LETTER

Reducing dispersal limitation via seed addition increases species richness but not above-ground biomass

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Abstract

Seed dispersal limitation, which can be exacerbated by a number of anthropogenic causes, can result in local communities having fewer species than they might potentially support, representing a potential diversity deficit. The link between processes that shape natural variation in diversity, such as dispersal limitation, and the consequent effects on productivity is less well known. Here, we synthesised data from 12 seed addition experiments in grassland communities to examine the influence of reducing seed dispersal limitation (from 1 to 60 species added across experiments) on species richness and productivity. For every 10 species of seed added, we found that species richness increased by about two species. However, the increase in species richness by overcoming seed limitation did not lead to a concomitant increase in above-ground biomass production. This highlights the need to consider the relationship between biodiversity and ecosystem functioning in a pluralistic way that considers both the processes that shape diversity and productivity simultaneously in naturally assembled communities.

Keywords

Biodiversity, community assembly, ecosystem function, grasslands, metacommunity ecology, seed addition, species pool.

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INTRODUCTION

Human activities directly and indirectly impact both the diversity and the functioning of ecosystems (Díaz *et al.* 2006; Moreno-Mateos *et al.* 2017; Chaplin-Kramer *et al.* 2019). Furthermore, the loss of species diversity itself is often thought to have a concomitant direct effect on the stability and function of ecosystems (Cardinale *et al.* 2013; Hooper *et al.* 2016). However, most studies that link biodiversity and ecosystem functioning (BEF) implicitly assume biodiversity is an independent variable driving ecosystem function, but this is increasingly recognised as unrealistic (Lepš 2004; De Laender *et al.* 2016; Grace *et al.* 2016; Wardle 2016; Veen *et al.* 2018). Instead, biodiversity in natural systems arises as the outcome of processes including environmental filtering, colonisation/extinction dynamics and species interactions, which in turn influence the functioning of ecosystems (Grace *et al.* 2016; Leibold *et al.* 2017; van der Sande *et al.* 2017). Providing more realistic manipulations to more fully understand the relationship between naturally variable levels of diversity and ecosystem functioning is an experimental challenge.

Habitat fragmentation and connectivity loss can have strong negative effects on diversity (e.g. Damschen 2006; Haddad *et al.* 2015; Damschen *et al.* 2019). While this loss of diversity via reductions in dispersal rates might cascade to affect ecosystem processes (e.g. Isbell *et al.* 2017), this remains largely unexplored. For example, species exhibit trade-offs in the ability to disperse and colonise vs. the ability to persist and compete (Hastings 1980; Tilman 1994). In low-diversity communities, such as small patches in fragmented landscapes, species are unlikely to be a random subset of diverse communities (Smith & Knapp 2003). Instead, they are likely a biased subset of species on this trade-off spectrum (Turnbull *et al.* 1999; Zavaleta & Hulvey 2004; Veen *et al.* 2018), affected by processes such as competition for resources. Which species can coexist locally depends on how well suited their traits are for a local environment (Leibold *et al.* 2017), and how species complement each other (Barry *et al.* 2019a), which can have varying implications for measures of ecosystem function above and below ground (Barry *et al.* 2019b).

At the regional scale, connectivity among patches in a metacommunity facilitates dispersal (i.e. the quantity of propagules arriving to a local community), which can influence the diversity and composition of species in local areas (e.g. Ricklefs 1987, 2004; Vellend 2016; Leibold & Chase 2017). This altered diversity and composition, can in turn influence patterns of ecosystem functioning (Bond & Chase 2002; Mouquet & Loreau 2003; Leibold *et al.* 2017; Thompson & Gonzalez 2017).

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For example, a dispersal-limited community may not be saturated with species that would be otherwise well-adapted to local environmental conditions, thus limiting potential ecosystem function. In contrast, a community with an excess of dispersal might allow poorly competitive species to persist via mass effects, and this might also limit ecosystem function (Leibold *et al.* 2017). In short, varying rates of dispersal might influence patterns of both species diversity and ecosystem function in other interdependent ways, producing a variety of possible correlational patterns between diversity and function. For example, the relationship between biodiversity and ecosystem functions is typically asymptotic (Cardinale *et al.* 2013; Hooper *et al.* 2016), and if dispersal-mediated diversity increases are near the asymptote, dispersal could increase diversity without influencing ecosystem functions in a significant way.

In this study, we tested the local-scale relationship between seed dispersal-mediated changes in species diversity and one commonly reported measure of ecosystem function, above-ground plant biomass. We analysed the results from seed-addition experiments in plant communities of grassland ecosystems. A common experimental approach to understand the importance of seed dispersal is to add seeds of species from the regional species pool to discern to what degree local communities are seed limited (e.g. Tilman 1997; Turnbull *et al.* 2000; Zobel *et al.* 2006; Poulsen *et al.* 2007; Myers & Harms 2009). Such an approach is among the most realistic available to test seed dispersal effects on diversity in an experimental setting, as the only factor manipulated is the realised seed dispersal rates. As a result, we can also directly estimate the influence of dispersal on both changes in diversity and changes in measures of ecosystem functions such as plant biomass, allowing us to test a number of possible outcomes. First, a local community can be saturated with species and not dispersal limited, in which case we would expect no effect of seed addition on species richness or plant biomass. Second, seed addition could lead to an increase in species richness, but no change in biomass, if, for example, the biodiversity-ecosystem functioning relationship is asymptotic and added species are largely redundant with those already present. Third, seed addition could increase both richness and biomass if the local community is highly dispersal limited, and increased dispersal facilitates complementary species to establish and persist. Finally, seed addition could lead an increase in species richness, but a decline in biomass if excess dispersal allows competitively inferior species to persist and use resources less effectively.

We examined how increasing number of species added as seeds (ranging from 1 to 60 added species) influenced local species richness, community evenness, species composition and above-ground biomass production, per species of seed added in a synthesis across 12 previously published seed-addition experiments in grasslands (Table 1). We also quantified the relationship between the responses of richness and biomass to this seed addition gradient. Local species richness increased with seed dispersal across experiments, though biomass remained unaffected overall. Positive increases in species richness were not necessarily associated with large biomass gains within experiments.

MATERIALS AND METHODS

Data collation

We searched for seed addition studies where the experiment included: (1) an unmanipulated control and a treatment of diverse seed mixtures selected from the regional species pool, (2) the number and identity of every species added as seed and (3) measured species richness and the relative contribution of each species to community biomass (that were not weeded or otherwise altered). Because these criteria were relatively stringent, we did not restrict ourselves to formally standardised literature searches, but rather attempted to find as many datasets as possible that met our search criteria.

We began by consulting published meta-analyses (Cadotte 2006; Clark *et al.* 2007; Myers & Harms 2009; Grainger & Gilbert 2016), and other experimental data sources (e.g. U.S. Long Term Ecological Research [LTER] websites). We then used different combinations of standardised search strings including terms related to biodiversity ('richness', 'diversity'), biomass ('ecosystem function', 'above-ground biomass') and seed addition ('propagule arrival', 'BEF experiment', 'seeding'). For each experiment identified, we scanned the paper to determine whether it met our inclusion criteria. For some studies, we were able to download or extract data directly. For the rest, we contacted authors to request species-level data and other needed information (i.e. seeded richness).

We found a total of 12 studies that tested the effect of seed addition on species richness and biomass in grassland habitats, where the identity and number of seeds per species added was known (Table 1, Table S1, Fig. S1). Eight of the studies were conducted in the United States (two in California, two in Minnesota, two in Kansas, and one each in Michigan and Texas) and four studies were conducted in Germany. In all studies, species added via the seed addition treatments were part of the broader regional species pool (Pärtel *et al.* 1996), and were added to each community through a high density of seed mixes added to treatment (but not control) plots (Table S1).

Several experiments included treatments other than the primary focus of this study (e.g. disturbance, nutrient addition), which we omitted from all analyses. We also removed treatments with unknown richness of added seeds (e.g. hay). This led to some experiments having an unbalanced design between controls and treatments. Community level biomass was sometimes measured directly within plots, and other times estimated from percent cover or coarser samples (e.g. biomass strip) (Table S1). Where biomass was measured indirectly (sampled on smaller subplots), the percent cover of each species was divided by the plot percent cover and multiplied by the community biomass (g/m^2) sample from a neighbouring plot or biomass strip with the same treatment, and per species biomass estimates were then summed to the plot level (Axmanová *et al.* 2012). We standardised data for each experiment in a hierarchical experimental design: plots nested in blocks, nested in sites. The experiments varied in the number of species added (hereafter seeded richness), the density of seeds added and length of experiment (Table 1, Table S1). Combined, the study-level treatments resulted in a 'seeded richness gradient' ranging from 1 to 60 species (See Table 1).

TABLE 1 Twelve experiments testing the effects of seed arrival on plant species richness and biomass. All experiments include a non-seeded control where the seeded richness was 0. (More see Table S1)

Experiment short name	Experiment	Location	Climate	Grassland type	Management	Number of sites	Seeded richness	Data obtained for years since treatment
California.1	Seabloom et al. (2003)	Sedgwick Reserve, USA-CA	Mediterranean	Invaded natural	None	2	5	1,2,3,4,5
California.2	Seabloom (2010)	Sedgwick, Hastings, & McLaughlin Reserve USA-CA	Mediterranean	Invaded natural	None	3	1,3	1,2,3,4
CedarCreek.4	Clark & Tilman (2010)	Cedar Creek LTER, USA-MN	Temperate	Successional old field	None	1	10	1,2
CedarCreek.93	Tilman (1997)	Cedar Creek LTER, USA-MN	Temperate	Natural savanna	None	1	5,10, 15, 20,25,30, 35,40, 54	1,2,3,6,7, 13,17
Halle	Maron et al. (2014)	Halle (Salle), Germany	Temperate	Semi-natural	Mowing	10	20	2,3
Jena	Roscher et al. (2004); Petermann et al. (2010)	Jena Experiment, Germany	Temperate	Established grassland (3 years prior to seed addition)	Mowing	1	1,2,4,8, 16,60	2,3
Jena2	(Buchmann & Roscher, Unpublished)	Jena Region, Germany	Temperate	Semi-natural	Mowing	6	30	2
Kansas.Hay.Meadow	Foster (2016a)	Kansas University Field Station LTER, USA-KS	Temperate	Abandoned hay meadow	None	1	41	1-15
Kansas.Old.Field	Foster (2016b)	Kansas University Field Station LTER, USA-KS	Temperate	Successional old field	Herbicide, plowed, & disked prior to study	1	50	1-14
Michigan	Reynolds et al. (2007)	Allegan State Game Area, USA-MI	Temperate	Successional pasture	None	1	43	1,2,3
Montane	Stein et al. (2008)	Frankenwald & Thuringer Schiefergebirge, Germany	Temperate	Semi-natural/ Successional old field	Mowing	20	60	1,2,3
Texas.Temple.Prairie	Wilsey & Polley (2003)	Temple, USA-TX	Temperate	Successional/ natural	None	1	20	1

Data analysis

We examined how seed addition influenced plot level plant diversity and biomass (g/m^2) using a number of complementary metrics, and two different statistical models. Specifically, we quantified how species richness, evenness, species composition and biomass responded to seed addition using multilevel regression models.

Species richness and biomass were obtained directly from each experiment (Fig. S1). We calculated evenness using individual plant biomass as the probability of interspecific encounter (PIE) transformed to an effective number of species (S_{PIE}), equivalent to a diversity of order $q = 2$ in the Hill number scheme (Jost 2006; Chase et al. 2018). The PIE is typically calculated as the probability that two individuals sampled from a random community are different species, and higher values represent more even communities (Hurlbert 1971). Here, we had percent cover, not individual-based data, and so we calculated PIE using biomass of each species as the measure of relative abundance rather than the number of individuals, however, the qualitative information on the evenness of communities remains the same. The changes in S_{PIE} indicate that seeding treatments influenced species relative abundances, and in particular, the number of relatively common species in the sample; a more uneven a community will have a larger difference between species richness and S_{PIE} than a more even community (Chase et al. 2018).

To quantify the effect of seed addition on species composition of treatments compared to controls, we calculated the turnover and nestedness components of Jaccard's dissimilarity index using the R package beta.part (Baselga 2009; Baselga & Orme 2012; Baselga et al. 2018). Specifically, we calculated the dissimilarity components between each control (no seeds added) and each treatment (seeds added) plot within each

experiment, site, block and year combination as a pairwise comparison (Marion *et al.* 2017). This allowed us to ask what the effect of seed addition was on the species composition in control plots vs. treated plots, which we refer to as community composition hereafter. If adding seeds simply added species to the community, we would expect most of the difference in community composition between treatments would be due to the nestedness component. Alternatively, if adding seeds also led to some replacement of some species by others, this would be identified in the turnover component.

We fit separate univariate multilevel regression models for each metric (richness, biomass, evenness, turnover and nestedness) to quantify the effect of seed addition on these complementary components of community diversity, composition and function. These models were fit to species richness, biomass (log transformed) and evenness, with Gaussian error distributions. To quantify the joint response of richness and biomass to seed addition, we also fit a multivariate multilevel regression model. Finally, the turnover model assumed a zero-one inflated beta error distribution, and nestedness a zero-inflated beta distribution; zero-one and zero-inflation were required as the beta-distribution does not include zero or one, but our responses variables did.

For all models, we quantified the effect of seed addition using the seeded richness (i.e. the number of species of seed added in seeding treatments), modelled as a continuous fixed effect. This estimates the overall effect on species richness and biomass per species of seed added. The control plots had a seeded richness of zero and each treatment plot had a seeded richness value that equalled the number of species of seed in the associated treatment seed mixture. We fit models with seeded richness as a continuous effect to account for differences in seeded richness within and across experiments, rather than treating different levels of seeded richness as the same (categorical) fixed effect of seeding. For all univariate models, experiment, site (nested within experiment), block (nested within site) and year (nested within blocks to account for repeat samples through time) were all included as random intercepts, and the seeded richness slope was allowed to vary for all groups. However, for the multivariate model assessing the joint response of richness and biomass, we could only allow the seeded richness slope to vary among experiments as it is not possible to model varying effects as correlated across grouping variables (Bürkner 2018).

We visually examined plots of residuals to assess whether model assumptions (e.g. homogeneity of variance) were met, and plots of posterior predictive checks to visually determine how well models reproduced the data (Fig. S2a–e). We present the effects of seed addition on species richness and biomass using the univariate models, as the residual inspection showed that including the additional grouping variables of site, block and year reduced heteroscedasticity (Supporting Information 1–3). We use the multivariate model to quantify the correlation between the response of species richness and biomass to seed addition.

To visualise the combined response of species richness and biomass to seed addition, we plotted the experiment-level slope estimates from the univariate models. Because our multivariate model estimates the strength of correlation in the

variation of the two responses to seed addition, we report the correlation estimated from the multivariate model.

For Bayesian inference and estimates of uncertainty, all models were fit using the Hamiltonian Monte Carlo (HMC) sampler Stan (Carpenter *et al.* 2017), and coded using the 'brms' package (Bürkner 2018) in the R for Statistical Computing and graphics environment [v.3.5.2; (R Core Development Team 2019)]. All models were fit with 4 chains and 2000 iterations, with 1000 used as a warmup. We used weakly regularising default priors and visual inspection of the HMC chains showed excellent convergence (Supporting Information 1–3).

RESULTS

Seeding treatments

Across all experiments included in our synthesis, seed addition increased the realised plot level species richness (0.13, 95% CI: 0.049 to 0.20 richness increase per species seeded; Fig. 1a and b). This means that for every ten species of seed added to a plot, there were on average, a bit less than two species gained in realised richness. For species richness, about half (five out of twelve) of the experiments had an effect estimate that was significantly greater than zero (i.e. the 95% CI did not overlap zero); the other seven did not differ from zero (Fig. 1b). Seed addition had a positive overall effect on evenness (0.041, 95% CI: 0.0024 to 0.07 effective species per species seeded; Fig. S3a). Five out of 12experiments had an effect estimate that was significantly greater than zero; the other seven did not differ from zero (Fig. S3b). In terms of community composition, seed addition per seed added had no effect on the turnover (0.002, 95% CI: −01 to 0.015) or nestedness components (0.002, 95% CI: −0.006 to 0.010) of Jaccard's dissimilarity between treatments and control plots overall, or within any experiments (Fig. S4a-d).

Seed addition and subsequent effects on diversity estimates did not affect realised biomass overall (0.002, 95% CI: −0.002 to 0.007 log(grams)/m^2 biomass per species added; Fig. 2a and b). Two out of 12 experiments had an effect estimate that was greater than zero (10 were not different from zero) (Fig. 2b).

Relationship between richness & biomass

The multivariate response model estimated the correlation between the response of species richness and biomass to seed addition across experiments as 0.58, with a high degree of uncertainty that overlaps zero (95% CI: −0.13 to 0.95, Supporting Information 4). In two experiments (Kansas.Old.-Field, Jena) seeded richness did have a positive effect on realised biomass and also a positive effect on species richness (Fig. 3). In all other experiments where the effect of seeded richness was strong on species richness (e.g. Michigan, Halle), biomass remained unaffected (Fig. 3).

DISCUSSION

We found that on the whole, if additional species added as seed successfully established, they contributed to increased
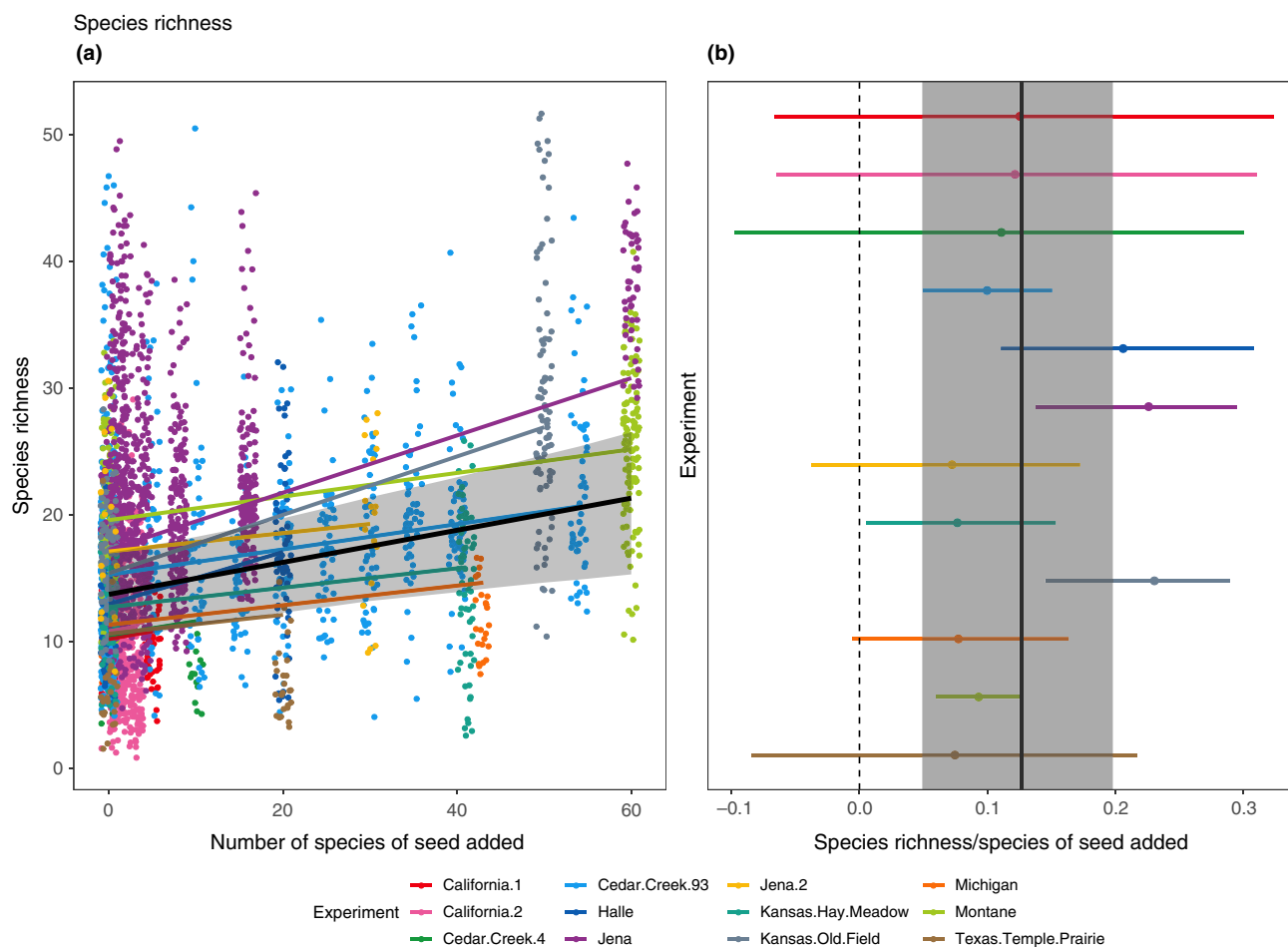
Species richness

FIGURE 1 Effect of seeded richness on plot species richness. Models fit in a Bayesian hierarchical framework with a random effects structure of experiment, site, block, and length of experiment (years). (a) Each plot is represented by a jittered point. Coloured lines represent the slope of every experiment as a random effect. The solid black line represents the overall effect estimate, and the grey shading around this black line shows the 95% credible interval. (b) Each point represents the slope of each experiment, error bars represent 95% credible intervals, and the dashed reference line at 0 represents a slope of 0 for species richness. The solid black line represents the overall slope, while the grey shading around this black line shows the 95% credible interval.

community diversity. Despite some variation among studies, species richness increased with the addition of seeds; on average, for every 10 species added, a bit less than two species established and contributed to community-level patterns. Seed addition treatments also generally had higher evenness using the S_{PIE} metric, which weights common species much more than rarer species. This indicates that increased diversity due to seed addition was not simply due to the addition of a few rare individuals of established species, but that treatments allowed species to establish and become important members of the community. This result, while interesting, is not particularly surprising as there is considerable evidence for dispersal limitation to play an important role in the local diversity of a number of communities (e.g. Ricklefs 1987; Hubbell 2001; Cornell & Harrison 2014). In experiments, dispersal in general (Grainger & Gilbert 2016), and seed addition treatments in grasslands specifically (Myers & Harms 2009), are well known to often increase the numbers of species (and other measures of diversity). While the effects of seed addition here were found to persist over a range of time-scales, it is unknown

how long these effects persist for, which is an interesting area for future research with many interesting applications such as in ecological restoration.

What is less well known, however, is how the connection between processes that influence species diversity (seed addition in this case) indirectly influence patterns of ecosystem functioning (above-ground biomass in this case). Here, despite the fact that seed addition increased species richness and evenness, we found little evidence that this had consequent effects on above-ground biomass in most studies. That is, the positive biodiversity-ecosystem function relationships that are often found in both experimental and observational studies did not seem to play much of a role in the studies we analysed here, where species diversity was altered as a consequence of reducing the influence of dispersal limitation. One reason for this could have been because biodiversity-ecosystem function relationships are unlikely to be linear in most communities, but rather are asymptotic (Tilman *et al.* 2014). If control communities were already near the asymptote along the biodiversity-ecosystem functioning relationship, increases in species
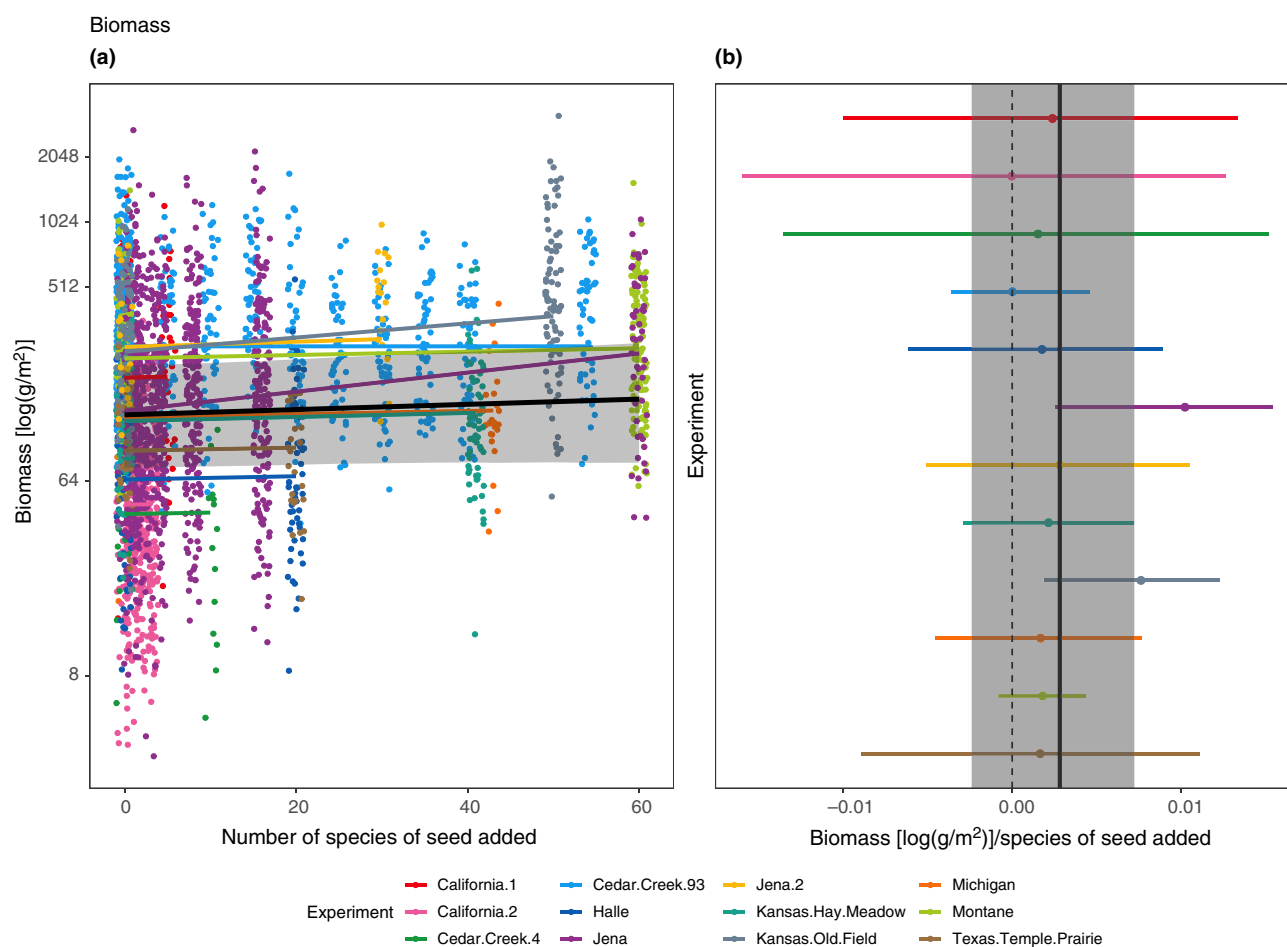
Biomass

(a)   **(b)**

FIGURE 2 Effect of Seeded Richness on Plot Biomass. Models fit in a Bayesian hierarchical framework with a random effects structure of experiment, site, block, and length of experiment (years). (a) Each plot is represented by a jittered point. Coloured lines represent the slope of every experiment as a random effect. The solid black line represents the overall effect estimate, and the grey shading around this black line shows the 95% credible interval b) Each point represents the slope of each experiment, error bars represent 95% credible intervals, and the dashed reference line at 0 represents a slope of 0 for aboveground biomass. The solid black line represents the overall slope, while the grey shading around this black line shows the 95% credible interval.

richness via removal of dispersal limitation would not necessarily lead to increases in biomass.

Despite the overall general pattern of an increase in species richness, but not biomass, in experiments with seed additions, there were some exceptions. Specifically, in two communities (Jena and Kansas.Old Field) seed addition had a positive effect on both species richness and biomass (Fig. 3). Importantly, these two cases with the strongest species richness response were seeded with much higher than average levels of species richness (Jena: 60 species, Kansas.Old.Field: 50 species). As a result, those studies may have had a higher chance of seeding species that were exceptionally productive. Alternatively, both of these sites are also on relatively degraded and reclaimed land. It could be that the 'control' diversity in these plots was lower such that increases in species richness via seed additions was further down the asymptotic biodiversity-ecosystem function curve.

We found that overall, *c.* 20% of the species seeded successfully colonised plots. Seeding success and the variability in the strength of the response of local diversity to dispersal can be related to several potential mechanisms, which we

unfortunately cannot fully parse owing to the fact that we were only able to include 12 studies in our synthesis owing to our data requirements. Nevertheless, potential mechanisms influencing diversity responses could include the degree of environmental variability (Davis *et al.* 2000); opportunity for gap filling in unsaturated starting communities (Rychtecká *et al.* 2014); facilitation from already established species (Pywell *et al.* 2004; Kulmatiski *et al.* 2008); elimination due to priority effects (Delory *et al.* 2019); and the background environmental conditions at the site, including levels of disturbance and productivity (Myers & Harms 2009). These dynamics underlying community assembly can have varying effects on the outcomes of dispersal on species richness and biomass, and on the relationship between the two variables.

Finally, we found little effect of seed addition on the turnover and nestedness components of compositional change within the time-span of the experiments examined here. The lack of an effect on turnover indicates an absence of competitive exclusion from the added species. The lack of an effect on nestedness could be linked to the saturation of the starting local community. However, it is worth nothing that these
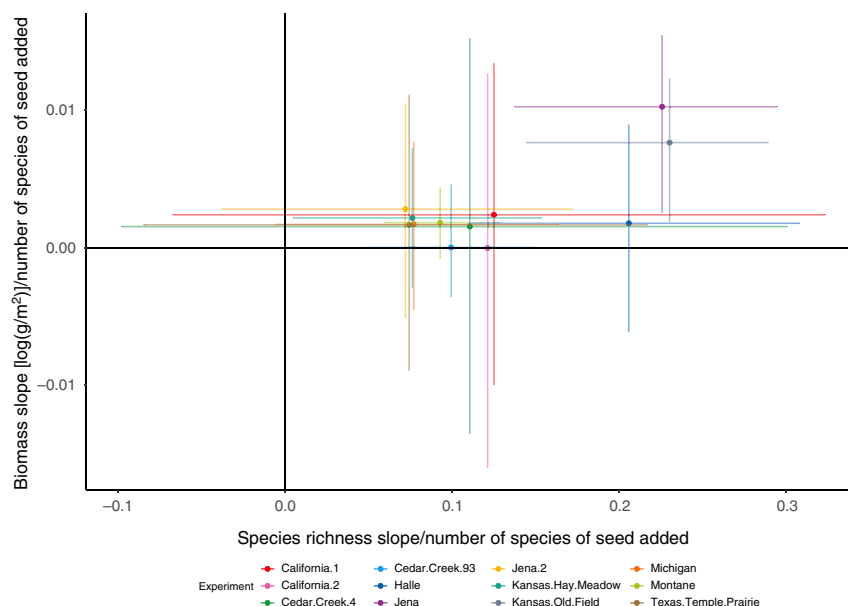
FIGURE 3 Relationship between the response of species richness and biomass per number of species of seed added. Each point represents the slope an experiment, error bars represent the 95% credible intervals.

dynamics could be observed across different time spans, and, that while there was no systematic effect of seed addition on turnover, the turnover component of dissimilarity was higher in treated plots than nestedness, and that there was greater variation among experiments in the turnover component.

Ways forward and conclusions

Experiments examining the complex relationships between regional species pools, dispersal, local species richness, species traits and ecosystem function can better help us understand the workings of real-world ecosystems. Local communities assemble as a result of multi-scale processes, and relationships between regional and local processes need to be further recognised and explicitly tested (Bond & Chase 2002; Mouquet & Loreau 2003; Thompson & Gonzalez 2016; Leibold *et al.* 2017). Direct examinations of the interdependencies between biodiversity and biomass will improve the understanding of the ultimate causal drivers of diversity and ecosystem function. Additionally, there is increasing evidence that biodiversity affects other properties of ecosystems, such as stability (Borer *et al.* 2012; Hautier *et al.* 2015), resilience (Ratcliffe *et al.* 2017) and persistence (Staples *et al.* 2019), suggesting that the selection of a measure of ecosystem function, health and overall condition may depend on environmental conditions, dispersal dynamics, community assembly processes or competition.

Our results suggest that increases in biodiversity do not necessarily translate into more biomass, but rather other mechanisms including community assembly processes, and environmental conditions may be affecting these two responses interdependently, and differently in local plant communities in different places. Thus, even though habitat fragmentation can lead to lowered diversity in many cases, and lowered diversity can lead to lower ecosystem functions such

as biomass, we would caution making such a direct link (e.g. Isbell *et al.* 2015) without understanding these interdependencies more thoroughly. We suggest that integrating community assembly processes more directly will increase our understanding of biodiversity-ecosystem function relationships.

AUTHORS CONTRIBUTIONS

J.M. C., E. L. and W. S. H. conceived the idea. E.L., H.A. C.R. and E. W. S. collected data. E.L. and S.A.B. conducted analyses. E.L. wrote the first draft, and all authors contributed to revisions.

DATA AVAILABILITY STATEMENT

All collected data has permission to be shared open access. Code and data necessary to reproduce all results and figures is archived in a GitHub repository (https://github.com/emma-ladouceur/SeedAdditionSynthesis/) and archived at Zenodo (https://doi.org/10.5281/zenodo.3889325) (10.6084/m9.figshare.12319682).

REFERENCES

Axmanová, I., Tichý, L., Fajmonová, Z., Hájková, P., Hettenbergerová, E., Li, C.-F. *et al.* (2012). Estimation of herbaceous biomass from species composition and cover. *Appl. Veg. Sci.*, 15(580), 589.

Barry, K.E., Mommer, L., van Ruijven, J., Wirth, C., Wright, A.J., Bai, Y. *et al.* (2019a). The future of complementarity: disentangling causes from consequences. *Trends Ecol. Evol.*, 34, 167–180.

Barry, K.E., van Ruijven, J., Mommer, L., Bai, Y., Beierkuhnlein, C., Buchmann, N. *et al.* (2019b). Limited evidence for spatial resource partitioning across temperate grassland biodiversity experiments. *Ecology*, 101(1), 1–13.

Baselga, A. (2009). Partitioning the turnover and nestedness components of beta diversity. *Glob. Ecol. Biogeogr.*, 19(134), 143.

Baselga, A. & Orme, C.D.L. (2012). betapart: an R package for the study of beta diversity. *Methods Ecol. Evol.*, 3(808), 812.

Baselga, A., Orme, D., Villéger, S., Bortoli, J.D., Leprieur, F., Logez, M.*et al.* (2018). Partitioning Beta Diversity into Turnover and Nestedness Components [R package betapart version 1.5.1]. CRAN.

Bond, E.M. & Chase, J.M. (2002). Biodiversity and ecosystem functioning at local and regional spatial scales. *Ecol. Lett.*, 5, 467–470.

Borer, E.T., Seabloom, E.W. & Tilman, D. (2012). Plant diversity controls arthropod biomass and temporal stability. *Ecol. Lett.*, 15, 1457–1464. https://doi.org/10.1111/ele.12006

Bürkner, P.-C. (2018). Advanced bayesian multilevel modeling with the R Package brms. *R Journal*, 10(395), 411.

Cadotte, M.W. (2006). Dispersal and species diversity: a meta-analysis. *Am. Nat.*, 167, 913–924.

Cardinale, B.J., Gross, K., Fritschie, K., Flombaum, P., Fox, J.W., Rixen, C. *et al.* (2013). Biodiversity simultaneously enhances the production and stability of community biomass, but the effects are independent. *Ecology*, 94(1697), 1707.

Carpenter, B., Gelman, A., Hoffman, M.D., Lee, D., Goodrich, B., Betancourt, M. *et al.* (2017). Stan: a probabilistic programming language. *J. Stat. Softw.*, 76(1), 32.

Chaplin-Kramer, R., Sharp, R.P., Weil, C., Bennett, E.M., Pascual, U., Arkema, K.K. *et al.* (2019). Global modeling of nature's contributions to people. *Science*, 366, 255–258.

Chase, J.M., McGill, B.J., McGlinn, D.J., May, F., Blowes, S.A., Xiao, X. *et al.* (2018). Embracing scale-dependence to achieve a deeper understanding of biodiversity and its change across communities. *Ecol. Lett.*, 21, 1737–1751.

Clark, C.M., Cleland, E.E., Collins, S.L., Fargione, J.E., Gough, L., Gross, K.L. *et al.* (2007). Environmental and plant community determinants of species loss following nitrogen enrichment. *Ecol. Lett.*, 10(596), 607.

Clark, C.M. & Tilman, D. (2010). Recovery of plant diversity following N cessation: effects of recruitment, litter, and elevated N cycling. *Ecology*, 91(3620), 3630.

Cornell, H.V. & Harrison, S.P. (2014). What are species pools and when are they important? *Annu. Rev. Ecol. Evol. Syst.*, 45(45), 67.

Damschen, E.I. (2006). Corridors increase plant species richness at large scales. *Science*, 313, 1284–1286.

Damschen, E.I., Brudvig, L.A., Burt, M.A., Fletcher, R.J., Haddad, N.M., Levey, D.J. *et al.* (2019). Ongoing accumulation of plant diversity through habitat connectivity in an 18-year experiment. *Science*, 365, 1478–1480.

Davis, M.A., Grime, J.P. & Thompson, K. (2000). Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol.*, 88, 528–534.

De Laender, F., Rohr, J.R., Ashauer, R., Baird, D.J., Berger, U., Eisenhauer, N. *et al.* (2016). Reintroducing environmental change drivers in biodiversity-ecosystem functioning research. *Trends Ecol. Evol.*, 31, 905–915.

Delory, B.M., Weidlich, E.W.A., von Gillhaussen, P. & Temperton, V.M. (2019). When history matters: The overlooked role of priority effects in grassland overyielding. *Funct. Ecol.*, 33(12), 2369–2380

Díaz, S., Fargione, J., Iii, F.S.C. & Tilman, D. (2006). Biodiversity loss threatens human well-being. *PLoS Biol.*, 4, e277.

Foster, B. (2016a). Long-term studies of secondary succession and community assembly in the prairie-forest ecotone of eastern Kansas, Hay meadow restoration experiment. LTER Network Data Portal. Available at: https://doi.org/10.6073/pasta/5703e8819c81da0beed4660f 467c288e. Last accessed 4 May 2018

Foster, B. (2016b). Long-term studies of secondary succession and community assembly in the prairie-forest ecotone of eastern Kansas, Old-field succession experiment. LTER Network Data Portal. Available at: https://doi.org/10.6073/pasta/a30d5b90676008cfb7987f31b4343a35. Last accessed 4 May 2018

Grace, J.B., Anderson, T.M., Seabloom, E.W., Borer, E.T., Adler, P.B., Harpole, W.S. *et al.* (2016). Integrative modelling reveals mechanisms linking productivity and plant species richness. *Nature*, 529, 390–393.

Grainger, T.N. & Gilbert, B. (2016). Dispersal and diversity in experimental metacommunities: linking theory and practice. *Oikos*, 125, 1213–1223.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D. *et al.* (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, 1, 1–9.

Hastings, A. (1980). Disturbance, coexistence, history, and competition for space. *Theor. Popul. Biol.*, 18, 363–373.

Hautier, H., Tilman, D., Isbell, F., Seabloom, E.W., Borer, E.T. & Reich, P.B. (2015). Anthropogenic environmental changes affect ecosystem stability via biodiversity. *Science*, 348, 336–340. https://doi.org/10.1126/science.aaa1788

Hooper, D.U., Chapin, F.S. III, Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S. *et al.* (2016). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.*, 75, 3–35.

Hubbell, S.P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography (MPB-32)*. Princeton, NJ: Princeton University Press.

Hurlbert, S.H. (1971). The nonconcept of species diversity: A critique and alternative parameters. *Ecology*, 52, 577–586.

Isbell, F., Gonzalez, A., Loreau, M., Cowles, J., Diaz, S., Hector, A. *et al.* (2017). Linking the influence and dependence of people on biodiversity across scales. *Nature*, 546(65), 72.

Isbell, F., Tilman, D., Polasky, S. & Loreau, M. (2015). The biodiversity-dependent ecosystem service debt. *Ecol. Lett.*, 18, 119–134.

Jost, L. (2006). Entropy and diversity. *Oikos*, 113, 363–375.

Kulmatiski, A., Beard, K.H., Stevens, J.R. & Cobbold, S.M. (2008). Plant–soil feedbacks: a meta-analytical review. *Ecol. Lett.*, 11, 980–992.

Leibold, M.A. & Chase, J.M. (2017). *Metacommunity Ecology*. Princeton, NJ: Princeton University Press.

Leibold, M.A., Chase, J.M. & Ernest, S.K.M. (2017). Community assembly and the functioning of ecosystems: how metacommunity processes alter ecosystems attributes. *Ecology*, 98, 909–919.

Lepš, J. (2004). What do the biodiversity experiments tell us about consequences of plant species loss in the real world? *Basic Appl. Ecol.*, 5(529), 534.

Marion, Z.H., Fordyce, J.A. & Fitzpatrick, B.M. (2017). Pairwise beta diversity resolves an underappreciated source of confusion in calculating species turnover. *Ecology*, 98(933), 939.

Maron, J.L., Auge, H., Pearson, D.E., Korell, L., Hensen, I., Suding, K.N. *et al.* (2014). Staged invasions across disparate grasslands: effects of seed provenance, consumers and disturbance on productivity and species richness. *Ecol Lett*, 17, 499–507.

Moreno-Mateos, D., Barbier, E.B., Jones, P.C., Jones, H.P., Aronson, J., López-López, J.A. *et al.* (2017). Anthropogenic ecosystem disturbance and the recovery debt. *Nat. Commun.*, 8, 14163.

Mouquet, N. & Loreau, M. (2003). Community patterns in source-sink metacommunities. *Am. Nat.*, 162, 544–557.

Myers, J.A. & Harms, K.E. (2009). Seed arrival, ecological filters, and plant species richness: a meta-analysis. *Ecol. Lett.*, 12(1250), 1260.

Pärtel, M., Zobel, M., Zobel, K., van der Maarel, E. & Partel, M. (1996). The species pool and its relation to species richness: evidence from Estonian plant communities. *Oikos*, 75, 111.

Petermann, J.S., Fergus, A.J.F., Roscher, C., Turnbull, L.A., Weigelt, A. & Schmid, B. (2010). Biology, chance, or history? The predictable reassembly of temperate grassland communities. *Ecology*, 91, 408–421.

Poulsen, J.R., Osenberg, C.W., Clark, C.J., Levey, D.J. & Bolker, B.M. (2007). Plants as reef fish: Fitting the functional Form of seedling recruitment. *Am. Nat.*, 170(2), 167–183

Pywell, R.F., Bullock, J.M., Walker, K.J., Coulson, S.J., Gregory, S.J. & Stevenson, M.J. (2004). Facilitating grassland diversification using the hemiparasitic plant Rhinanthus minor: facilitating grassland diversification. *J. Appl. Ecol.*, 41, 880–887.

R Core Development, (2019). R: A language and environment for statistical computing.

Ratcliffe, S., Wirth, C., Jucker, T., van der Plas, F., Scherer-Lorenzen, M., Verheyen, K. *et al.* (2017). Biodiversity and ecosystem functioning relations in European forests depend on environmental context. *Ecol. Lett.*, 20, 1414–1426.

Reynolds, H.L., Mittlebach, G.G., Darcy-Hall, T.L., Houseman, G.R. & Gross, K.L. (2007). No effect of varying soil resource heterogeneity on plant species richness in a low fertility grassland. *J. Ecol.*, 95(723), 733.

Ricklefs, R.E. (1987). Community diversity: Relative roles of local and regional processes. *Science*, 235(167), 171.

Ricklefs, R.E. (2004). A comprehensive framework for global patterns in biodiversity. *Ecol Letters*, 7, 1–15.

Roscher, C., Schumacher, J., Baade, J., Wilcke, W., Gleixner, G., Weisser, W.W. *et al.* (2004). The role of biodiversity for element cycling and trophic interactions: an experimental approach in a grassland community. *Basic Appl. Ecol.*, 5, 107–121.

Rychtecká, T., Lanta, V., Weiterová, I. & Lepš, J. (2014). Sown species richness and realized diversity can influence functioning of plant communities differently. *Naturwissenschaften*, 101, 637–644.

van der Sande, M.T., Peña-Claros, M., Ascarrunz, N., Arets, E.J.M.M., Licona, J.C., Toledo, M. *et al.* (2017). Abiotic and biotic drivers of biomass change in a Neotropical forest. *J. Ecol.*, 105, 1223–1234.

Seabloom, E.W. (2010). Spatial and temporal variability in propagule limitation of California native grasses. *Oikos*, 120(291), 301.

Seabloom, E.W., Harpole, W.S., Reichman, O.J. & Tilman, D. (2003). Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proc. Natl Acad. Sci.*, 100(13384), 13389.

Smith, M.D. & Knapp, A.K. (2003). Dominant species maintain ecosystem function with non-random species loss. *Ecol Letters*, 6, 509–517.

Staples, T.L., Dwyer, J.M., England, J.R. & Mayfield, M.M. (2019). Productivity does not correlate with species and functional diversity in Australian reforestation plantings across a wide climate gradient. *Glob. Ecol. Biogeogr.*, 35(23), 13.

Stein, C., Auge, H., Fischer, M., Weisser, W.W. & Prati, D. (2008). Dispersal and seed limitation affect diversity and productivity of montane grasslands. *Oikos*, 117, 1469–1478.

Thompson, P.L. & Gonzalez, A. (2016). Ecosystem multifunctionality in metacommunities. *Ecology*, 97, 2867–2879.

Thompson, P.L. & Gonzalez, A. (2017). Dispersal governs the reorganization of ecological networks under environmental change. *Nat Ecol Evol*, 1, 1–8.

Tilman, D. (1994). Competition and biodiversity in spatially structured habitats. *Ecology*, 75, 2–16.

Tilman, D. (1997). Community invasibility, recruitment limitation and grassland biodiversity. *Ecology*, 78, 81–92.

Tilman, D., Isbell, F. & Cowles, J.M. (2014). Biodiversity and ecosystem functioning. *Annu. Rev. Ecol. Evol. Syst.*, 45, 471–493.

Turnbull, L.A., Crawley, M.J. & Rees, M. (2000). Are plant populations seed-limited? A review of seed sowing experiments. *Oikos*, 88, 225–238.

Turnbull, L.A., Rees, M. & Crawley, M.J. (1999). Seed mass and the competition/colonization trade-off: a sowing experiment. *J. Ecol.*, 14, 899–912.

Veen, G.F., van der Putten, W.H. & Bezemer, T.M. (2018). Biodiversity-ecosystem functioning relationships in a long-term non-weeded field experiment. *Ecology*, 446(E6), 11.

Vellend, M. (2016). *The Theory of Ecological Communities*. Princeton, NJ: Princeton University Press.

Wardle, D.A. (2016). Do experiments exploring plant diversity-ecosystem functioning relationships inform how biodiversity loss impacts natural ecosystems? *J Veg Sci*, 27, 646–653.

Wilsey, B.J. & Polley, H.W. (2003). Effects of seed additions and grazing history on diversity and productivity of subhumid Grasslands. *Ecology*, 84(920), 931.

Zavaleta, E.S. & Hulvey, K.B. (2004). Realistic species losses disproportionately reduce grassland resistance to biological invaders. *Science*, 306, 1175–1177.

Zobel, M., Öpik, M., Moora, M. & Pärtel, M. (2006). Biodiversity and ecosystem functioning: It is time for dispersal experiments. *J. Veg. Sci.*, 17, 543–547.

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