values of b_A were estimated at each spatial scale by drawing 5000 replicate combinations of local plots and estimating the slope of the relationship between their aggregated biomass and their unique species in log–log space. Local scale plots were 81 m^2 and the max spatial scale corresponds to 24 plots aggregated together. The dark grey shows the results when the species identities from the experimental plots were used to estimate γ-diversity, the light grey shows the results when all plots were assumed to consist of unique species. The solid line indicates the mean across all 14 years in the dataset, the bands show the interquartile range.

other two scaling mechanisms in most landscapes, and in controlled experiments, such as in our analysis of the Cedar Creek experiment. This expectation is based on the fact that the overall magnitude of change in the BEF slope was up to 10 times greater in case V (incomplete compositional turnover) than in the other two cases. These findings are consistent with other studies that have demonstrated the importance of β-diversity in maintaining ecosystem functioning at landscape scales [16–19]. Our approach with the Cedar Creek experimental data, where we created simulated landscapes by randomly combining local scale plots, is similar to the approach taken by Pasari *et al.* [16], van der Plas *et al.* [17] and Hautier *et al.* [19]. However, we have done this over a range of spatial scales, rather than at a single larger spatial scale, which allows us to more generally consider how scale affects the BEF relationship. Further to the direct effect of incomplete compositional turnover, these empirical studies also highlight how spatial differences in dominance and productivity of individual species can lead to positive BEF effects. Such spatial insurance effects may be important drivers of how the BEF relationship changes with spatial scale [32], and are not included in the mechanisms that we have identified here. In addition, variation in local species richness or the local slope of the BEF relationship would increase the relative contributions of these scaling mechanisms (cases III and IV) to BEF scaling across the landscape. However, this variation would have to be much higher, probably unrealistically high, to reveal effects on scale dependence of similar magnitude as those that can result from incomplete compositional turnover. Therefore, we expect that increases in the BEF slope are most likely to be driven in nature by the loss or gain of species that are shared across multiple local sites in a region, because it is these shared species that cause changes in α-diversity to proportionally exceed changes in γ-diversity.

The range of spatial areas over which we should expect the slope of the BEF relationship to increase remains unresolved and depends in part on the shape of the SAR, which captures how species accumulate across space. When the SAR saturates quickly, reflecting low β-diversity, we expect the BEF slope to

peak at small spatial areas, and then decline with increasing area sampled. In such scenarios, the slope of the BEF relationship at large spatial extents may be lower than it is at local scales. By contrast, when the SAR is slow to saturate with increasing area sampled, we expect the BEF slope to rise more slowly with increasing area, and remain high over a larger range of scales. This pattern is consistent with what has been shown for the invariability–area relationship [11], where invariability in ecosystem functioning increases at local scales, but then saturates at regional scales. Of course, our analysis has not considered very large scales (e.g. continental), where species area relationships have been found to steepen again [33,34]. In this case, we may expect to see a further steepening of the BEF relationship, as has been found for invariability [11].

Our results provide a theoretical expectation for how and why the BEF relationship should depend on the spatial scale at which it is observed. They suggest that the way that this scale dependence is realized in real ecosystems will depend on the abiotic and biotic processes that determine patterns of α-, β- and γ-diversities, and rates of ecosystem functioning. Because our goal was simply to develop basic theoretical expectations for how and why the BEF relationship should change with spatial scale, we intentionally omitted these processes from our simulations. Further development of this theory should now consider the ecological processes that would determine how this scale dependence will play out in real landscapes. An obvious next step would be to develop expectations for how environmental heterogeneity across time and space [32], should cause the BEF relationship to change with scale, via its influence on β-diversity. Linking these expectations to observed environmental conditions and patterns of β-diversity could give us predictions about how the BEF relationship should change with scale in a given landscape. Furthermore, metacommunity processes such as dispersal and spatial connectivity are known to alter patterns of biodiversity, community composition and the strength of the BEF relationship (i.e. spatial insurance) [13,20,21]. For example, dispersal can both increase and decrease β-diversity, and can be an important determinant of the

number of species present at a site, and whether they are well suited to the prevailing conditions. Future progress on this topic should focus on understanding how these ecological processes lead to scaling via the mathematical mechanisms that we have identified in this paper.

To accomplish these goals, we see three obvious avenues forward: (i) simulation models that allow composition to depend on the local abiotic and biotic conditions in each local habitat patch and the spatial gradients of abiotic conditions and connectivity of patches; (ii) experiments that vary α, β and γ-diversities across a range of spatial scales; and (iii) field observations (e.g. [17,28]) where community properties can be nested at multiple spatial scales to estimate the effects of biodiversity on ecosystem functioning. Simulation models offer the opportunity to further develop this theory and incorporate additional ecological processes that we expect should be critical in determining the scale dependence of the BEF relationship. Experiments and field observations offer the opportunity to test and isolate the contribution of the different scaling mechanisms that we have identified here. Furthermore, field experiments can also provide information on how much natural ecosystems vary in the parameters that we have found to be drivers of BEF scaling. In our analysis of the Cedar Creek data, we were able to identify that the BEF relationship depends on spatial scale in empirical data, but unfortunately this experimental design did not allow us to tease apart the specific contributions of the different mechanisms, although it appears that compositional turnover is important. However, experiments could be designed that would differentiate these mechanisms, for example, by manipulating levels of spatial compositional turnover in species richness. Variation in the slope of the BEF relationship could be removed by calculating the predicted levels of ecosystem functioning in each local patch based only on the number of species in the patch, and the average BEF relationship in the experiment.

Our conclusion, that a scale-dependent BEF relationship is expected, extends previous theory on this topic [23], which suggested that the BEF relationship should be consistent across spatial scales. In their case, Cardinale *et al.* [23] assumed that all species in a region were present in every patch, and that the strength of the BEF relationship was constant across patches. These assumptions meet those of case I in our study, where the BEF relationship is not scale dependent. However, few (if any) real landscapes conform to these strict criteria. For example, environmental heterogeneity, spatial distance and stochastic factors lead to compositional turnover in space [35]. Therefore, we suggest that our expectation should be for a scale-dependent BEF relationship.

Our findings provide a theoretical understanding of why we should expect the BEF relationship to vary with the spatial scale at which it is observed. They suggest that we cannot simply apply our current understanding, which is almost exclusively based on small-scale experiments and observations [1–3], to understand the consequences of biodiversity change at larger spatial scales without a theoretical framework for scale-dependent change. We have identified three mechanisms, which drive the scale dependence of the BEF relationship. We must now apply this understanding to real landscapes [9], where patterns of biodiversity, composition and ecosystem functioning are determined by abiotic and biotic gradients, rather than by statistical probabilities, as they are in our simulations. To this end, our findings provide an important step towards linking our understanding of BEF science to the spatial scales that are relevant to conservation decisions and the provisioning of ecosystem services [10].

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