UC Riverside
UC Riverside Previously Published Works

Title

Beta diversity as a driver of forest biomass across spatial scales

Permalink

https://escholarship.org/uc/item/7rw894s7

Journal

Ecology, 103(10)

ISSN

0012-9658

Authors

Reu, Jacqueline C

Catano, Christopher P

Spasojevic, Marko J

et al.

Publication Date

2022-10-01

DOI

10.1002/ecy.3774

Copyright Information

Peer reviewed

ARTICLE

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Beta diversity as a driver of forest biomass across spatial scales

Jacqueline C. Reu[1] | Christopher P. Catano[1,2] | Marko J. Spasojevic[3] | Jonathan A. Myers[1]

[1]Department of Biology, Washington University in St. Louis, St. Louis, Missouri, USA

[2]Department of Plant Biology, Michigan State University, East Lansing, Michigan, USA

[3]Department of Evolution, Ecology, and Organismal Biology, University of California Riverside, Riverside, California, USA

Correspondence
Jacqueline C. Reu
Email: jreu@wustl.edu

Abstract

Despite the importance of biodiversity–ecosystem functioning (BEF) relationships in ecology and conservation, relatively little is known about how BEF relationships change across spatial scales. Theory predicts that change in BEF relationships with increasing spatial scale will depend on variation in species composition across space (β-diversity), but empirical evidence for this is limited. Moreover, studies have not quantified the direct and indirect role the environment plays in costructuring ecosystem functioning across spatial scales. We used 14 temperate-forest plots 1.4 ha in size containing 18,323 trees to quantify scale-dependence between aboveground tree biomass and three components of tree-species diversity—α-diversity (average local diversity), γ-diversity (total diversity), and β-diversity. Using structural-equation models, we quantified the direct effects of each diversity component and the environment (soil nutrients and topography), as well as indirect effects of the environment, on tree biomass across 11 spatial extents ranging from 400 to 14,400 m^2. Our results show that the relationship between β-diversity and tree biomass strengthened with increasing spatial extent. Moreover, β-diversity appeared to be a stronger predictor of biomass than α-diversity and γ-diversity at intermediate to large spatial extents. The environment had strong direct and indirect effects on biomass, but, in contrast to diversity, these effects did not strengthen with increasing spatial extent. This study provides some of the first empirical evidence that β-diversity underpins the scaling of BEF relationships in naturally complex ecosystems.

KEYWORDS
biodiversity, ecosystem functioning, net primary productivity, spatial scale, species diversity, species turnover, temperate forest

INTRODUCTION

Syntheses of hundreds of biodiversity–ecosystem functioning (BEF) studies show that biodiversity contributes to the magnitude and stability of ecosystem functions and services (Balvanera et al., 2006; Cardinale et al., 2011; Hooper et al., 2005). To date, most studies focused on how a single component of biodiversity—species richness in

---

J.C. Reu and C.P. Catano contributed equally to this manuscript.

local communities—influenced BEF relationships at small spatial scales (e.g., in grassland plots ranging from <1 to 100 m²) (Cardinale et al., 2011; Tilman et al., 2014). Key questions remain as to whether findings from small-scale studies shed light on BEF relationships at broader scales (Gonzalez et al., 2020; Isbell et al., 2018; Srivastava & Vellend, 2005). As spatial scale increases, a combination of local and regional processes—including local coexistence mechanisms, dispersal limitation, and environmental gradients—likely contribute to BEF relationships (Leibold et al., 2017). Therefore, one of the largest unresolved challenges for BEF research is "the question of scale" (Gonzalez et al., 2020)—how and why does the relationship between biodiversity and ecosystem functioning change with scale?

Scale dependence in BEF relationships can be understood by determining how the contributions of local, regional, and spatial components of biodiversity change with increasing spatial extent (Gonzalez et al., 2020; Isbell et al., 2018; Thompson et al., 2018). Total diversity at a given extent (γ-diversity) can be partitioned into local (α-diversity) and spatial (β-diversity) components (Anderson et al., 2011; Chase et al., 2018), whose differential effects on ecosystem functioning can provide insights into the roles of local and spatial processes for BEF relationships (Isbell et al., 2018). At small spatial extents, α-diversity can increase ecosystem functioning due to niche complementarity, which promotes local species coexistence (Liang et al., 2015; Tilman et al., 2014). As spatial extent increases, β-diversity can increase ecosystem functioning through spatial niche complementarity when species sort across environmental gradients (Barnes et al., 2016; Thompson et al., 2021), even when α-diversity is low and species cannot coexist locally (Catano et al., 2020; Hammill et al., 2018; Winfree et al., 2018). The relative importance of α-diversity and β-diversity can therefore provide insights into relationships between γ-diversity and ecosystem functioning across scales (Thompson et al., 2018).

Despite rising interest in the so-called question of scale in BEF research, the importance of different components of biodiversity in determining scale-dependent BEF relationships in natural ecosystems remains unknown (Gonzalez et al., 2020). First, relatively few empirical tests of scale dependence in BEF relationships have been conducted, and most come from aggregating small plots with similar environmental conditions in experiments originally designed to examine local species richness–productivity relationships (e.g., Thompson et al., 2018). Such studies may underestimate the role of β-diversity for ecosystem functioning in landscapes with more heterogeneous environments (Winfree et al., 2018). Second, most empirical BEF research focuses on a single diversity component (α-, β-, or γ-diversity) (Liang et al., 2016; Luo et al., 2019) and may not capture the multidimensional nature of biodiversity change relevant to real-world scenarios (McGill et al., 2015). For example, species invasions and disturbance can homogenize species composition by reducing β-diversity (Catano et al., 2017; McKinney & Lockwood, 1999), even with no net change in local species richness (Dornelas et al., 2014). Third, diversity in natural ecosystems is structured by the environment, yet BEF studies typically focus solely on diversity effects. Therefore, the extent to which variation in ecosystem functioning can be explained by the direct effects of the environment (e.g., energy flux), the direct effects of diversity (e.g., niche partitioning), or the indirect effects of the environment by structuring diversity remains unclear. These empirical gaps limit our understanding of the processes underlying the scaling of BEF relationships in heterogeneous environments typical of natural ecosystems.

We provide one of the first empirical tests of the importance of the environment and α-, β-, and γ-diversity in the scaling of biodiversity–biomass relationships in heterogeneous landscapes. Our study examined the effects of tree biodiversity on total aboveground tree biomass, a key ecosystem property associated with carbon dynamics, productivity, and several other ecosystem functions (Chisholm et al., 2013; Lutz et al., 2018; Stephenson et al., 2014). We conducted our study across 14 forest plots 1.44 ha in size in the Missouri Ozarks in the United States, each encompassing strong soil and topographic gradients. We used structural-equation models (SEMs) to quantify how the relationships between three diversity components (α-, β-, and γ-diversity), environmental variables (soil nutrients and topography), and aboveground tree biomass varied across 11 spatial extents ranging from 400 to 14,400 m². We predicted that α-diversity effects would be positive but scale invariant because average α-diversity is not expected to vary with increasing spatial extent, that β-diversity effects would increase with spatial extent because environmental heterogeneity should provide more opportunities for spatial niche complementarity (Thompson et al., 2021; Winfree et al., 2018), and that γ-diversity effects would be nonlinear, initially increasing with extent as new species are sampled across different environments but weaken as species accumulation saturates (Thompson et al., 2018). In contrast, we predicted that environmental variation would be an important predictor of tree biomass at all scales, both through direct effects and indirect effects via its influence on species diversity.

METHODS

Study system

We conducted our study in late-successional (undisturbed for ca. 80 years) oak-hickory forests at Tyson Research

Center, an 800-ha environmental field station located in the border region of the Ozark highlands, Missouri (38°31′ N, 90°33′ W; mean annual temperature 13.58°C; mean annual precipitation 957 mm). We established 14 forest plots each 1.44 ha (120 × 120 m) in size and each containing strong environmental gradients (Appendix S1: Figure S1). Each plot included three main habitats representative of Ozark oak-hickory forests: (1) mesic east-to-north-facing slopes, (2) hydric valleys with an intermittent stream, and (3) xeric west-to-south-facing slopes. Tree species composition and diversity vary strongly among these habitats (Myers et al., 2013; Spasojevic et al., 2016). Within the plots, elevational ranges varied from 15.5 to 32.3 m and soil fertility ranged from wet, pH-neutral soils with high macronutrient availability to dry, acidic soils with high iron and aluminum concentrations (Figure 1a) (Spasojevic et al., 2014). Therefore, each forest plot is a replicate landscape including this environmental gradient. Importantly, all plots are late-successional forests with similar land-use and disturbance history, which minimizes the potential confounding effects of history on contemporary biodiversity–biomass relationships.

Tree biodiversity, aboveground biomass, and environmental heterogeneity

In the period 2016–2017, we identified, mapped, and measured the diameters of all woody stems (excluding lianas) >1 cm diameter at breast height (dbh) within each of the 14 forest plots following ForestGEO protocols (Anderson-Teixeira et al., 2014). Each plot was divided into 36 grid cells (20 × 20-m quadrats) by installing permanent markers (rebar poles) at the corners of each quadrat. We focused on stems >2.5 cm dbh for which allometric equations were available to calculate aboveground biomass. We estimated the biomass of each stem using species-specific allometric regression equations from the U.S. Department of Agriculture Database of Diameter-based Biomass Regressions for North American Tree Species (Jenkins et al., 2004):

$$bm = e^{\beta_o + \beta_1 \ln(dbh)} \tag{1}$$

where bm is the total aboveground biomass (kg), dbh is the diameter at breast height (cm), and β_o and β_1 are species-specific constants. We calculated biomass for 18,323 stems (range = 898 to 1487 stems/plot) of 43 species (range = 22 to 29 species/plot) (Appendix S1: Table S1). Aboveground live tree biomass ranged from 170 to 237 Mg/ha (mean: 213 ± 17) across plots. Total tree biomass in this forest is strongly and positively associated with annual net primary productivity: 0.53 ± 0.03 (mean ± SE), $F_{1,98} = 184.8$, $p < 0.001$, $r = 0.8$ (Appendix S1: Figure S2).

We quantified environmental conditions within each forest plot using 14 abiotic variables that strongly influence the distributions of tree species and functional compositions in these forests (Spasojevic et al., 2014, 2016). We measured four topographic variables and 10 soil variables in 20 × 20-m quadrats in each forest plot ($n = 36$ quadrats/plot). Topographic variables included aspect,
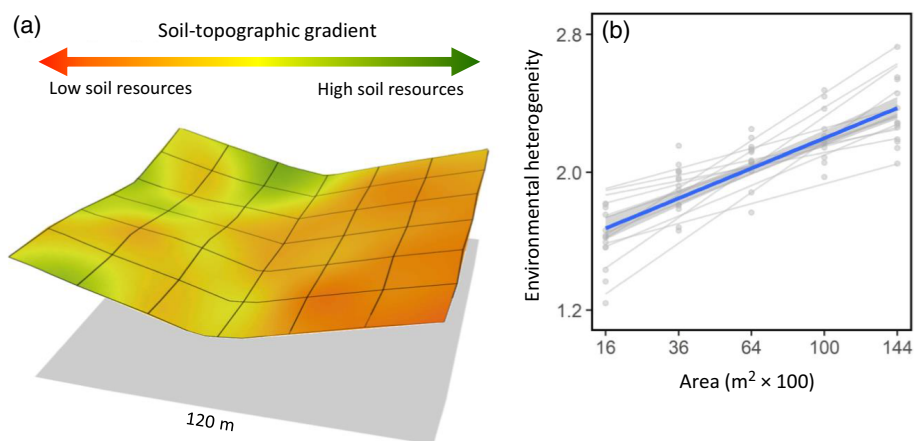

FIGURE 1 Environmental heterogeneity increases with spatial scale. (a) Map of soil resources and topography for one of the 14 forest plots, 120 × 120 m (1.44 ha) in size, analyzed in this study. The 20 × 20-m grid projected onto the forest plot shows the spatial grain where environmental variables were quantified. (b) Area-heterogeneity curve, where heterogeneity is the SD of environmental conditions (first principal component from 14 soil and topographic variables) across 20 × 20-m quadrats in each spatial extent. Gray points and lines are trends for each of the 14 plots, blue line is the mean trend and SE across all plots. Environmental maps for all 14 forest plots are provided in the supporting information (Appendix S1: Figure S1).

convexity, elevation, and slope (Spasojevic et al., 2014, 2016). Soil variables included seven exchangeable cations (Al, Ca, Fe, K, Mg, Mn, Na), soil pH, plant-available phosphorus, and organic matter content. See Appendix S2 for detailed soil sampling methods. We then used principal component analysis (PCA) to reduce the dimensionality of the environmental data. First, we normalized the raw data by log-transforming Ca, Fe, Mg, Mn, Na, P, and organic matter content and square-root transforming K, then standardized the variables (Z-scores) before PCA. Second, we extracted the first principal component axis (PC1) to serve as our environmental variable in downstream analyses. PC1 explained 31% of the environmental variation and is most strongly associated with a soil-resource gradient spanning acidic soils with high Al concentrations to more resource-rich alkaline soils with higher concentrations of organic matter, K, Mg, and P (Appendix S2: Figure S1). To visualize how environmental heterogeneity increases with extent in each plot (Figure 1b), we calculated the standard deviation of environmental conditions (first principal component from soil and topographic variables) across quadrats at five spatial extents (40 × 40 m, 60 × 60 m, 80 × 80 m, 100 × 100 m, and 120 × 120 m).

Spatial sampling design and diversity calculations

In each forest plot, we calculated the abundance of each tree species (number of stems per species) and total aboveground tree biomass (hereafter biomass) within four 10 × 10-m subquadrats in each 20 × 20-m quadrat (Figure 1a). We used a nested plot sampling design to calculate tree diversity and biomass at 11 different spatial extents, ranging from 20 × 20 m to 120 × 120 m for each plot (Figure 2). Because spatial structure in environmental conditions can influence the rate of species and biomass accumulation with increasing area depending on starting location, we repeated this procedure starting at every possible location for each spatial extent. For example, for the 20 × 20-m sample extent shown in Figure 2, we extracted the stems for each of the four 10 × 10-m subquadrats and assigned these to subsample i_1. We then systematically shifted the sampling extent 10 m and extracted the stems for the next four subquadrats and assigned these to subsample i_2. We repeated this procedure until all possible subsamples for a given spatial extent were recorded (Appendix S1: Table S2). We fixed the spatial grain size at 10 × 10 m
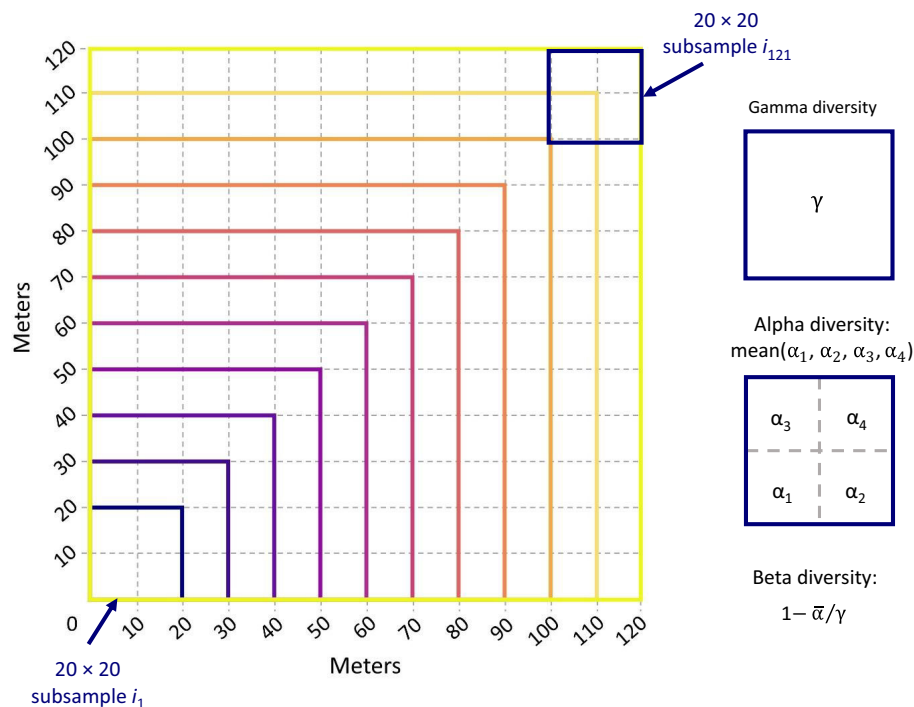

FIGURE 2   Nested sampling design. Tree biomass, the topo-edaphic environment, and alpha, beta, and gamma diversity were averaged across subsamples for each of the 11 spatial extents (shown in different colors) in each of 14 forest plots. For example, there are 121 total subsamples of the 20 × 20-m extent. The gray dotted lines indicate 10 × 10-m cells (spatial grain). For a given extent in each forest plot, alpha diversity is the mean tree diversity across 10 × 10-m cells in each extent; gamma diversity is the total tree diversity calculated after summing species abundances across all cells in each extent; beta diversity is 1 − (alpha/gamma) and indicates variation in species composition across cells in each extent.

because this is the unit in which we censused trees and corresponds to the scale at which prior studies showed that conspecific and heterospecific trees interact strongly (LaManna et al., 2016, 2017).

We calculated diversity using the probability of inter-specific encounter (PIE) converted to an effective number of species:

$$\text{ENS}_{\text{PIE}} = \left(1/\sum_{i=1}^{S} p_i^2 \right) \qquad (2)$$

where S is the number of species and p_i the proportional abundance of each species in the sample. ENS_{PIE} (equivalent to inverse Simpson's index) reflects the initial slope of the species rarefaction curve and is insensitive to differences in the number of individuals, thereby providing a scale-independent diversity metric (Chase et al., 2018). ENS_{PIE} is ideal for evaluating the effects of diversity on biomass because it integrates both species richness and relative abundances, so it captures the role of dominant species that disproportionately influence total biomass (Chase et al., 2018). Within each of the 14 forest plots, we calculated α-diversity (α_{PIE}) as the mean ENS_{PIE} across the 10×10-m cells within each subsample for a given spatial extent (Figure 2). We calculated γ-diversity (γ_{PIE}) as the ENS_{PIE} within each subsample for a given spatial extent (i.e., after summing species abundances across all 10×10-m cells). We calculated β-diversity (β_{PIE}) for each subsample for a given spatial extent as $1 - \alpha_{\text{PIE}}/\gamma_{\text{PIE}}$, a scale-independent metric of β-diversity that reflects the spatial aggregation of individuals within species (Chase et al., 2018); a larger β_{PIE} indicates greater variation in species composition across space. Finally, we averaged all variables over the subsamples for a given spatial extent in each of the 14 forest plots.

Statistical analysis

We quantified the scale-dependent effects of biodiversity and the environment on biomass through a two-step process. First, we developed SEMs to quantify the direct effects of each diversity metric on biomass, the direct effect of the environment on biomass, and the indirect effect of the environment through its effect on diversity (Figure 3 inset). We fitted separate piecewise SEMs for α_{PIE}, β_{PIE}, and γ_{PIE} at each scale (e.g., 11 spatial extents ranging from 400 to 14,400 m^2) using the R package piecewiseSEM version 2.1.2 (Lefcheck, 2016), where each forest plot is a replicate ($n = 14$) within the broader forest landscape. Therefore, we fitted 33 SEMs: one for each diversity metric at each of the 11 spatial extents.

Moreover, we fitted SEMs across forest plots to maintain equal sample sizes for each spatial extent, which allowed us to quantify biodiversity–biomass relationships across a broader range of scales (400–14,000 m^2) than prior studies. For example, Barry et al. (2021) quantified BEF scaling relationships in a tropical forest plot from 25 to 400 m^2; thus, their maximum spatial extent is equivalent to our minimum spatial extent. The larger scales in our study allowed us to capture a wider range of environmental conditions, where spatial niche partitioning is expected to be especially important for structuring tree species composition. We log$_e$-transformed biomass to linearize its relationship with diversity and the environment and ensured that final bivariate relationships in each SEM were approximately linear by plotting partial regression plots for each path (Appendix S1: Figures S3–S5). We also inspected residual diagnostic plots for each SEM (quantile-quantile plots for normality and fitted versus residual plots for homogenous errors) to confirm that linear functions were appropriate. Next, we extracted the standardized path coefficients from each SEM that represent the relative importance of biodiversity on biomass, direct environmental effects on biomass, and indirect environmental effects by structuring diversity. Last, we plotted the SEM path coefficients across spatial extents to evaluate the relative importance of different biodiversity metrics and the environment for scaling biomass.

RESULTS

Relationships between tree biodiversity and aboveground biomass varied across spatial extents (Figure 3). The relationships between biomass and all three diversity components (α_{PIE}, β_{PIE}, γ_{PIE}) appeared to increase in strength from intermediate (3600 m^2) to large (14,400 m^2) extents; however, only relationships between biomass and β_{PIE} became consistently stronger at the largest extents compared to the smallest extents (Figure 3; Appendix S1: Figures S3–S5). Moreover, the direct effects of β_{PIE} on biomass at the two largest extents (12,100 m^2: standardized [std.] coefficient = 0.42, df = 11, $p = 0.09$; 14,400 m^2: std. coefficient = 0.40, df = 11, $p = 0.09$) were about twice as large as those for α_{PIE} (12,100-m^2: std. coefficient = 0.18, df = 11, $p = 0.39$ and 14,400-m^2: std. coefficient = 0.17, df = 11, $p = 0.39$). Similarly, the direct effects of β_{PIE} on biomass at the largest extents were about twice as large as those for γ_{PIE} (12,100 m^2: std. coefficient = 0.21, df = 11, $p = 0.33$ and 14,400 m^2: std. coefficient = 0.18, df = 11, $p = 0.39$). All diversity components initially appeared to show weakening relationships with biomass when scaling up from small (400 m^2) to intermediate (3600 m^2) extents. The
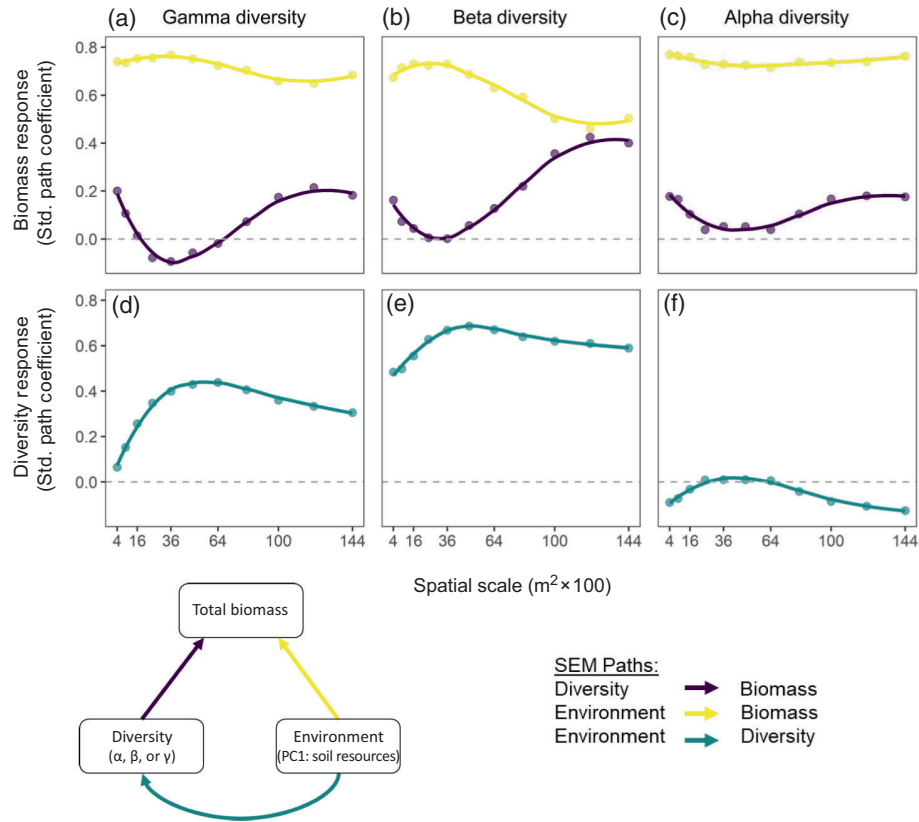
FIGURE 3 Scale-dependent effects of three biodiversity metrics (α_{PIE}, β_{PIE}, and γ_{PIE}) and environmental conditions (soil and topographic variables) on aboveground tree biomass. Each point is the effect size (standardized path coefficient) from a structural equation model (SEM, see inset). A separate SEM was fitted for each diversity component (α_{PIE}, β_{PIE}, and γ_{PIE}) across forest plots ($n = 14$) at 11 different spatial extents (33 total SEMs). (a)–(c) Path coefficients for direct effects of environment (yellow) and biodiversity (purple) on biomass. Larger positive values indicate stronger relationships between biomass and predictor variables (environment or diversity metrics). (d)–(f) Path coefficients for effects of environment on biodiversity (blue; note we multiply by -1 for visualization purposes to more easily compare the strength of these relationships to the other path coefficients). We used locally estimated scatterplot smoothing to visualize trends in effects with increasing spatial scale.

unstandardized path coefficients and standard errors for all SEMs are reported in Appendix S1: Tables S3–S5.

The environment had strong direct and indirect effects on tree biomass at all spatial extents, but, in contrast to diversity, the direct effects of the environment on tree biomass did not strengthen with increasing spatial extent (Figure 3a–c). In the SEMs with β_{PIE}, the environment–biomass relationships became weaker with increasing extent (Figure 3b). Moreover, the indirect effects of the environment on tree biomass (i.e., via its effects on β_{PIE}) were strong but did not consistently increase with spatial extent (Figure 3e). Therefore, though the environment is among the most important predictors of biomass at any extent, it is not responsible for the change in diversity–biomass relationships across scales. The amount of variation in biomass explained by the SEMs varied from 50% to 65%, depending on the diversity component and spatial extent (Appendix S1: Tables S3–S5).

DISCUSSION

Numerous studies have explored the relationships between biodiversity (typically species richness) and ecosystem functioning at local scales (Balvanera et al., 2006). In addition, a small number of recent studies explored these relationships at regional scales (Hammill et al., 2018; van der Plas et al., 2016; Winfree et al., 2018). Yet relatively few empirical studies have tested direct and indirect effects of the environment and β-diversity on BEF relationships across a continuum of spatial scales. Our results show that the relationship between β-diversity and tree biomass strengthened with increasing spatial extent. Moreover, β-diversity appeared to be a stronger predictor of tree biomass than α-diversity and γ-diversity at intermediate to large spatial extents. Environmental conditions related to soil nutrients and topography had strong direct and indirect effects on tree biomass, but in contrast to diversity the relationship

between the environment and tree biomass did not strengthen with increasing spatial extent. These findings provide some of the first empirical support for recent theory (Thompson et al., 2018, 2021) suggesting that β-diversity underpins the scaling of BEF relationships in naturally complex ecosystems.

The increasingly strong relationship between β-diversity and biomass at larger spatial extents (Figure 3) could be related to the increase in topographic and resource heterogeneity at these extents (Figure 1b). Metacommunity theory predicts environmental heterogeneity will increase variation in species composition by selecting for different species best adapted to local environmental conditions (species sorting) (Leibold et al., 2004). Species sorting is expected to maximize ecosystem functions like productivity because species are filtered into environments where their traits most efficiently convert resources into biomass (Hammill et al., 2018; Leibold et al., 2017; Winfree et al., 2018). Consistent with this mechanism, soil resources and topography were an important predictor of β-diversity, especially at larger spatial scales. Moreover, a prior study of leaf functional traits at our site showed that functional β-diversity and its associations with soil conditions increase from small to large spatial extents, suggesting traits may also contribute to scaling BEF relationships (Spasojevic et al., 2016). Our results provide support for recent theory that suggests β-diversity resulting from spatial niche complementarity strengthens BEF relationships across spatial scales in heterogeneous ecosystems (Gonzalez et al., 2020; Isbell et al., 2018; Thompson et al., 2021). However, the effect of the environment on β-diversity saturates at larger extents (Figure 3e), while the direct effect of β-diversity on biomass continues to rise, suggesting additional mechanisms may contribute to these scaling relationships. For example, dispersal limitation or other stochastic processes could contribute to patterns of β-diversity at larger scales that are not related to environmental conditions. Regardless, our results are likely to be general because both environmental heterogeneity and β-diversity increase with spatial scale in most natural ecosystems (Isbell et al., 2017).

The relationship between γ-diversity and biomass also increased with scale, but was generally weaker than the relationship between biomass and β-diversity (Figure 3). One potential reason for this is because as scale increases, the correlation between γ-diversity and its constituent α- and β-components decreases (Thompson et al., 2018). At large scales, similar values of γ-diversity could be explained by more permutations of species compositions in local communities (Thompson et al., 2018), thereby obscuring outcomes due to species sorting directly linked to β-diversity. Additionally, the relatively small species pool in our region (γ-diversity only varied between 22 and 29 species per forest plot) could also contribute to weak relationships between γ-diversity and biomass. Our study is consistent with others that generally found γ-diversity, relative to β-diversity, to be a weaker predictor of biomass dynamics at larger scales (Catano et al., 2020; Hammill et al., 2018). However, we did not find a strong hump-shaped relationship between γ-diversity and biomass, as predicted by Thompson et al. (2018). It is possible that the largest spatial extent in our study, 1.44 ha, was not large enough to capture the scales where saturation of species richness is strong enough to decrease the slope of the BEF. Alternatively, the functional form of BEF scaling relationships in our study may differ because the theory is based on richness measures that do not account for differences in species dominance or relative abundances that we quantify here.

Despite decades of theory and experiments in local communities demonstrating local biodiversity effects, we found the relationship between α-diversity and biomass was generally weak at all scales. This weak biodiversity effect may be attributed to the 10×10-m resolution used in our study: selection effects likely dominate at this small scale because little environmental heterogeneity is present. Also, the correlation between α-diversity and biomass could be weak if environmental variables, rather than diversity per se, directly influence biomass at these scales (Gonzalez et al., 2020). For example, soil resources and microclimate (e.g., temperature) could directly increase plant productivity due to higher energy inputs and faster individual growth rates regardless of the diversity of the communities. Consistent with this interpretation, our results show that environmental conditions related to soil nutrients were the most significant predictor of biomass at smaller scales in these forests. Our results suggest the need to include environmental components and other dimensions of biodiversity to understand variation in BEF relationships when moving from local communities to larger scales.

Our study highlights three main avenues for future research. First, though our results support predictions of stronger β-diversity effects with increasing scale, they demonstrate that certain aspects of BEF theory should be adapted to, and tested within, natural landscapes. For example, myriad assembly processes in natural ecosystems could modify the scaling relationships between biodiversity and ecosystem functions. Large-scale experiments that manipulate spatial/regional processes, including landscape-scale connectivity (Haddad et al., 2017), regional dispersal and species pools (Catano et al., 2021), and environmental heterogeneity (Reynolds et al., 2007), could reveal mechanistic insights into the scaling of BEF relationships in natural environments. Second, extensive empirical research in a variety of ecosystems is needed

before generalizations can be made concerning the scale dependency of biodiversity effects. Though our findings in a forest ecosystem mirror results from aquatic mesocosms (Hammill et al., 2018) and recent theory (Thompson et al., 2021), the processes underlying variation in species composition (e.g., species sorting, dispersal limitation, demographic stochasticity) are likely to vary greatly between ecosystems (Barnes et al., 2016; Myers et al., 2013) and may lead to distinct BEF relationships. Third, it is unclear how the scaling of biodiversity effects may differ for specific ecosystem functions. We focused on total forest biomass because it is a critical attribute that influences multiple ecosystem processes in forests, including carbon dynamics and primary productivity (Chisholm et al., 2013; Lutz et al., 2018; Stephenson et al., 2014). Future studies that explicitly focus on specific functions, such as net primary productivity and how they are influenced by various demographic processes (recruitment, growth, and mortality), could reveal novel insights into biodiversity effects on ecosystem functioning, which could be missed when focusing on aggregate properties like standing biomass (Liang et al., 2005). Moreover, α- and β-diversity effects may be stronger when considering multiple functions simultaneously (Hautier et al., 2017; Pasari et al., 2013).

In conclusion, our findings suggest that spatial variation in species composition is among the strongest determinants of BEF relationships at larger spatial scales. Though BEF research has historically focused on how random species loss influenced ecosystem functions at small scales, it is becoming increasingly clear that environmental change, species invasions, and environmental management can alter the distribution of species in non-random ways with or without net change in local species richness (Dornelas et al., 2014). Therefore, understanding change in both environmental conditions and species composition, not just species richness, is critical for anticipating the consequences of biodiversity change on ecosystems across scales.

ORCID

Christopher P. Catano https://orcid.org/0000-0002-4060-7291
Marko J. Spasojevic https://orcid.org/0000-0003-1808-0048
Jonathan A. Myers https://orcid.org/0000-0002-2058-8468

REFERENCES

Anderson, M. J., T. O. Crist, A. L. Freestone, and N. J. Sanders. 2011. "Navigating the Multiple Meanings of β Diversity: A Roadmap for the Practicing Ecologist." *Ecology Letters* 14: 19–28.

Anderson-Teixeira, K. J., S. J. Davies, A. C. Bennett, E. B. Gonzalez-Akre, H. C. Muller-Landau, S. Joseph Wright, K. Abu Salim, et al. 2014. "CTFS-ForestGEO: A Worldwide Network Monitoring Forests in an Era of Global Change." *Global Change Biology* 21(2): 528–49.

Balvanera, P., A. B. Pfisterer, N. Buchmann, J.-S. He, T. Nakashizuka, D. Raffaelli, and B. Schmid. 2006. "Quantifying the Evidence for Biodiversity Effects on Ecosystem Functioning and Services." *Ecology Letters* 9: 1146–56.

Barnes, A. D., P. Weigelt, M. Jochum, D. Ott, D. Hodapp, N. F. Haneda, and U. Brose. 2016. "Species Richness and Biomass Explain Spatial Turnover in Ecosystem Functioning across Tropical and Temperate Ecosystems." *Philosophical Transactions of the Royal Society B: Biological Sciences* 371: 20150279.

Barry, K. E., G. A. Pinter, J. W. Strini, K. Yang, I. G. Lauko, S. A. Schnitzer, A. T. Clark, et al. 2021. "A Graphical Null Model for Scaling Biodiversity-Ecosystem Functioning Relationships." *Journal of Ecology* 109: 1549–60.

Cardinale, B. J., K. L. Matulich, D. U. Hooper, J. E. Byrnes, E. Duffy, L. Gamfeldt, P. Balvanera, M. I. O. Connor, and A. Gonzalez. 2011. "The Functional Role of Producer Diversity in Ecosystems." *American Journal of Botany* 98: 572–92.

Catano, C. P., T. L. Dickson, and J. A. Myers. 2017. "Dispersal and Neutral Sampling Mediate Contingent Effects of Disturbance on Plant Beta-Diversity: A Meta-Analysis." *Ecology Letters* 20: 347–56.

Catano, C. P., T. S. Fristoe, J. A. Lamanna, and J. A. Myers. 2020. "Local Species Diversity, β-Diversity and Climate Influence the Regional Stability of Bird Biomass across North America." *Proceedings of the Royal Society B: Biological Sciences* 287: 20192520.

Catano, C. P., E. Grman, E. Behrens, and L. A. Brudvig. 2021. "Species Pool Size Alters Species–Area Relationships during Experimental Community Assembly." *Ecology* 102: 1–7.

Chase, J. M., B. J. McGill, D. J. McGlinn, F. May, S. A. Blowes, X. Xiao, T. M. Knight, O. Purschke, and N. J. Gotelli. 2018. "Embracing Scale-Dependence to Achieve a Deeper Understanding of Biodiversity and its Change across Communities." *Ecology Letters* 21: 1737–51.

chcatano. 2022. "chcatano/SPFD_tree_diversity-biomass: data and analysis scripts: Reu et al. beta diversity as a driver of forest biomass across scales." Ecology (v1.0). Zenodo. https://doi.org/10.5281/zenodo.6506797.

Chisholm, R. A., H. C. Muller-Landau, K. Abdul Rahman, D. P. Bebber, Y. Bin, S. A. Bohlman, N. A. Bourg, et al. 2013. "Scale-Dependent Relationships between Tree Species Richness and Ecosystem Function in Forests." *Journal of Ecology* 101: 1214–24.

Dornelas, M., N. J. Gotelli, B. McGill, H. Shimadzu, F. Moyes, C. Sievers, and A. E. Magurran. 2014. "Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss." *Science* 344: 296–9.

Gonzalez, A., R. M. Germain, D. S. Srivastava, E. Filotas, L. E. Dee, D. Gravel, P. L. Thompson, et al. 2020. "Scaling-up Biodiversity-Ecosystem Functioning Research." *Ecology Letters* 23: 757–76.

Haddad, N. M., A. Gonzalez, L. A. Brudvig, M. A. Burt, D. J. Levey, and E. I. Damschen. 2017. "Experimental Evidence Does Not Support the Habitat Amount Hypothesis." *Ecography* 40: 48–55.

Hammill, E., C. P. Hawkins, H. S. Greig, P. Kratina, J. B. Shurin, and T. B. Atwood. 2018. "Landscape Heterogeneity Strengthens the Relationship between β-Diversity and Ecosystem Function." *Ecology* 99: 2467–75.

Hautier, Y., F. Isbell, E. T. Borer, E. W. Seabloom, W. S. Harpole, E. M. Lind, A. S. MacDougall, et al. 2017. "Local Loss and Spatial Homogenization of Plant Diversity Reduce Ecosystem Multifunctionality." *Nature Ecology & Evolution* 2: 50–6.

Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, et al. 2005. "Effects of Biodiversity on Ecosystem Functioning: A Consensus of Current Knowledge." *Ecological Monograms* 75: 3–35.

Isbell, F., J. Cowles, L. E. Dee, M. Loreau, P. B. Reich, A. Gonzalez, A. Hector, and B. Schmid. 2018. "Quantifying Effects of Biodiversity on Ecosystem Functioning across Times and Places." *Ecology Letters* 21: 763–78.

Isbell, F., A. Gonzalez, M. Loreau, J. Cowles, S. Díaz, A. Hector, G. M. Mace, et al. 2017. "Linking the Influence and Dependence of People on Biodiversity across Scales." *Nature* 546: 65–72.

Jenkins, J. C., D. C. Chojnacky, L. S. Heath, and R. A. Birdsey. 2004. *Comprehensive Database of Diameter-Based Biomass Regressions for North American Tree Species*. Newton Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station.

LaManna, J. A., S. A. Mangan, A. Alonso, N. A. Bourg, W. Y. Brockelman, S. Bunyavejchewin, L. Chang, et al. 2017. "Plant Diversity Increases with the Strength of Negative Density Dependence at the Global Scale." *Science* 356: 1389–92.

LaManna, J. A., M. L. Walton, B. L. Turner, and J. A. Myers. 2016. "Negative Density Dependence Is Stronger in Resource-Rich Environments and Diversifies Communities when Stronger for Common but Not Rare Species." *Ecology Letters* 19: 657–67.

Lefcheck, J. S. 2016. "piecewiseSEM: Piecewise Structural Equation Modeling in R for Ecology, Evolution, and Systematics." *Methods in Ecology and Evolution.* 7: 573–9.

Leibold, M., A. M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, et al. 2004. "The Metacommunity Concept: A Framework for Multi-Scale Community Ecology." *Ecology Letters* 7: 601–13.

Leibold, M. A., J. M. Chase, and S. K. M. Ernest. 2017. "Community Assembly and the Functioning of Ecosystems: How Metacommunity Processes Alter Ecosystems Attributes." *Ecology* 98: 909–19.

Liang, J., J. Buongiorno, and R. A. Monserud. 2005. "Growth and Yield of all-Aged Douglas-Fir – Western Hemlock Forest Stands: A Matrix Model with Stand Diversity and Diversity Effects." *Canadian Journal of Forest Research* 35: 2368–81.

Liang, J., T. W. Crowther, N. Picard, S. Wiser, M. Zhou, G. Alberti, E. D. Schulze, et al. 2016. "Positive Biodiversity-Productivity Relationship Predominant in Global Forests." *Science* 354: 196.

Liang, J., M. Zhou, P. C. Tobin, A. D. McGuire, and P. B. Reich. 2015. "Biodiversity Influences Plant Productivity through Niche-Efficiency." *Proceedings of the National Academy of Sciences of the United States of America* 112: 5738–43.

Luo, W., J. Liang, R. Cazzolla Gatti, X. Zhao, and C. Zhang. 2019. "Parameterization of Biodiversity–Productivity Relationship and its Scale Dependency Using Georeferenced Tree-Level Data." *Journal of Ecology* 107: 1106–19.

Lutz, J. A., T. J. Furniss, D. J. Johnson, S. J. Davies, D. Allen, A. Alonso, K. J. Anderson-Teixeira, et al. 2018. "Global Importance of Large-Diameter Trees." *Global Ecology and Biogeography* 27: 849–64.

McGill, B. J., M. Dornelas, N. J. Gotelli, and A. E. Magurran. 2015. "Fifteen Forms of Biodiversity Trend in the Anthropocene." *Trends in Ecology & Evolution* 30: 104–13.

McKinney, M. L., and J. L. Lockwood. 1999. "Biotic Homogenization: A Few Winners Replacing Many Losers in the Next Mass Extinction." *Trends in Ecology & Evolution* 14: 450–3.

Myers, J. A., J. M. Chase, I. Jiménez, P. M. Jørgensen, A. Araujo-Murakami, N. Paniagua-Zambrana, and R. Seidel. 2013. "Beta-Diversity in Temperate and Tropical Forests Reflects Dissimilar Mechanisms of Community Assembly." *Ecology Letters* 16: 151–7.

Pasari, J., T. Levi, E. Zavaleta, and D. Tilman. 2013. "Several Scales of Biodiversity Affect Ecosystem Multifunctionality." *Proceedings of the National Academy of Sciences of the United States of America* 110: 10219–22.

van der Plas, F., P. Manning, S. Soliveres, E. Allan, M. Scherer-lorenzen, K. Verheyen, C. Wirth, et al. 2016. "Biotic Homogenization Can Decrease Landscape-Scale Forest Multifunctionality." *Proceedings of the National Academy of Sciences* 113: 3557–62.

Reynolds, H. L., G. G. Mittelbach, T. L. Darcy-Hall, G. R. Houseman, and K. L. Gross. 2007. "No Effect of Varying Soil Resource Heterogeneity on Plant Species Richness in a Low Fertility Grassland." *Journal of Ecology* 95: 723–33.

Spasojevic, M. J., B. L. Turner, and J. A. Myers. 2016. "When Does Intraspecific Trait Variation Contribute to Functional Beta-Diversity?" *Journal of Ecology* 104: 487–96.

Spasojevic, M. J., E. A. Yablon, B. Oberle, and J. A. Myers. 2014. "Ontogenetic Trait Variation Influences Tree Community Assembly across Environmental Gradients." *Ecosphere* 5: 129.

Srivastava, D. S., and M. Vellend. 2005. "Biodiversity-Ecosystem Function Research: Is it Relevant to Conservation?" *Annual Review of Ecology, Evolution, and Systematics* 36: 267–94.

Stephenson, N. L., A. J. Das, R. Condit, S. E. Russo, P. J. Baker, N. G. Beckman, D. A. Coomes, et al. 2014. "Rate of Tree

Carbon Accumulation Increases Continuously with Tree Size." *Nature* 507: 90–3.

Thompson, P. L., F. Isbell, M. Loreau, M. I. O'connor, and A. Gonzalez. 2018. "The Strength of the Biodiversity-Ecosystem Function Relationship Depends on Spatial Scale." *Proceedings of the Royal Society B: Biological Sciences* 285: 20180038.

Thompson, P. L., S. Kéfi, Y. R. Zelnik, L. E. Dee, S. Wang, C. de Mazancourt, M. Loreau, and A. Gonzalez. 2021. "Scaling up Biodiversity Ecosystem Functioning Relationships: The Role of Environmental Variability in Space and Time." *Proceedings of the Royal Society B* 288: 20202779.

Tilman, D., F. Isbell, and J. M. Cowles. 2014. "Biodiversity and Ecosystem Functioning." *Annual Review of Ecology, Evolution, and Systematics* 45: 471–93.

Winfree, R., J. R. Reilly, I. Bartomeus, D. P. Cariveau, N. M. Williams, and J. Gibbs. 2018. "Species Turnover Promotes the Importance of Bee Diversity for Crop Pollination at Regional Scales." *Science* 359: 791–3.

SUPPORTING INFORMATION

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

How to cite this article: Reu, Jacqueline C., Christopher P. Catano, Marko J. Spasojevic, and Jonathan A. Myers. 2022. "Beta Diversity as a Driver of Forest Biomass across Spatial Scales." *Ecology* e3774. https://doi.org/10.1002/ecy.3774