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RESEARCH ARTICLE

Early positive spatial selection effects of beta-diversity on ecosystem functioning

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Abstract
Context Metacommunity theory predicts that diversity arising at larger spatial scales (spatial β-diversity) may increase ecosystem functioning if there are positive spatial selection effects whereby species dominate in mixtures at places where they are most productive in monocultures. However, beta-diversity effects on ecosystem functioning remain understudied and unquantified experimentally.
Objectives Our experiment tests for spatial selection effects in survivorship among transplanted seedlings of the dominant species of five major habitats (grassland, oak savanna, deciduous forest, coniferous forest, bog) at Cedar Creek Ecosystem Science Reserve.
Methods We established monocultures and mixtures of dominant species in five habitats and estimated survivorship at the end of the first growing season of the experiment, partitioning net biodiversity effects into its components of complementarity effects and selection effects, which include spatial selection effects. Results: At this early experimental stage, we found positive selection effects, due mostly to average selection effects across all habitats. We also found a significantly positive spatial selection effect, indicating that the habitats where species tended to be more abundant in mixtures were also those where they tended to survive more in monocultures.
Results At this early experimental stage, we found positive selection effects, due mostly to average selection effects across all habitats. We also found a significantly positive spatial selection effect, indicating that the habitats where species tended to be more abundant in mixtures were also those where they tended to survive more in monocultures.
Conclusion Overall, our results are consistent with theoretical predictions that additional effects of plant diversity on ecosystem functioning, beyond those observed in local experiments within local habitats, may arise at landscape scales from dispersal and spatial sorting of species across a heterogeneous landscape. Further study will be needed to determine how survivorship patterns develop over time within and among habitats and how growth and reproduction contribute to plant productivity and other ecosystem functions.

Keywords Net biodiversity effect · Complementarity effect · Overyielding · Environmental heterogeneity · Metacommunity · Scale

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10980-023-01786-9.

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Introduction

The effect of biodiversity on ecosystem functioning, and by extension ecosystem services, has gained increasing research attention over recent decades (Loreau et al. 2001, 2021; Reich et al. 2001, 2012; Tilman et al. 2014; Isbell et al. 2017). At the local scale, empirical studies have revealed a generally positive, but decelerating, relationship between richness and various ecosystem functions (Hooper et al. 2005; Balvanera et al. 2006; O'Connor et al. 2017), which has been related to the way species interact with resources in time and space (Loreau 1998; Yachi and Loreau 1999). Despite considerable progress in understanding how ecosystem functioning depends on local plant diversity (Hooper et al. 2005; Balvanera et al. 2006; Tilman et al. 2014), it remains largely unclear whether and how much additional effects of diversity on ecosystem functioning arise at larger spatial scales (Isbell et al. 2017; Mori et al. 2018; Gonzalez et al. 2020). A large-scale approach to Biodiversity-Ecosystem Functioning (BEF) relationship will include important considerations from metacommunity theory of dispersal-dependent processes, as well as environmental heterogeneity and disturbance rates in the region that ultimately determine community structure and its relation to ecosystems (Leibold et al. 2017). Furthermore, we will be able to better integrate the multiscale nature of BEF (Mori et al. 2018). Locally, loss of α-diversity can reduce ecosystem functioning within times and places (Tilman et al. 1997), affecting the provisioning of numerous ecosystem services to society (Balvanera et al. 2006; Isbell et al. 2017; van der Plas 2019). A more diverse species pool can contain and be dominated by those species that most contribute to ecosystem functioning than a smaller species pool (Tilman et al. 1997), leading to positive selection effects of local biodiversity on productivity (Loreau and Hector 2001). Furthermore, increasing plant diversity can reduce competition, increase facilitation, or both, manifesting as local complementarity effects of local plant diversity on productivity (Loreau and Hector 2001).

Much less understood are the potentially widespread consequences of loss of spatial β-diversity (i.e., turnover in dominant plant species across space) (van der Plas et al. 2023). This knowledge gap regarding the effects of β-diversity has limited our ability to quantify the consequences of large-scale biodiversity loss (Isbell et al. 2017; Mori et al. 2018; Gonzalez et al. 2020). At intermediate dispersal rates (Loreau et al. 2003; Leibold et al. 2017), β-diversity may increase plant productivity at landscape scales if there are positive spatial selection effects (Loreau et al. 2003; Mori et al. 2018), which occurs when species become more dominant in mixtures when and where they are most productive in monoculture (Yachi and Loreau 1999; Isbell et al. 2018). These positive effects of spatial β-diversity on landscape productivity (i.e., spatial selection effects) that emerge from dispersal and spatial heterogeneity can be quantified alongside well-studied effects of local diversity on local productivity (e.g., complementarity effects) that arise from local species interactions (Isbell et al. 2018; Loreau et al. 2021). Fundamentally, we seek to understand how β-diversity effects arise on ecosystem functioning. For example, different plant species may become dominant in different habitats (e.g., grasslands, savannas, deciduous forests, coniferous forests, and bogs), and this spatial β-diversity may contribute to landscape productivity. Since local communities rarely assemble independently from larger-scale processes, it is critical to study the role of landscape beyond local processes (Bond and Chase 2002; Loreau et al. 2003; Mouquet and Loreau 2003; Thompson and Gonzalez 2016). Thus, large spatial scale biodiversity effects might be overlooked until we understand how they arise from different species being dominant at different places across large landscapes.

Spatial heterogeneity may allow the expression of spatial complementarity of resource use as species exploit suitable conditions for their establishment (Griffin et al. 2009), potentially influencing long-term coexistence (Chesson 1991) and ecosystem functioning (Thompson et al. 2021). At large spatial scales, the effects of biodiversity can be largely driven by environmental heterogeneity (i.e., the degree of dissimilarity in environmental conditions, e.g., temperature, moisture, light availability) among sites, or between time points, which sets the scale of species turnover (Loreau et al. 2003; Griffin et al. 2009). At local scales, when there are positive selection effects but not positive complementarity effects, relatively low levels of biodiversity can maintain ecosystem functioning; however, greater environmental heterogeneity and beta diversity may still be needed to sustain functioning at larger scales (Isbell et al. 2018, Thompson et al. 2021). Therefore, the strength of the

BEF relationship is expected to vary with environmental context across sites.

Alternatively, there may instead be mismatches between the places where species are currently most dominant and where they are most productive. For example, metacommunity theory predicts that dispersal limitation can lead to species failing to arrive at the locations where they would otherwise be most productive (Loreau et al. 2003; Leibold et al. 2017). Furthermore, niche theory acknowledges that species not only affect productivity, they also respond to it (Leibold 1995). Sometimes, species modify their environment in ways that disfavor their continued dominance, which can lead to succession (Connell and Slatyer 1977). In such cases, spatial β-diversity may decrease, rather than increase, landscape level productivity. In other words, there may be negative spatial selection effects, due to species lingering in dominance at places where they now tend to be less productive. Finally, neutral spatial selection effects may arise if species relative abundance varies stochastically across the landscape, independently of where they are most productive across the landscape. Given the importance of the establishment phase for dispersal processes, early community development may provide insights into the mechanisms and processes maintaining productivity at large spatial scales, however spatial selection effects remain unquantified from the seedling stage. We experimentally test the following hypotheses in early establishing communities:

I. Dominant species have higher survivorship at the same places where they have higher survivorship in monocultures, creating positive spatial selection effects of β-diversity on seedling survivorship. II. Alternatively, there may be mismatches between the places where species survive most in mixtures or monocultures, leading to negative or neutral spatial selection effects of β-diversity on seedling survivorship.

We established the same biodiversity experiment in five major habitats: a grassland, a savanna, a deciduous forest, a coniferous forest, and a bog. In each habitat, we established monocultures and mixtures by transplanting seedlings of a grass *Andropogon gerardii*, and tree species *Quercus macrocarpa*, *Acer rubrum*, *Pinus strobus* and *Larix laricina*. These five species respectively dominate in the five major habitats where the experiment was established, and they are known to exhibit a range of tolerances to environmental filters that may be relevant for their spatial sorting (Table S1). Here we present the initial results for seedling survivorship and additive partitioning of biodiversity during the first growing season of this experiment. Seedling survivorship during this early stage of establishment is a component of ecosystem productivity and is used as a proxy for ecosystem functioning. To our knowledge, this is the first study to experimentally test the role of spatial selection effects. We do so by considering dominant species survivorship across environmentally heterogenous habitats.

Methods

Study habitats, species, and experimental design

To test our alternative hypotheses, we established a multi-habitat biodiversity experiment, named BetaDIV that is designed to test effects of spatial β-diversity on ecosystem functioning. The experimental habitats (henceforth, habitats) are located at Cedar Creek Ecosystem Science Reserve (CCESR) in Minnesota, USA. Cedar Creek is characterized by a continental climate, with mean annual precipitation of 682 mm and mean annual temperature of 7 ºC, and glacial outwash soils (Isbell et al. 2019; Cedar Creek Weather Station).

The five experimental habitats included: (1) an oak savanna (45.392005; − 93.169304), where *Quercus macrocarpa* dominates; (2) a coniferous forest (45.417500 − 93.201667), where *Pinus strobus* dominates; (3) a mixed deciduous forest (45.422186, − 93.196079), where *Acer rubrum* dominates; (4) a bog (45.422536, − 93.186333), where *Larix laricina* dominates; (5) an old field grassland (45.403554, − 93.182780) where *Andropogon gerardii* dominates (45.403554, − 93.182780). Since 1964, the oak savanna habitat, which is located in Burn Unit 103 of experiment E133 at Cedar Creek, has been burned approximately four out of every five years in the spring and it was burned just before the BetaDIV plots were established in 2022. None of the other habitats in the BetaDiv experiment have had prescribed burning. The grassland habitat, which is located in old field 67A at Cedar Creek, was formerly cropped and abandoned from agriculture in 1962, undergoing passive recovery and succession for six decades prior to the establishment of the BetaDiv experiment. None of the other habitats in the BetaDiv experiment are known to have had cropping. The bog habitat, which is located on the West side of Beckman Bog, has some standing water that fluctuates in depth. The deciduous and coniferous forests have been kept unmanaged in recent decades. Thus, the habitats are extended across a gradient of heterogeneous environmental filters and species-specific tolerance to them (Table S1).

The entire study consists of 100 plots (20 plots per habitat × 5 habitats). Each of the five habitats includes two true replicate monocultures for each of the five species and two true replicates for each of the five possible mixture compositions of four species (leaving each one out in turn to eventually explore the effect of species identity). Each plot is 1.5 by 1.5 m, with 12 seedlings planted 0.5 m apart in a 4×4 square grid, except in the plot corners (Fig. 1, Fig. S1). This spacing of tree seedlings is similar to that used in a nearby tree diversity experiment that found local tree diversity effects on productivity, even in the first year (Grossman et al. 2017). The five habitats can be considered spatial blocks of the study. We do not have replicate habitats for each major habitat because our aim is not to test for significant differences between these specific habitats (e.g., between bogs and savannas). Instead, our aim is to test whether common plant species tend to have higher rates of survivorship in mixtures at the sites where they have the higher survivorship

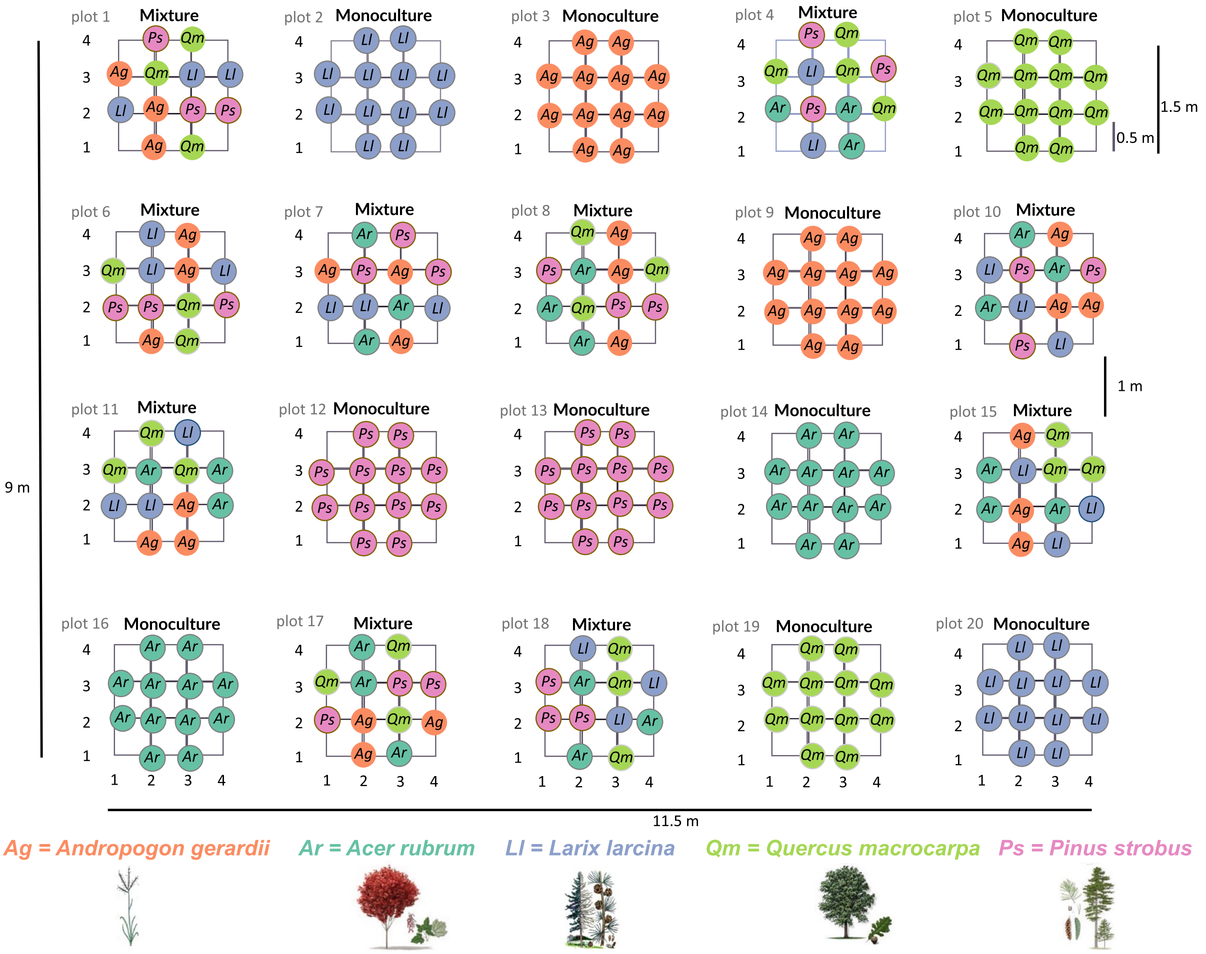


Fig. 1 Illustration of BetaDIV experimental plot set up with seedlings of five dominant species planted in monoculture and mixtures at Cedar Creek Ecosystem Science Reserve, Minnesota, USA

in monocultures (i.e., testing our spatial selection effect hypothesis). Our study is designed to test this aim across all five habitats, rather than testing this for each specific type of habitat. No habitat preparation or other manipulations were done prior to seedling planting because we wanted to test how seedlings survived under the unmodified and naturally heterogeneous conditions present in each habitat.

Seedling transplant

We obtained seedlings from a local plant nursery (Out Back Nursery & Landscaping, Hasting, MN) and their initial heights ranged from 5 to 30 cm. In the early June 2022, we tagged and planted all seedlings (i.e., bareroot seedlings for trees and plugs for the grass *A. gerardii*). For the first two weeks after the initial planting, we watered seedlings three times a week, except when there was a rain event on the day of watering. Within these two weeks, we noticed high mortality of *L. laricina* across all habitats and obtained new seedlings from a different plant nursery (Paint Creek Nursery and Tree Farm, Cadott, WI) due to the lack of seedling availability from the former supplier. Two weeks after the initial transplanting, we replaced all dead seedlings from any of the five species that had failed to survive the transplant shock. Subsequently, we did no further watering or seedling replacements to study how seedling survival (presented here) and growth and reproduction (to be studied in future years) responded to local habitat conditions.

Seedling census

We conducted a seedling census for each of the 1200 tagged seedlings (12 seedlings per plot × 100 plots). We recorded species as alive if green leaves were present or green stems could be determined by carefully scratching the seedling bark (Fagundes et al. 2018). The seedling census was conducted in early September, two months after the two-week initial establishment period, at the end of the growing season of the first year of this experiment.

Environmental variables

We measured soil moisture and soil temperature before seedlings were transplanted in June 2022. We took five measurements of soil moisture (m^3 of water/m^3 of soil) and soil temperature (°C) in the upper 10 cm of each plot (averaging across five measurements per plot: four in the plot corners and one in the center) using a Decagon 5TM probe (METER Group, Pullman, WA, USA). We estimated light interception by taking two-point measurements of photosynthetically active radiation (PAR, μmol m^{-2} s^{-1}) above the plant canopy (i.e., below adult trees canopy) and below the plant canopy (i.e., just above litter layer) in each plot and using a Meter Accupar—LP-80 (METER Group, Pullman, WA, USA). Each light measurement comprises eighty sensors that are averaged in an 80 cm long probe. We then averaged the two-point measurements to obtain an overall averaged plot-level PAR.

Statistical analysis

Partitioning complementarity and selection effects within and among habitats

The net biodiversity effect (NBE) is simply the difference in performance (survivorship, in our study) between mixtures and monocultures. It is positive when a greater proportion of the planted individuals survive in mixtures than in monocultures. The NBE can also be negative, such as due to chemical or physical interference competition, though this has rarely been found (O'Connor et al. 2017). More individuals may survive in mixture for two types of reasons: (i) complementarity effects, which are positive when there is less competition and/or more facilitation in mixtures than in monocultures (e.g., due to resource partitioning or escape from specialized natural enemies in mixtures), and (ii) selection effects, which are positive when species that survive most in monoculture also tend to survive most in mixtures (e.g., if the species that is best-adapted to the local environment tends to outcompete other species). More specifically, positive complementarity effects occur when many species survives more in mixture than expected in monoculture, whereas positive selection effects occur when the species that survive most in monoculture disproportionately survive more in mixture than expected from monoculture. Note that these two types of biodiversity effects are not mutually exclusive. For example, in communities of interacting species, rare species can be partly released from intraspecific competition, which may lead to disproportionate survivorship in mixtures, and dominant species can be somewhat adapted to local conditions, which may lead to incomplete dominance and moderately positive selection effects.

First, to quantify the local biodiversity effects that arise within each habitat, we used Loreau and Hector's (2001) additive partition:

$$NBE_\alpha = \sum_{i}^{N} \Delta RY_i M_i = N\overline{\Delta RY}\bar{M} + Ncov\left(\Delta RY_i, M_i\right) \tag{1}$$

where i indexes one of N species in the community, $CE_\alpha = N\overline{\Delta RY}\,\overline{M}$ is the local complementarity effect, $SE_\alpha = Ncov\left(\Delta RY_i, M_i\right)$ is the local selection effect, $\Delta RY_i = RY_{O,i} - RY_{E,i}$ and $RY_{O,i} = Y_{O,i}/M_i$ and $RY_{O,i}$ is the relative yield (survivorship, in this case) observed in mixture, Y_i and M_i are respectively the observed yield (survivorship, in this case) in mixture and monoculture, and $RY_{E,i}$ is the expected relative survivorship (initial proportion) for species i, and the subscript α denotes that the biodiversity effect was calculated at the local scale, within a habitat. These local biodiversity effects were calculated for each mixture plot, with each of the five habitats treated as a separate block of the experiment. For example, mean monoculture values were calculated within habitats.

Next, to quantify the landscape-scale biodiversity effects that arise across all habitats, we used Isbell et al.'s (2018) additive partition, which generalizes equation E1 to multiple habitats:

$$NBE_\gamma = \sum_{k}^{H} \sum_{i}^{N} \Delta RY_{ik} M_{ik} = HN\overline{\overline{\Delta RY}}\,\overline{\overline{M}} + HNcov\left(\Delta RY_{ik}, M_{ik}\right) \tag{2}$$

where k indexes one of H habitats, $HN\overline{\overline{\Delta RY}}\,\overline{\overline{M}}$ is the total complementarity effect (CE_γ), summed across all habitats and species, and $HNcov\left(\Delta RY_{ik}, M_{ik}\right)$ is the total selection effect (SE_γ), summed across all habitats and species, and the subscript γ denotes that the biodiversity effect is quantified at the landscape scale, across rather than within habitats. Thus, landscape biodiversity effects were calculated across all mixture plots across all habitats. Note that the net biodiversity effect is equivalent regardless of whether it is quantified at local scales using Eq. 1 and then summed across plots and habitats or quantified at the landscape scale using Eq. 2. In contrast, local complementarity effects and selection effects cannot simply be summed across all times and places to quantify their total effects because the sum of products does not necessarily equal the product of sums (means). Consequently, local complementarity effects within habitats can turn into total selection effects across the landscape, and vice versa (Isbell et al. 2018).

Finally, we further partitioned the total selection effect into its components (Isbell et al. 2018):

$$SE_\gamma = HNcov\left(\Delta RY_{ik}, M_{ik}\right) = HNcov\left(\Delta RY_{O,ik}, M_{ik}\right) + HNcov\left(\overline{\Delta p_i}, \overline{M_i}\right) + HNcov\left(\Delta p_{ik}, M_{ik}\right) \tag{3}$$

where $HNcov\left(\Delta RY_{O,ik}, M_{ik}\right)$ is the nonrandom overyielding effect, $HNcov(\overline{\Delta p_i}, \overline{M_i})$ is the average selection effect, and $HNcov(\Delta p_{ik}, M_{ik})$ is the spatial selection effect, with $RY_{O,ik} - p_{O,ik} = \Delta RY_{O,ik}$ as the change in observed relative yield, with the O subscript serving as a reminder that this difference is with respect to the observed, rather than expected, proportion, and $p_{O,ik} - RY_{E,ik} = \Delta p_{ik}$ as the change in dominance for species i in habitat k. The nonrandom overyielding effect quantifies the extent to which the species that survive most in monoculture tend to survive the most in mixtures; greater survival is measured against an expectation based on monoculture survivorship and observed, rather than initial, relative abundance in mixture (Isbell et al. 2018). The average selection effect quantifies the extent to which the species that survive most in monoculture also tend to be the same species that are most dominant (i.e., greatest relative abundance) in mixtures, on average across all habitats. The spatial selection effect quantifies the extent to which each species dominates mixtures to a greater extent in the habitats where it survives the most in monocultures. Spatial selection effects were formerly referred to as spatial insurance effects, following Yachi and Loreau's (1999) definition of 'performance-enhancing insurance effects,' but are now known as spatial selection effects, given that they are a component of the selection effect (Isbell et al. 2018), and to avoid confusion with other types of 'buffering insurance effects' in the diversity-stability literature (Loreau et al. 2021).

No seedlings survived in the two true replicates of the *P. strobus* monocultures in the grassland.

This creates division by zero when quantifying relative yields for this species in this habitat. That is, if any individuals survive in mixture, then the diversity effect approaches infinity because no individuals survived in monoculture. There are several options for addressing this issue. For example, one could avoid division by zero by excluding plots or species where this occurs, or by changing the zero to a small nonzero value. We caution against the latter two options, as excluding some species in some plots creates a data imbalance that can create a nonzero spatiotemporal selection effect (Isbell et al. 2018) and results can be highly sensitive to the nonzero values added. Here we simply removed the eight mixture plots in the grassland that included *P. strobus*. We did this consistently across all analyses of diversity effects so that results would be comparable across scales. We calculated landscape CE_{γ} and SE_{γ} mean and error bars by bootstrapping sampling. To choose bootstrap samples, we randomly sampled one of the two true replicate plots for each mixture species composition at each site 42 times, which is the number of experimental units. Local scale within sites had two true replicates and thus the mean and standard errors indicate the same source of within-site plot-to-plot variation among true replicates, similarly as previous biodiversity experiments that were conducted at only one site.

We further tested the effects of monoculture survivorship, calculated as the percent of individuals surviving, on the mixture relative abundance for each species. We used the function *predict* to extract predicted results for the GLMM model and illustrate fitted values of mixture relative abundance and monoculture survival. The level of significance for all statistical tests was $\alpha < 0.05$ and marginal significance was $0.1 \leq \alpha \geq 0.05$. We used the function *glmmPQL* in the MASS package (Venables and Ripley 2002) in RStudio (R Development Core Team 2016).

Environmental variables

We used a generalized linear mixed effects model (GLMM) gamma error distribution (inverse link) for continuous variables to test whether environmental variables differed between the diversity treatments (single-species monocultures and four-species mixtures) and habitats. Plot was a random intercept term to account for plot heterogeneity. Because both above and below PAR were correlated, we kept above canopy measurements only in our analysis, as this corresponds to the light available to the seedlings (whereas the ground-level measurements may be more relevant for seed germination). Henceforth, above PAR is referred to as light availability. We used the function *predict* to obtain predicted results for the GLMM model to calculate predicts means and standard errors. The level of significance for all statistical tests was $\alpha < 0.05$ and marginal significance was $0.1 \leq \alpha \geq 0.05$. We used the *glmer* function in the *lme4* package (Bates et al. 2015). We explored how environmental variables were distributed across habitats by plotting them in the 3D space with the function *plot_ly* in the *plotly* package (Sievert 2020) in RStudio (R Development Core Team 2016).

Seedling survivorship in response to environmental factors

We calculated seedling survivorship based on proportional data of seedlings alive per species per plot. To test the effects of the environmental variables on focal seedling survivorship, we tested environmental variables (as single variables and condensed as scores [PC1 and PC2] derived from principal component analysis (PCA)) as main effects in GLMM with a quasibinomial error distribution for the proportional response variable. Fixed effects were tested as non-interactive terms. We also tested the environmental factors effects on survivorship for species in monoculture and mixture in the different habitats as main effects. Plot and species nested within major habitat (bog, coniferous forest, deciduous forest, grassland, and savanna) was a random intercept term to account for plot and habitat heterogeneity. The level of significance for all statistical tests was $\alpha < 0.05$ and marginal significance was $0.1 \leq \alpha \geq 0.05$. We used the function *glmmPQL* in the MASS package (Venables and Ripley 2002) in RStudio (R Development Core Team 2016).

Seedling survivorship in response to distance from home habitat and diversity

Distance from home habitat for each species was calculated as the Euclidian distance from home habitat centroids to plot-level PCA scores in other habitats. Home habitats were places where a species is the dominant plant species outside of the experiment, whereas away habitats were places outside a species dominance. We then estimated the influence of habitat distance from home habitat, diversity (monoculture or mixture) and species identity on seedling survivorship by using a GLMM with a quasibinomial error distribution for the proportional response variable. Fixed effects were tested as interaction terms. Plot nested within major habitat (bog, coniferous forest, deciduous forest, grassland, and savanna) was a random intercept term. The level of significance for all statistical tests was $\alpha < 0.05$ and marginal significant effects were $\alpha < 0.05$ and marginal significance was $0.1 \leq \alpha \geq 0.05$. We used the *glmmPQL* in the MASS package (Venables and Ripley 2002) in RStudio (R Development Core Team 2016).

Results

Partitioning complementarity and selection effects within and among habitats

At this establishment stage of our study, at local scales, within habitats, we found positive CE_α and slightly negative SE_α (Fig. 2a, local). These local effects were counterbalancing. Thus, about half of the individuals survived through the first growing season in both monoculture and mixtures, leading to a net biodiversity effect not significantly different from zero on average across all plots (t-test = 0.28, $p = 0.78$).

At the landscape scale, across all habitats, we found the opposite: a negative CE_γ and a positive SE_γ (Fig. 2a, landscape). This positive landscape-scale selection effect was due mostly to a positive average selection effect (Fig. 2b), whereby the species that tend to survive most in monocultures also tend to be those that survived most in mixtures, on average across sites (Fig. 3). *Andropogon gerardii* and *P. strobus* respectively exhibited high or low survivorship in all habitats (Fig. 3, Table S2–3). Interestingly, the experiment was established during a dry growing season and the wide range in survivorship among species (Fig. 3) seems to partly reflect their drought tolerances (Table S1). Importantly, we also found a significantly positive spatial selection effect (Fig. 2b), indicating that the habitats where species tended to survive more in mixtures were also those where they tended to survive more in monocultures (Fig. 3).

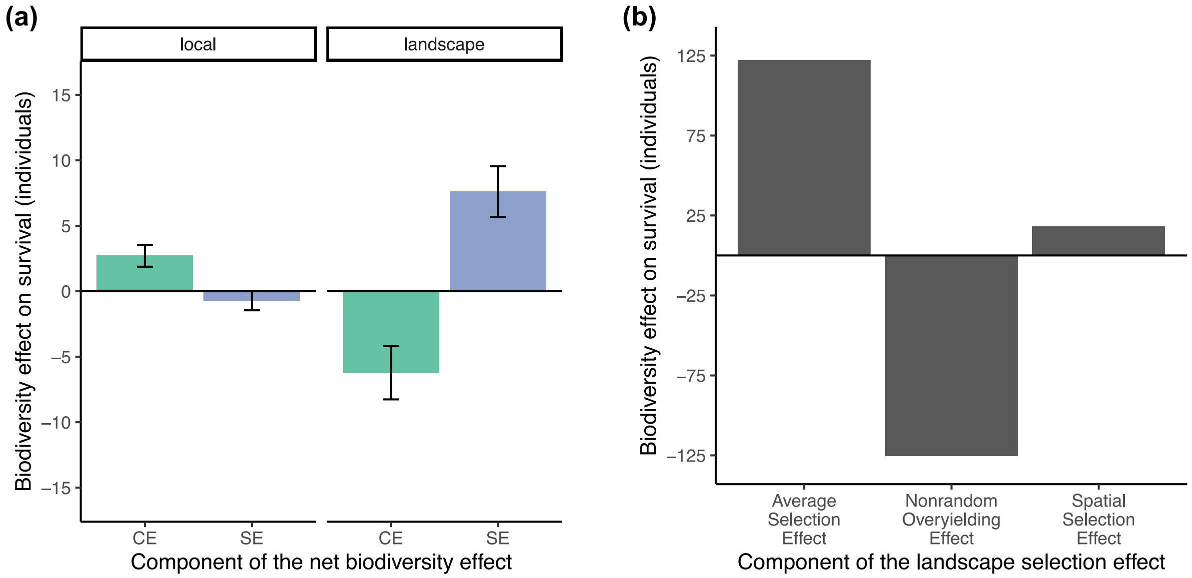
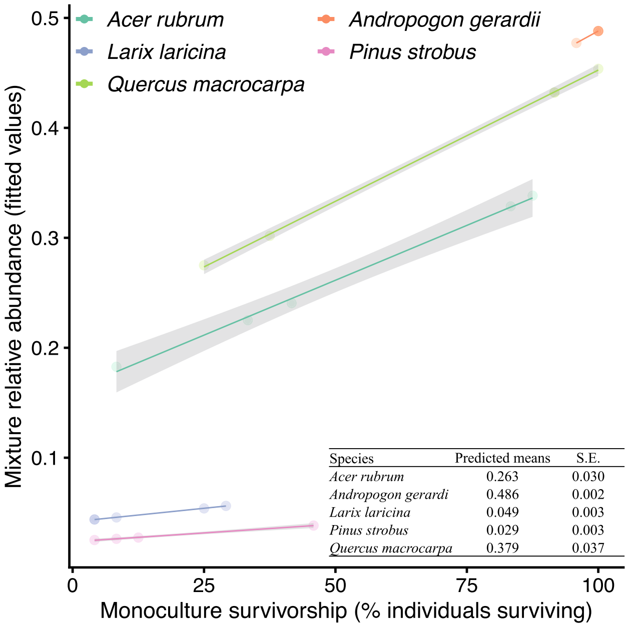


Fig. 2 Magnitudes of **a** local and landscape scale complementarity effects (CE) and selection effects (SE) and **b** components of the landscape selection effect on seedling survival for the BetaDiv experiment



Species	Predicted means	S.E.
Acer rubrum	0.263	0.030
Andropogon gerardi	0.486	0.002
Larix laricina	0.049	0.003
Pinus strobus	0.029	0.003
Quercus macrocarpa	0.379	0.037

Fig. 3 Covariation between monoculture survivorship (% individuals surviving) and mixture relative abundance (based on fitted values) for the BetaDIV experiment. Mixture relative abundance was plotted from fitted values from the generalized linear mixed model on the effects of monoculture survivorship and species on mixture relative abundance. Positive sloping lines indicate that species increasingly dominated mixtures across habitats in which they were most productive in monoculture, consistent with a positive spatial selection effect. Inset table: GLMM predicted mean values and standard errors for each species. Study species and their respective dominant habitat are: *Andropogon gerardii* (grasslands), *Quercus macrocarpa* (savannas), *Acer rubrum* (deciduous forests), *Pinus strobus* (coniferous forests) and *Larix laricina* (bogs)

Environmental variables

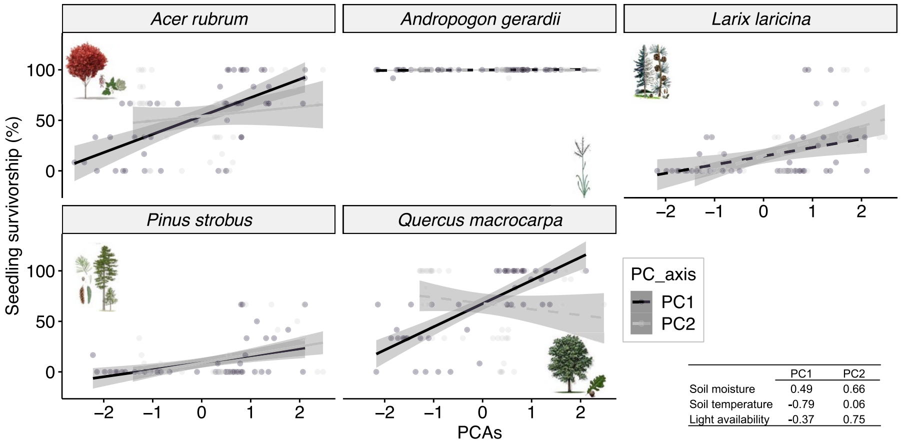
Soil moisture ($\chi^2(1)=0.45$, $p=0.50$), soil temperature ($\chi^2(1)=3.66$, $p=0.05$) and light availability ($\chi^2(1)=1.83$, $p=0.18$) marginally differed between monocultures and mixtures, and varied across the landscape more than plots within habitats (Table S4). Environmental variables were separated into habitats in the 3D space (Fig. S3). The savanna and grassland were characterized by high soil temperature and light availability, whereas the bog was characterized by high soil moisture and light availability (Table S4). The coniferous and deciduous forests were characterized by relative low light availability and intermediate levels of soil temperature and soil moisture relative to the other habitats (Table S4).

Seedling survivorship in response to environmental factors

Acer rubrum and *P. strobus* survivorship increased with lower soil temperature (PC1) and slightly increased with more light availability and soil moisture (PC2) (Fig. 4 and Table S5-6). *Quercus macrocarpa* survivorship increased only when soil temperature was lower (PC1). For the remaining species, *L. laricina* survivorship tended to increase with increased soil moisture and light availability, where *A. gerardii* had high survivorship across all environmental conditions.

Seedling survivorship in response to distance from home habitat and diversity

At this early stage of establishment, we found that only one of the five species had higher survivorship in its home habitat, where it is the dominant plant



	PC1	PC2
Soil moisture	0.49	0.66
Soil temperature	-0.79	0.06
Light availability	-0.37	0.75

Fig. 4 Relationship between principal component analysis (PCA) scores of condensed environmental variables (soil moisture, soil temperature and light availability) and seedling survivorship (%)

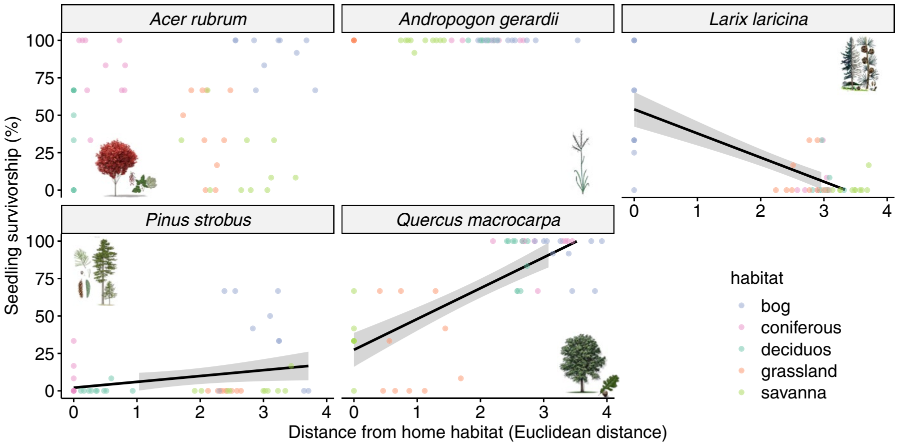


Fig. 5 Seedling survivorship (%) along an environmental distance gradient from the home habitat (i.e., where they dominate) to away habitats (i.e., where they do not dominate), measured as Euclidean distance. Study species and their respective dominant habitat are: *Andropogon gerardii* (grasslands), *Quercus macrocarpa* (savannas), *Acer rubrum* (deciduous forests), *Pinus strobus* (coniferous forests) and *Larix laricina* (bogs)

species outside of the experiment (Fig. 5, Table 1). The opposite was true for another two species, and the remaining species exhibited similar survivorship in their home habitats as elsewhere.

Larix laricina survivorship was 56% in its home habitat and 5% in away habitats. In contrast, *Q. macrocarpa* survivorship was 31% in its home habitat compared to 92% in away habitats, whereas *P. strobus* had low overall survivorship and its survivorship was 3% in home habitats compared to 13% in away habitats. *Acer rubrum* and *A. gerardii* did not differ significantly between habitats, while *A. gerardii* has had nearly 100% survivorship across all plots. We did not detect any significant main effects of diversity (consistent with a NBE not significantly different from zero) or significant interactions between home habitat distance and diversity, or species and diversity, or among home habitat distance, species, and diversity ($P > 0.05$).

Discussion

At this early experimental stage, we found positive selection effects, primarily due to average selection effects, as well as spatial selection effects arising among habitats, which supports our hypothesis for positive spatial effects of β-diversity on seedling

Table 1 Effects of habitat distance, diversity (monoculture vs. mixture) and species identity on seedling survivorship based on a generalized linear mixed model with quasibinomial error distribution. Plot nested within experimental habitat were a random intercept term in this analysis

Predictor	X^2	df	p
Distance	1.01	1	0.32
diversity	0.33	1	0.56
species	216.19	4	**< 0.001**
distance*diversity	0.72	1	0.40
distance*species	16.19	4	**< 0.01**
diversity*species	2.72	4	0.61
distance*diversity*species	8.59	4	*0.07*

Shown are Chi^2 and *p*-values (*p*). Significant effects ($p<0.05$) are given in bold and marginally significant effects ($p<0.10$) in italics. Study species: *Quercus macrocarpa*, *Andropogon gerardii*, *Acer rubrum*, *Pinus strobus* and *Larix laricina*. Respective dominated sites: savanna, grassland, deciduous forest, coniferous forest, and bog

survivorship. A significantly positive spatial selection effect indicates that the habitats where species tended to survive more in mixtures were also those where they tended to survive more in monocultures. Taken together, these early experimental results are consistent with theoretical predictions that additional effects of plant diversity on ecosystem functioning, beyond those previously studied in local experiments conducted within a particular habitat, may arise at landscape scales from dispersal and spatial sorting of species across heterogeneous landscapes (Loreau et al. 2003; Leibold et al. 2017). Here, we use survivorship as an early-stage proxy for ecosystem functioning; therefore, further investigation of the spatially and temporally fluctuating environmental heterogeneity will help inform how survivorship, growth, and relevant plant traits contribute to plant productivity and other ecosystem functions (Leibold et al. 2004, 2017; Griffin et al. 2009; Isbell et al. 2018; Polley et al. 2020).

We partitioned the net biodiversity effects into complementarity effects and selection effects based on seedling survivorship at the local and landscape scale. At the local scale, we found results consistent with previous studies that showed positive complementarity effects (Loreau and Hector 2001; Fargione et al. 2007) and negative selection effects (Isbell et al. 2009) when considering local α-diversity. Uniquely, we also found that the direction of these effects was reversed at the landscape scale as β-diversity effects resulted in negative complementarity effects and positive selection effects on seedling survival. Local complementarity effects can turn into positive landscape selection effects when there are positive spatial selection effects of β-diversity (Isbell et al. 2018). Although, we did not directly manipulate metacommunity processes, such as dispersal, we tested whether a large-scale distribution of species exhibit survivorship consistent with optimal sorting after arriving in a variety of habitats. At a landscape scale spanning multiple habitats and larger than previous local experiments, our study provides evidence for species sorting and dispersal across a spatially heterogeneous environment to influence ecosystem functioning, as expected by theory (Figure S1) (Loreau et al. 2003; Leibold et al. 2004, 2017).

The early results of our experiment highlight the importance of the influence of spatial processes (i.e., metacommunity dynamics) of community assembly processes in mediating biodiversity ecosystem function relationships. As part of the components of landscape selection effect, a positive average selection effect resulted from increased rates of survival in mixture as survival in monoculture increased for the study species on average across the landscape. For example, seedlings of *A. gerardii* and *P. strobus* respectively exhibited high or low survivorship in all habitats. Furthermore, for most species, relative abundance in mixture was positively correlated across sites with survivorship in monocultures, leading to a positive spatial effect (Figure S1). Thus, surprisingly, we can already observe ß-diversity effects at this early stage of species establishment that may eventually contribute to effects of ß-diversity on productivity. Early biodiversity effects on biomass production at the seedling stage have also been observed within habitats in previous local biodiversity experiments, such as in mixed deciduous forests (Anujan et al., unpublished), Mediterranean forests (Bastias et al. 2021), the mixed temperate forests at our site (Grossman et al. 2017), and in many other local tree diversity experiments (Guerrero-Ramírez et al. 2017). Finally, a negative nonrandom overyielding effect was likely due to a combination of observation error and biological processes that are not yet well understood (Isbell et al. 2018). Interestingly, only *L. laricina* survived more in its home bog habitat where its adult trees dominate, whereas some other species survived more, in both monocultures and mixtures, in habitats currently dominated by adults of other plant species. This may indicate the potential for long-term transitions from one forest type to another in some of these habitats, rather than the continued dominance of the same tree species in each of these habitats forever.

Spatial heterogeneity has increasingly and experimentally been considered in the biodiversity-ecosystem functioning framework, which is important to dictate the extent to which differences between species in patterns of resource use can be expressed (Loreau et al. 2003; Griffin et al. 2009; Isbell et al. 2018). Spatial heterogeneity in environmental conditions that affects the survival and growth of seedlings may act as filters that differentially affect species performance (Harper 1977). In our environmentally heterogenous landscape, decreased soil temperature, more soil moisture and intermediate levels of light availability were associated with higher rates of survival for most species, including those species where their home habitats were mostly characterized by high temperatures. For example, for *Q. macrocarpa*, mesic, nutrient-rich, shaded conditions were important environmental factors in the early stages of development which are characteristic of forested habitats but also flooded habitats like the bog. The home habitat of this species is the oak savanna, *Q. macrocarpa* had higher rates of survival as the distance increased away from it, likely because soil temperatures were relatively high in its home habitat. Conversely, only *L. laricina* out of the five species had higher survivorship in its home habitat, where soil moisture was high, as expected for its seedlings that require abundant light and a constant but suitable water level (Uchytil 1991). The deciduous tree *A. rubrum* and *P. strobus* exhibited similar survival rates across all habitats, but especially high survivorship in environmental conditions that were similar to their home habitats. Interestingly, one species, the only grass species *A. gerardii*, had high survival across all environmental conditions. Light could have hindered *A. gerardii* establishment in habitats with a dense litter layer (Tilman 1993), but light availability was not a limitation yet for *A. gerardii* seedling survival, which has been previously observed for this species in natural ecosystems with increasing habitat productivity (Grman 2013).

However, the potential for spatial heterogeneity across environments to maintain species survival will depend on interactions of different sources of heterogeneity across spatial and temporal scales. Species may track temporal fluctuations environmental conditions, thereby influencing net biodiversity effects on ecosystem functioning (Isbell et al. 2018). Alternatively, the interaction between space and time may play a role in influencing species dominance (Loreau et al. 2003; Isbell et al. 2018). Because metacommunities experience a wide range variation across multiple temporal scales, temporal drivers such as disturbance and multi-year dynamics alter the relative strength and interactions among the biological processes of dispersal, environmental filtering and species interactions (Holyoak et al. 2020). Disturbances (e.g., fire, flooding), demographic stochasticity, soil fungal community diversity, and species reproductive capacity in each habitat are expected to play a role in the dominance of species with time (Beckage and Clark 2003; Nash et al. 2020). For example, establishment of *Q. macrocarpa* seedlings might be short-lived in forest habitats because survival might not reflect its ability to grow (Seiwa 2007) or survive in the long-term (Signell et al. 2005). In shaded understory forests, seedling persistence is strongly affected by the abundance and activity of herbivores and pathogens, in addition to a negative correlation with growth rates under in both small and large gaps (Seiwa 2007). In addition, *Q. macrocarpa* are typically low to intermediate shade tolerant (Barnes and Wagner 1981), and this leads to a “sapling bottleneck” in shaded conditions, where *Q. macrocarpa* seedlings are unable to survive after their acorn energy reserves are depleted (Nowack et al. 1990). However, longer establishment in home habitats will strengthen species ability to persist. Persistence of *Q. macrocarpa* in the oak savanna will also likely depend on fire or other disturbances that limit the establishment of less fire-tolerant and more shade-tolerant woodland species (Signell et al. 2005). In contrast, seedlings of *P. strobus* tolerate limited shade from herbaceous ground cover better than other pine species (Torbert et al. 1988) and this might have influenced higher survival away from forest habitats that are also shaded at some extent. In addition, this species has its establishment enhanced in acidic conditions, which is provided in the bog (Raynal et al. 1982). Finally, the ability of energy reserves to capitalize on favorable growth conditions will influence the species-specific correlation between species survival and growth.

Our early findings that additional effects of plant diversity on ecosystem functioning may arise at heterogeneous landscape scales strengthen the importance of multiscale knowledge at the intersections of spatial scales, especially in the context of biodiversity loss (Isbell et al. 2017; Mori et al. 2018, Plas et al. 2019; Gonzalez et al. 2020). Cascading impacts of human activities on biodiversity and ecosystems, as well as the ecosystem services (e.g., production of wood in forests, livestock forage in grasslands and carbon storage in bog ecosystems) that are provided for people, will likely increase at larger spatial and temporal scales (Isbell et al. 2017). Therefore, understanding how these relationships shift with scale will help in the assessment of the sustainability of ecosystem services in the face of biodiversity loss (Balvanera et al. 2014; Isbell et al. 2017).

Conclusion

In this experiment, we extended experimental tests of biodiversity effects on ecosystem functioning from single to multiple habitats. Our results show positive spatial selection effects, indicating that the habitats where species tended to be more abundant in mixtures were also those where they tended to survive more in monocultures. These findings support theoretical predictions that plant diversity can have additional effects on ecosystem functioning beyond those observed in local experiments within local habitats. Our results also emphasize the importance of metacommunity processes as drivers of biodiversity and ecosystem functioning, as well as environmental heterogeneity that ultimately determine community structure and its relation to ecosystems. Further study will be needed to determine how survivorship patterns develop over time within and among habitats and how not only survivorship, but also growth and reproduction, contribute to plant productivity and other ecosystem functions.

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Author contributions FI conceived the study. KC and FI established the experiment. KC collected the data; KC and FI analyzed and interpreted the data and wrote the manuscript. All authors made edits and approved the final manuscript.

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Data availability Upon publication of this article, data will be made available on the Environmental Data Initiative (EDI).

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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