

## LETTER

# Dispersal and neutral sampling mediate contingent effects of disturbance on plant beta-diversity: a meta-analysis

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### Abstract

A major challenge in ecology, conservation and global-change biology is to understand why biodiversity responds differently to similar environmental changes. Contingent biodiversity responses may depend on how disturbance and dispersal interact to alter variation in community composition ( $\beta$ -diversity) and assembly mechanisms. However, quantitative syntheses of these patterns and processes across studies are lacking. Using null-models and meta-analyses of 22 factorial experiments in herbaceous plant communities across Europe and North America, we show that disturbance diversifies communities when dispersal is limited, but homogenises communities when combined with increased immigration from the species pool. In contrast to the hypothesis that disturbance and dispersal mediate the strength of niche assembly, both processes altered  $\beta$ -diversity through neutral-sampling effects on numbers of individuals and species in communities. Our synthesis suggests that stochastic effects of disturbance and dispersal on community assembly play an important, but underappreciated, role in mediating biotic homogenisation and biodiversity responses to environmental change.

### Keywords

Biotic homogenisation, community assembly, community size, ecological drift, global change, metacommunity theory, niche selection, null models, seed addition, species pools.

*Ecology Letters* (2017) **20**: 347–356

## INTRODUCTION

A major challenge in ecology, conservation and global-change biology is to understand why biodiversity often responds differently to similar environmental disturbances (Lawton 1999; Vellend 2010). Biodiversity is multidimensional (McGill *et al.* 2015), but hypotheses to explain how disturbance alters biodiversity have predominantly focused on the maintenance of local species richness ( $\alpha$ -diversity) (Connell 1978), and remain controversial (Fox 2013; Huston 2014). Meanwhile some of the largest changes in biodiversity worldwide are occurring through changes to site-to-site variation in species composition ( $\beta$ -diversity) (Dornelas *et al.* 2014; Magurran *et al.* 2015), rather than through systematic changes in  $\alpha$ -diversity (Vellend *et al.* 2013; Dornelas *et al.* 2014). As a component of biodiversity that links patterns at local and regional scales (Anderson *et al.* 2011),  $\beta$ -diversity can provide key insights into mechanisms through which environmental change influences community assembly (Chase & Myers 2011), biotic homogenisation (Olden *et al.* 2004), ecosystem stability (Wang & Loreau 2016) and conservation of regional biodiversity (Socolar *et al.* 2015).

Despite rising interest in how disturbance alters biodiversity across scales, the effects of disturbance on  $\beta$ -diversity appear to be highly variable (Chase 2007; Vanschoenwinkel *et al.* 2013; Velle *et al.* 2014; Hawkins *et al.* 2015; Myers *et al.* 2015). Disturbance can be broadly defined as any discrete event causing mortality and the loss of individuals or biomass (*sensu* Sousa 1984). In this way, disturbance can alter patterns of  $\beta$ -diversity by mediating, or interacting with, three fundamental community assembly processes: niche-selection, ecological drift and dispersal (Vellend 2010).

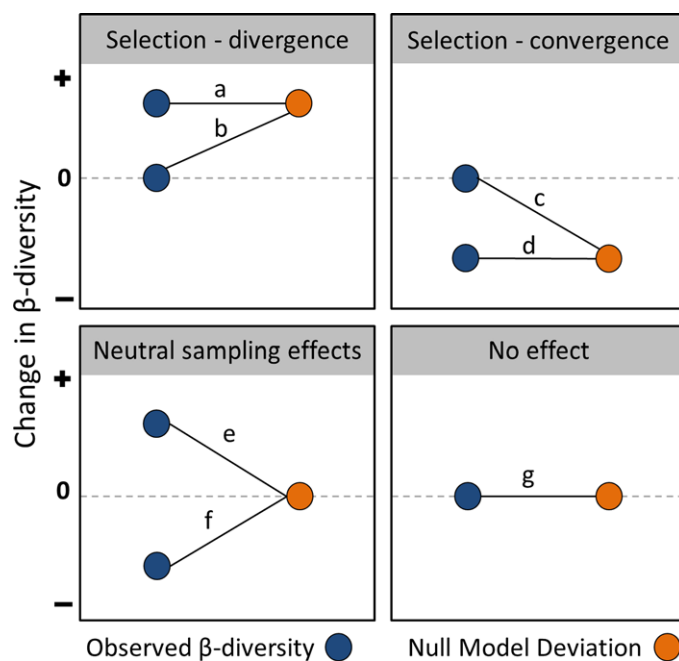
First, disturbance can homogenise community composition by selectively filtering species from the regional species pool in a similar way across local communities, resulting in low  $\beta$ -diversity (Chase 2007; Lepori & Malmqvist 2009; Püttker *et al.* 2014). For example relatively frequent disturbances like treefall gaps can select for species that colonise and reproduce rapidly (Connell 1978; Huston 2014), whereas severe or prolonged disturbances like drought can select for species with stress-tolerance traits (Chase 2007). Alternatively, disturbance can increase  $\beta$ -diversity through species sorting when it increases environmental heterogeneity among local communities in a landscape (Questad & Foster 2008; Hawkins *et al.* 2015) or by decreasing competition from regionally dominant species (Velle *et al.* 2014; Stubbington *et al.* 2015). Second, disturbance can increase  $\beta$ -diversity by causing stochastic colonisation or extinction processes that create ecological drift (Lepori & Malmqvist 2009; Myers *et al.* 2015). Drift may be especially likely when disturbance increases demographic stochasticity by reducing the number of individuals in a community (community size) (Orrock & Watling 2010).

Third, the effects of disturbance on  $\beta$ -diversity may depend on dispersal dynamics (Vanschoenwinkel *et al.* 2013; Vellend *et al.* 2014). High dispersal rates can decrease  $\beta$ -diversity by increasing distributions of regionally dominant competitors (Mouquet & Loreau 2003; Cadotte 2006). Disturbance can enhance these homogenising regional effects by decreasing local constraints on establishment (Foster *et al.* 2004). Alternatively, when disturbance increases environmental heterogeneity, high dispersal rates can increase  $\beta$ -diversity by increasing species sorting and the strength of species-environment relationships (Questad & Foster 2008). Interactive effects

of dispersal and disturbance may be especially important in ecosystems where environmental change (e.g. habitat loss & fragmentation) and restoration practices (e.g. habitat restoration & corridors) simultaneously alter disturbance regimes and dispersal rates.

Our understanding of how disturbance and dispersal influence  $\beta$ -diversity in natural ecosystems is currently limited by at least three key empirical gaps. First, most studies of disturbance effects on  $\beta$ -diversity are observational, where dispersal dynamics are either not considered or inferred using proxies for spatial processes (e.g. geographical distance) (Myers *et al.* 2015). Therefore, the extent to which results from controlled laboratory experiments (e.g. Cadotte 2007; Altermatt & Holyoak 2012) can be generalised to complex natural ecosystems is largely unknown (Vanschoenwinkel *et al.* 2013). Second, observed patterns of  $\beta$ -diversity cannot be used to infer the strength of underlying assembly mechanisms (e.g. local niche-selection) when they are confounded by changes in  $\alpha$ -diversity or community size that are neutral with respect to species identity (neutral sampling effects) (Chase *et al.* 2011; Kraft *et al.* 2011; Myers *et al.* 2015). For example if disturbance increases mean  $\alpha$ -diversity by simply altering the number of individuals in a community, observed  $\beta$ -diversity would necessarily decline if regional ( $\gamma$ ) diversity is unchanged (e.g.  $\beta = \gamma/\alpha$ ). This decline in  $\beta$ -diversity would be indistinguishable from a pattern based on random sampling from the species pool and therefore would not reflect selective homogenisation (Chase *et al.* 2011). Third, although dispersal can modify how disturbance alters patterns of  $\beta$ -diversity through its influence on niche-selection or ecological drift (Vellend *et al.* 2014), quantitative syntheses across empirical studies are lacking. Together, these three gaps limit our understanding of the contingencies or generalities by which natural communities respond to environmental change.

We quantified the extent to which disturbance and dispersal alter  $\beta$ -diversity by synthesising data from 22 field experiments conducted in plant communities across Europe and North America. Each experiment included a fully factorial manipulation of disturbance and dispersal, thereby allowing us to compare the independent and combined effects of disturbance and dispersal on  $\beta$ -diversity. Dispersal treatments in these experiments increased immigration of species from the regional pool; a process that often occurs during restoration, species invasions or natural succession after disturbance. We then used two different null models and a meta-analysis across experiments to determine the extent to which changes in  $\beta$ -diversity were caused by changes in the strength of niche-selection and neutral sampling effects (Fig. 1). We found that when dispersal was limited, disturbance increased  $\beta$ -diversity. In contrast, when dispersal was increased,  $\beta$ -diversity declined regardless of disturbance. Moreover, the combined effects of disturbance and dispersal on  $\beta$ -diversity appear to primarily reflect neutral sampling effects on the number of individuals and species in local communities, rather than systematic changes in the strength of niche-selection. Our synthesis provides new insights into why environmental change causes context-dependent patterns of biodiversity and biotic homogenisation across ecosystems.



**Figure 1** Hypothetical scenarios to infer changes in  $\beta$ -diversity and community assembly mechanisms. The alternative hypotheses are differentiated based on two criteria: 1) the difference between observed and null patterns; and 2) the region of the graph in which they fall. Blue circles are the observed differences in  $\beta$ -diversity between treatments and controls [increase (+), no difference (0), decrease (–)]. Null model deviations (orange circles) farther from the dotted grey line at 0 indicate stronger selection. Scenarios: Observed increase in  $\beta$ -diversity reflects niche-selection (a); neutral sampling effect obscures the influence of selection on community divergence (b) or convergence (c); observed decrease in  $\beta$ -diversity reflects niche-selection (d); neutral sampling effects explain observed increase in  $\beta$ -diversity, e.g. ecological drift (e), or observed decrease in  $\beta$ -diversity, e.g. resulting from increases in richness or community size that are random with respect to species identity (f); treatments have no effect on  $\beta$ -diversity or assembly mechanisms (g).

## MATERIAL AND METHODS

### Experimental data sets

In October 2014 we used ISI Web of Knowledge and Google Scholar to identify field experiments that manipulated disturbance and dispersal in plant communities. We focused on experiments in plant communities because of the relatively large number of studies that include factorial manipulations of disturbance and dispersal where a similar method (seed addition) was used for dispersal treatments (Cadotte 2006; Clark *et al.* 2007; Myers & Harms 2009a). We used Web of Knowledge to search titles, abstracts and author key words for: ‘disturbance’ AND (‘seed augmentation’ OR ‘seed addition’) AND (‘diversity’ OR ‘richness’). In Google Scholar, we searched the entire text of published peer-reviewed articles using the same keywords to locate additional studies.

We determined the suitability of each study using the following criteria: (1) experiments were conducted in natural environments; (2) disturbance and dispersal were factorially manipulated in a similar way (see 3 and 4), with controls for each treatment; (3) disturbance directly imposed mortality

and/or removal of biomass (*sensu* Sousa 1984); and (4) dispersal was manipulated by increasing immigration into plots from species pools. We excluded studies published from overlapping data sets. After filtering the literature based on these criteria, we identified 24 published studies with experiments suitable for our analysis.

We performed all analyses using the raw data from each study because most did not measure  $\beta$ -diversity. Therefore, our final set of experiments was dependent on data provided by the authors (see Table S1 in Appendix SA1). Meta-analyses based on primary data are rare in ecology and evolutionary biology (< 5%), but offer substantial advantages such as the ability to standardise data aggregation and analysis across all experiments thereby yielding more comparable effect sizes (Koricheva *et al.* 2013). We compiled data sets of 22 experiments in herbaceous plant communities representing a diversity of European and North American grassland/savanna ecosystems (Fig. 2; Table S1).

### $\beta$ -diversity & null-model analyses

We examined how responses of  $\beta$ -diversity to disturbance may be influenced by variation in assembly mechanisms and dispersal using a three-tiered approach (Fig. 1). For each experiment, we first calculated the observed dissimilarity in species composition among replicate plots within each of four treatments: control (unmanipulated), disturbance, dispersal and disturbance with dispersal. Because most of the experiments recorded only species' presences and absences, we calculated observed dissimilarity for all 22 experiments using Jaccard's incidence-based measure. For the subset of experiments that recorded species' abundances (individual frequencies or stem densities;  $n = 10$  experiments), we calculated observed dissimilarity using the Bray–Curtis abundance-based measure.

Second, we used a modified Raup–Crick null model to determine how much variation in composition was due only to sampling effects on  $\alpha$ -diversity (richness) that are neutral with respect to species identity (Chase *et al.* 2011). Changes in compositional dissimilarity after accounting for this neutral

sampling effect are often interpreted to reflect the influence of deterministic, niche-assembly mechanisms (Chase *et al.* 2011); with some caveats (see below). To generate the expected dissimilarity under the Raup–Crick null model we first defined the species pool as the total number of species and their observed occupancy across all plots in an experiment. Species were then randomly sampled from the pool (the probability of being drawn was determined by the proportion of plots in which they were observed) and assigned to local communities until reaching the observed  $\alpha$ -diversity. We repeated this procedure 10 000 times to generate a null distribution of the expected number of shared species between each pair-wise plot combination. We then estimated the probability of obtaining the observed or fewer shared species given random sampling from the species pool, rescaled to range from  $-1$  to  $1$  (Chase *et al.* 2011). Values closer to  $1$  indicate greater dissimilarity than expected from stochastic changes in  $\alpha$ -diversity, whereas those closer to  $-1$  indicate lower dissimilarity than expected (Table S2).

Incidence-based null models, however, may fail to differentiate among assembly mechanisms that operate primarily through changes in relative abundance (Gotelli & Ulrich 2012; Tucker *et al.* 2016) or when  $\alpha$ -diversity is low (Chase *et al.* 2011). Therefore, we used an additional null model for the subset of experiments that recorded species' abundances. This null model can be used to disentangle processes that cause non-random abundance changes, for example caused by environmental filtering or dispersal limitation, from those that emerge from neutral sampling effects on community size or changes in species pools (Myers *et al.* 2015). To simulate the expected dissimilarity caused by changes in community size, we first defined species pools as the total number of species and their abundances observed across all plots in a treatment. Next, while preserving the treatment species pool (relative abundance distribution and total species richness observed across all plots in a treatment), we randomly assigned individuals to local communities until reaching the observed community size. We repeated this procedure 10 000 times to generate a null distribution of the expected dissimilarity. We then



**Figure 2** Geographical distribution of experiments across North America and Europe ( $n = 22$ ). Points are sized proportional to the number of unique experiments (as labelled when there is more than one) located within particular regions (see Table S1 for experiment details). Countries include: United States of America ( $n = 13$  experiments), Austria (3), Canada (2), Italy (1), Germany (1), Estonia (1) and Finland (1).

calculated a standardised deviation from this null model ( $\beta$ -deviation) as the difference between Bray–Curtis dissimilarity and the mean expected dissimilarity, divided by the standard deviation of the mean expected values. Positive deviations indicate greater dissimilarity than expected from changes in community size or treatment species pools, whereas negative values indicate lower dissimilarity than expected (Table S2).

For observed dissimilarity and the expected dissimilarity generated by both null models, we calculated  $\beta$ -diversity using the bootstrapped mean distance between the multivariate locations of each replicate plot and the treatment centroids (distance-to-centroid) to account for non-independence of dissimilarities (Anderson *et al.* 2011). This provides the additional advantage of making the effect sizes for all measures of  $\beta$ -diversity directly comparable. To aid interpretations of null models, we also evaluated treatment effects on  $\alpha$ -diversity (mean plot richness), community size (mean number or frequency of stems per plot) and species-pool diversity (evenness and richness). We calculated  $\beta$ -diversity using the `betadisper()` function in the R package ‘vegan’, version 2.3-0 (Oksanen *et al.* 2015).

### Meta-analysis

We conducted meta-analyses across experiments to estimate independent and combined effects of disturbance and dispersal on  $\beta$ -diversity and underlying assembly mechanisms. Our meta-analyses included two steps. First, for each experiment we calculated the difference between  $\beta$ -diversity for each treatment and the unmanipulated control using Hedges’  $d$  metric – a mean difference that standardises the effect based on the pooled variance and adjusts for small sample size (Koricheva *et al.* 2013). We followed the suggestion of Gurevitch *et al.* (2001) and focused on Hedges’  $d$  to incorporate standard errors and increase comparability with previous meta-analyses that evaluated the impacts of dispersal and/or environmental filters on  $\alpha$ -diversity (Cadotte 2006; Myers & Harms 2009a). Unstandardised log response-ratios yielded similar results.

Second, we calculated mean treatment effects across experiments with random-effects models, which allow for conservative inferences more suitable for broad generalisation (Borenstein *et al.* 2009; Koricheva *et al.* 2013). Mean effects are typical of meta-analyses, but can mask variation in treatment effects across studies that are caused by differences in experimental or environmental conditions (Koricheva *et al.* 2013). Therefore, we estimated the total variation in effect sizes among studies ( $T^2$ ) using the DerSimonian and Laird method (Borenstein *et al.* 2009). Next, we determined the proportion of this variation that could be caused by differences in experimental or environmental conditions across studies ( $I^2$ ), as opposed to that simply due to sampling variance within studies. Finally, we evaluated the extent to which the effects of dispersal, disturbance or their interaction co-varied with latitude, disturbance frequency, dispersal magnitude (frequency and number of arriving species), plot size and study length (See Appendix SA2 for supplemental methods).

We conducted a leave-one-out sensitivity analysis to evaluate the influence of each experiment and diagnose outliers. We ensured there was no skewness in effect sizes from publication bias; funnel plots of standard errors on effect sizes were

symmetric for all treatments (Fig. S1). All meta-analyses were performed with the R package ‘metafor’, version 1.9-5 (Viechtbauer 2010).

## RESULTS

### Increased dispersal modified the effect of disturbance on observed $\beta$ -diversity

Across all experiments ( $n = 22$ ), disturbance increased Jaccard  $\beta$ -diversity (*effect size* = 0.12, SE = 0.11), but not significantly ( $P = 0.254$ ) (Figs 3a and 4a). In contrast, dispersal significantly decreased Jaccard  $\beta$ -diversity (*effect size* =  $-0.41$ , SE = 0.18,  $P = 0.023$ ) (Figs 3b and 4b). Moreover, the combined effect of disturbance and dispersal further decreased Jaccard  $\beta$ -diversity (*effect size* =  $-0.76$ , SE = 0.23,  $P < 0.001$ ) (Figs 3c and 4c). Sensitivity analyses demonstrated that the effects of disturbance, dispersal and their combined effect on Jaccard  $\beta$ -diversity were robust to experiment inclusion (direction of changes were consistent and had negligible effects on  $P$ -values). Treatment effects on Bray–Curtis  $\beta$ -diversity were qualitatively similar for the subset of experiments for which species’ abundances were included ( $n = 10$ ) (Fig. 3g–i).

### $\beta$ -diversity responses to disturbance and dispersal are mediated by neutral sampling effects

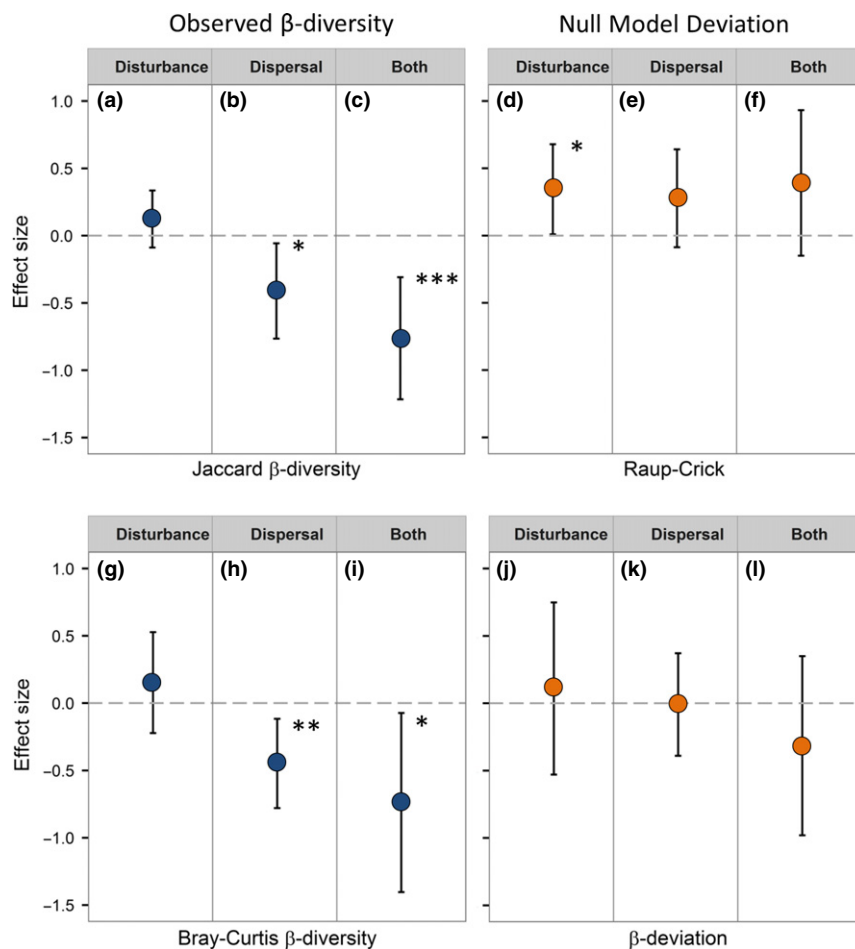
We used two different null models to determine the extent to which changes in observed  $\beta$ -diversity may reflect non-neutral assembly mechanisms (niche-selection) or neutral sampling effects.

#### *Raup–Crick effect sizes*

Patterns of Jaccard  $\beta$ -diversity were strongly influenced by increases in  $\alpha$ -diversity that were neutral with respect to species identity (Fig. 3d–f). Dispersal and disturbance both significantly increased  $\alpha$ -diversity (Fig. 5a–c). After accounting for increases in  $\alpha$ -diversity, disturbance significantly increased  $\beta$ -diversity (*Raup–Crick effect size for disturbance* = 0.35, SE = 0.17,  $P = 0.043$ ) (Fig. 3d). In contrast, the homogenising effect of dispersal in both undisturbed and disturbed communities disappeared after accounting for increases in  $\alpha$ -diversity that were neutral with respect to species identity (*Raup–Crick effect size for dispersal* = 0.28, SE = 0.19,  $P = 0.136$ ; *Raup–Crick effect size for disturbance with dispersal* = 0.39, SE = 0.28,  $P = 0.156$ ) (Fig. 3e and f). This neutral sampling effect also caused substantial shifts in the distribution of effect sizes within experiments for all three treatments (Fig. 4).

#### *$\beta$ -deviation effect sizes*

Patterns of Bray–Curtis  $\beta$ -diversity were strongly influenced by increases in community size that were neutral with respect to species identity (Fig. 3j–l). As with  $\alpha$ -diversity, dispersal and disturbance both significantly increased community size (Fig. 5d–f). Increases in community size did not qualitatively change the effect of disturbance on  $\beta$ -diversity ( *$\beta$ -deviation effect size for disturbance* = 0.11, SE = 0.33,  $P = 0.738$ ) (Fig. 3j). In contrast, the homogenising effect of dispersal in



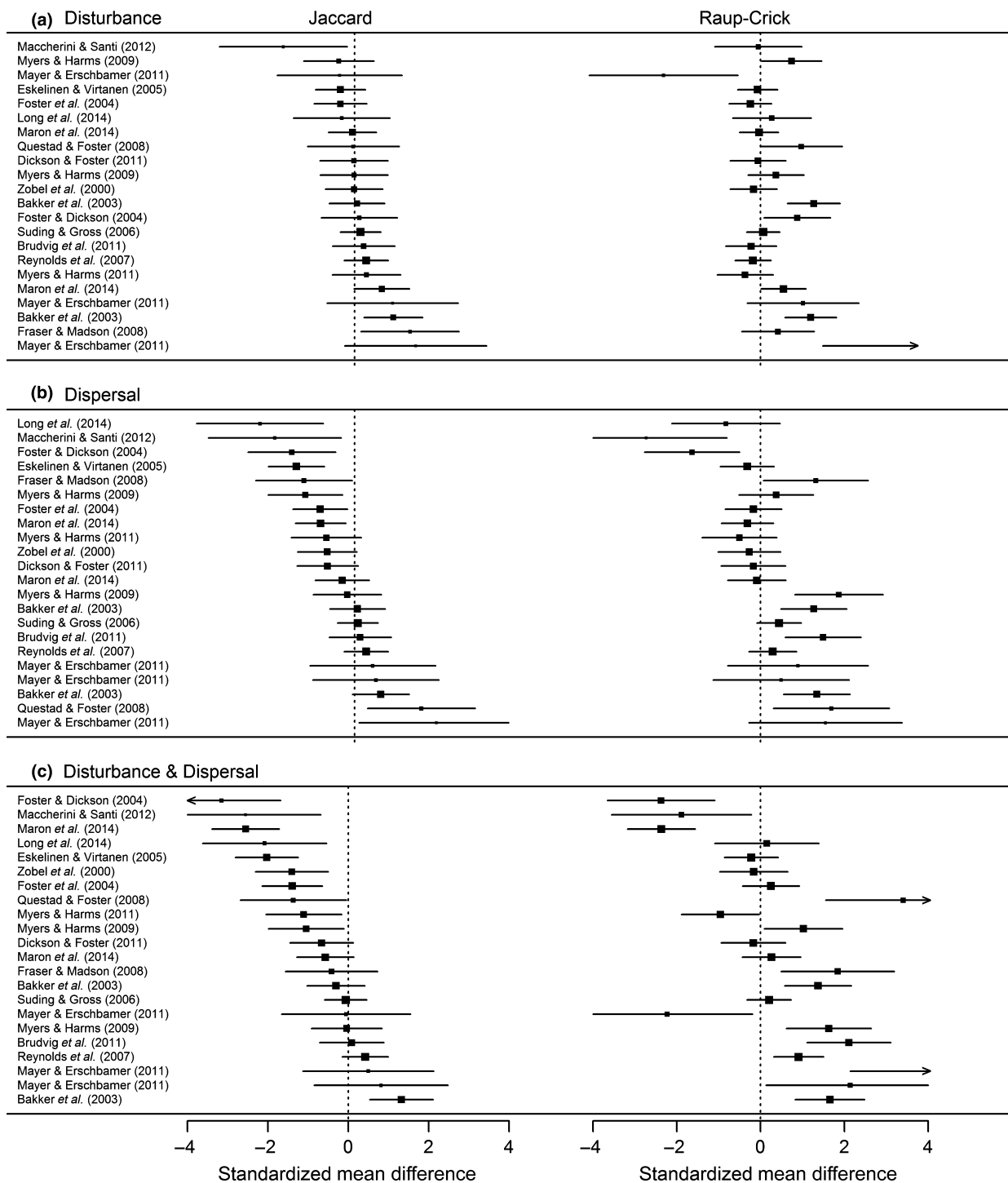
**Figure 3** Meta-analysis effect sizes (95% confidence intervals) of disturbance, dispersal and disturbance with dispersal (Both) on observed  $\beta$ -diversity and  $\beta$ -diversity from null model deviations. (a–c) Observed  $\beta$ -diversity using Jaccard dissimilarity and (d–f) Raup–Crick  $\beta$ -diversity across all 22 experiments. (g–i) Observed  $\beta$ -diversity using Bray–Curtis dissimilarity and (j–l)  $\beta$ -deviations across the ten experiments with abundance data. Effect sizes are the grand mean of the standardised mean differences between treatments and unmanipulated controls calculated with random effects models. Dashed lines at zero indicate no difference between treatments. Stars indicate significant effects (\*\*\* $P < 0.001$ , \*\* $P < 0.01$ , \* $P < 0.05$ ). Significant null model deviations indicate observed patterns are caused by non-random processes (e.g. niche-selection). Non-significant deviations indicate the observed pattern can be explained by neutral sampling effects, either caused by (d–f) stochastic change in species richness or (j–l) change in community size.

both undisturbed and disturbed communities disappeared after accounting for increases in community size that were neutral with respect to species identity ( $\beta$ -deviation effect size for dispersal =  $-0.01$ , SE = 0.19,  $P = 0.961$ ;  $\beta$ -deviation effect size for disturbance with dispersal =  $-0.32$ , SE = 0.34,  $P = 0.352$ ) (Fig. 3k and l). Furthermore, observed decreases in  $\beta$ -diversity in both the dispersal treatments and the combined dispersal with disturbance treatments were significantly correlated with increases in community size, but weakly or uncorrelated with changes in regional diversity (evenness or richness) (Fig. S2 and S3). These results indicate that observed changes in  $\beta$ -diversity were mediated primarily by changes in local community size rather than changes in regional diversity.

#### Other factors influencing variation in effect sizes across experiments

Variation in effect sizes among studies ( $I^2$ ) (Table S3) was influenced by the number of times a disturbance treatment

was applied in an experiment, species richness of seeds added in dispersal treatments, and study length (Table S3; Figs S4–S6). The number of times a disturbance treatment was applied explained 12% of the variation in Raup–Crick effect sizes. Disturbance had no effect on mean  $\beta$ -diversity when applied once (Raup–Crick effect size = 0.05,  $P = 0.822$ ), but increased mean  $\beta$ -diversity when applied multiple times (Raup–Crick effect size = 0.67,  $P = 0.009$ ) (Fig. S4). Dispersal decreased  $\beta$ -diversity more when the species richness of added seeds was greater, but this effect explained little variation among studies ( $R^2 < 1$  and 3% for observed  $\beta$ -diversity and Raup–Crick  $\beta$ -diversity respectively) (Fig. S5a and b). Dispersal decreased  $\beta$ -diversity more in longer studies, explaining 6 and 28% of the variation in observed  $\beta$ -diversity and Raup–Crick  $\beta$ -diversity respectively (Fig. S5c and d). Disturbance with dispersal also reduced  $\beta$ -diversity more in longer studies ( $R^2 = 5\%$  for both observed  $\beta$ -diversity and Raup–Crick  $\beta$ -diversity) (Fig. S6). Plot size, latitude and the number of dispersal treatments did not explain variation in effect sizes across studies.

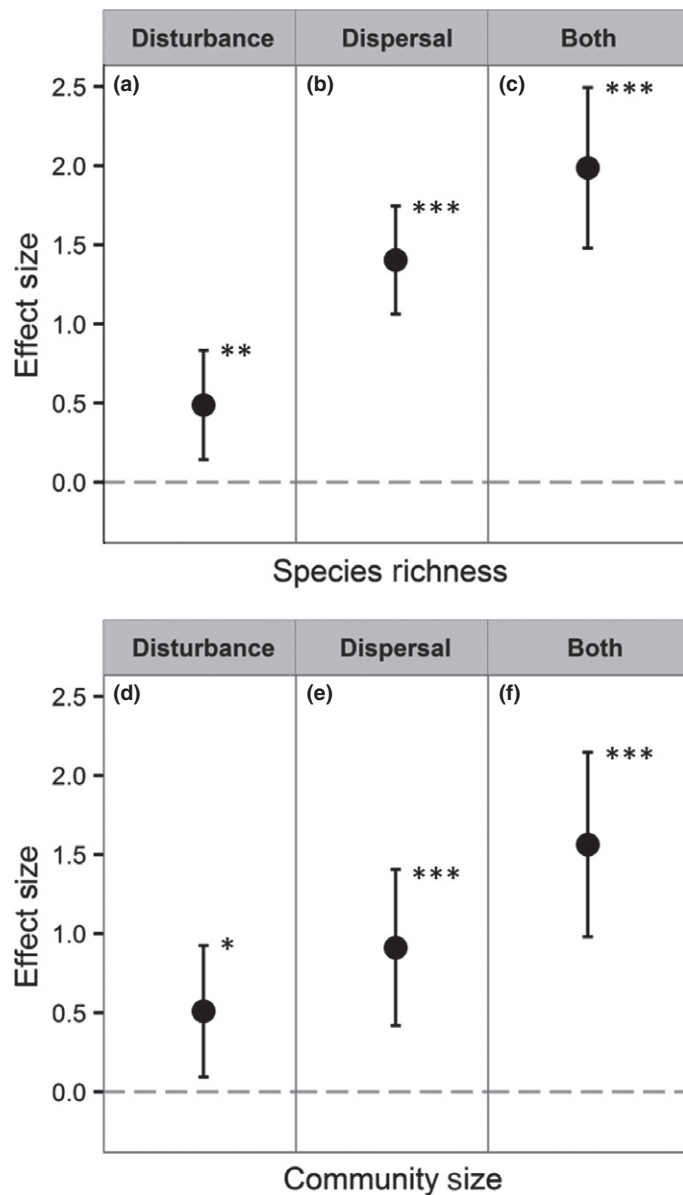


**Figure 4** Effect sizes (95% confidence intervals) of (a) disturbance, (b) dispersal and (c) disturbance with dispersal on observed  $\beta$ -diversity (Jaccard dissimilarity) and Raup–Crick  $\beta$ -diversity for individual experiments. Boxes are standardised mean differences between treatment and unmanipulated controls (dotted grey line), sized according to their proportional weight in the random effects model (inverse of their within-study variance). Negative differences (relative to the control) in observed  $\beta$ -diversity (Jaccard) indicate treatments homogenised species composition across local communities; positive differences indicate divergence in species compositions. Significant differences in Raup–Crick  $\beta$ -diversity (confidence intervals do not overlap dotted grey line) indicate non-random processes (e.g. niche-selection) contribute to the observed patterns; non-significant differences indicate stochastic changes in species richness among local communities (neutral sampling effects) contribute to the observed patterns.

## DISCUSSION

A major challenge in ecology, conservation and global-change biology is to understand why biodiversity often responds

differently to similar environmental changes (Lawton 1999; Vellend 2010). Yet comparative studies of the effects of ecological disturbance on spatial patterns of biodiversity and the underlying community assembly mechanisms are rare. Our



**Figure 5** Effect sizes (95% confidence intervals) of disturbance, dispersal and disturbance with dispersal (Both) on (a–c) mean species richness per plot and (d–f) mean total number of individuals per plot (community size). Species richness was calculated for all 22 experiments. Community size was calculated for the subset of 10 experiments with abundance data. Effect sizes are the grand mean of the standardised mean differences between treatments and unmanipulated controls calculated with random effects models. Dashed lines at zero indicate no difference between treatments. Stars indicate significant effects (\*\*\* $P < 0.001$ , \*\* $P < 0.01$ , \* $P < 0.05$ ).

meta-analysis suggests that contingent effects of disturbance on  $\beta$ -diversity depend on dispersal and are strongly mediated by neutral sampling effects.

#### Dispersal causes contingent effects of disturbance on $\beta$ -diversity

Our results suggest that the amount of dispersal into communities alters the perceived effects of disturbance on spatial patterns of biodiversity. In communities with natural

(unmanipulated) dispersal, disturbance did not significantly change observed  $\beta$ -diversity (Fig. 3a and g). In contrast, increased dispersal into disturbed communities homogenised community composition (Fig. 3c and i). Two non-mutually exclusive mechanisms could explain this result.

First, high dispersal rates may override the influence of local disturbance on patterns of biodiversity. When dispersal from the regional pool increases local species richness (Cadotte 2006; Myers & Harms 2009a),  $\beta$ -diversity can be reduced through source-sink dynamics (Mouquet & Loreau 2003; Leibold *et al.* 2004). Consistent with this mechanism, communities were more homogenised in experiments where the number of immigrating species (species richness of seed-additions) was higher (Fig. S5a and b). Second, disturbance and dispersal may interactively homogenise species composition by selecting for species arriving with disturbance-tolerant traits (Vanschoenwinkel *et al.* 2013; Vellend *et al.* 2014). Although we found that disturbance and dispersal together decreased  $\beta$ -diversity more than the additive effects of disturbance and dispersal, and that  $\beta$ -diversity trended lower in communities with disturbance and increased dispersal (Fig. 3a–c and g–i), these effects were not significantly greater than the effects of dispersal alone. Therefore, our results provide limited evidence that disturbance and dispersal interactively homogenised community composition. However, it is important to consider that experimental conditions often simplify dispersal (e.g. constant dispersal rates) (Grainger & Gilbert 2016) and environmental variation, both of which could contribute to interactive effects in natural ecosystems (Questad & Foster 2008). In summary, our results illustrate how explicit consideration of dispersal dynamics can help explain contingent effects of disturbance on  $\beta$ -diversity.

#### Neutral sampling effects, rather than changes in the strength of community assembly mechanisms, mediate effects of disturbance and dispersal on $\beta$ -diversity

Although disturbance and dispersal are often hypothesised to influence  $\beta$ -diversity by altering the relative importance of different community assembly mechanisms (Mouquet & Loreau 2003; Chase 2007; Chase & Myers 2011), observed patterns of  $\beta$ -diversity cannot be used to unambiguously separate changes in assembly mechanisms from neutral sampling effects (Myers *et al.* 2015). Our meta-analysis revealed that disturbance and dispersal influence observed  $\beta$ -diversity primarily through changes in local species richness ( $\alpha$ -diversity) and community size that appear to be neutral with respect to species identity. In particular, neutral sampling effects influenced patterns of  $\beta$ -diversity in two ways: (1) through homogenisation when disturbance and dispersal increase species richness and community size; and (2) by obscuring the effect of disturbance on non-random assembly processes.

First, our null-model analyses revealed that the homogenisation caused by dispersal and the combined effect of disturbance and dispersal were explained by increases in richness and community size that would be expected if assembly was random with respect to species' identities (Fig. 3e, f, k and i). These patterns could reflect stochastic recruitment of immigrating species

or insufficient time for deterministic influences of dispersal (e.g. competition-colonisation trade-offs) to manifest in relatively short-term experiments. Consistent with this second possibility, we found that communities were more homogenised in longer experiments (Figs S5c, d and S6). In addition, disturbance and dispersal could together influence stochastic community assembly. For example disturbance decreases recruitment limitation by opening space for colonisation from the species pool (Foster *et al.* 2004). Under these conditions, disturbance and dispersal may jointly contribute to biotic homogenisation by increasing the strength of regional controls (dispersal assembly & species-pool influences) on community assembly.

Second, neutral sampling effects obscured the influence of disturbance on non-random assembly mechanisms that diversify community composition. After accounting for increases in local species richness that would be expected if recruitment was neutral with respect to species' identities (Fig. 5a), disturbance increased incidence-based (Jaccard)  $\beta$ -diversity (Fig. 3d). In contrast, disturbance did not alter abundance-weighted (Bray–Curtis)  $\beta$ -diversity even after accounting for changes in community size and species pools (Fig. 3j). These results suggest that disturbance altered community assembly primarily through its influence on local species richness, and to a lesser degree through its influence on species abundances. This could occur if disturbance decreases occupancy of poor dispersing, but regionally dominant competitors (Velle *et al.* 2014; Stubbington *et al.* 2015) or increases deterministic species sorting across environmental gradients (Questad & Foster 2008; Hawkins *et al.* 2015). In the seven experiments where disturbance increased  $\beta$ -diversity more than expected by chance (Fig. 4a), the disturbance treatments reduced densities of dominant competitors (e.g. removal by animal disturbance, herbicide or clipping; Table S1). Therefore, weaker homogenisation (less negative Raup–Crick values) observed in disturbed relative to undisturbed communities (Table S2) may reflect changes in dominance and reduced interspecific competition, which could increase opportunities for recruitment from the seed bank or stochastic immigration from the regional species pool (Zobel *et al.* 2000; Foster *et al.* 2004; Myers & Harms 2009a).

In contrast to recent studies (e.g. Lepori & Malmqvist 2009; Myers *et al.* 2015), we did not find evidence to support the hypothesis that disturbance increases  $\beta$ -diversity by decreasing community size. Ecological drift is most likely to increase  $\beta$ -diversity when disturbance equalises fitness differences among species or increases demographic stochasticity by reducing community size (Orrock & Watling 2010). Across the experiments included in our study, in contrast, disturbance generally increased community size (Fig. 5d); a pattern that likely emerged from a combination of higher resource availability and recruitment in disturbed communities (e.g. Zobel *et al.* 2000; Myers & Harms 2009b). These results highlight the importance of understanding mechanisms by which disturbances increase or decrease community size and how changes in community size contribute to diversity-disturbance relationships (Vellend *et al.* 2014; Myers *et al.* 2015).

Surprisingly, we found little evidence to support the hypothesis that disturbance homogenises community composition through deterministic processes (Chase 2007; Lepori & Malmqvist 2009; Püttker *et al.* 2014).  $\beta$ -diversity was generally

higher in disturbed relative to undisturbed communities, and only one of 22 experiments had significantly lower  $\beta$ -diversity in disturbed communities (Fig. 4a–Raup–Crick). In this study, experimental ungulate trampling reduced the cover of a dominant sedge; however, it also increased mortality of seedlings by desiccation in gaps exposed by the disturbance (Mayer & Erschbamer 2011). Disturbance may have reduced facilitation by this dominant species thus increasing the susceptibility of others to drought. This result is consistent with other studies that found drought homogenised species composition, presumably by selecting for species with stress-tolerant traits (Chase 2007; Lepori & Malmqvist 2009). One factor that could explain why disturbance did not homogenise most communities in our meta-analysis is that the disturbances generally reflected pulse perturbations. Press disturbances that impose constant selection pressures (e.g. long-term nutrient enrichment or climate change) are more likely to cause deterministic homogenisation. Also, we focused on relatively sessile organisms (primarily herbaceous plants) where low dispersal is known to strongly limit population sizes (Clark *et al.* 2007) and local diversity (Cadotte 2006; Myers & Harms 2009a). Dispersal limitation may thus maintain spatial patterns of diversity during disturbance and reduce source-sink dynamics that can erode  $\beta$ -diversity.

Our meta-analysis highlights the importance of determining when and how dispersal may contribute to both stochastic and deterministic assembly (Vellend *et al.* 2014; Myers *et al.* 2015). Variable effects of disturbance on community assembly mechanisms and spatial patterns of diversity may strongly depend on variation in the traits that influence organisms' dispersal abilities (Lowe & McPeck 2014) and immigration rates (Vellend *et al.* 2014). For example using the same null model (Raup–Crick), Vanschoenwinkel *et al.* (2013) found that disturbance and dispersal jointly increased  $\beta$ -diversity for active dispersing aquatic invertebrates, but decreased  $\beta$ -diversity for passive dispersers (although they found the opposite result using observed  $\beta$ -diversity). Furthermore, Vellend *et al.* (2014) propose that differences in the total number of individuals and the relative abundances of species arriving to a community can alter the perceived strength of deterministic and stochastic assembly. Our results provide one of the most comprehensive tests supporting the hypothesis that one of the largest sources of contingent biodiversity responses to disturbance may be explained by variation in dispersal dynamics (which are generally not quantified) within and across ecosystems.

#### Limitations and future directions

Our results suggest three fruitful avenues for future studies investigating mechanisms of diversity-disturbance relationships. First, most experimental manipulations of disturbance and/or dispersal fail to capture the complexity of these phenomena in nature. For example natural disturbances can vary in magnitude, duration, frequency and spatio-temporal variation (Sousa 1984), and have varying effects on biodiversity. In our analysis, changes in  $\beta$ -diversity appeared to reflect increasing selection pressures as disturbance became more frequent (Fig. S4). Similarly, in most field experiments dispersal is meant to increase



immigration (staged invasions), rather than movement of residents among patches within a meta-community. Therefore, there is a critical need for field experiments to manipulate more comprehensive features of disturbance and dispersal to generalise to natural communities (Grainger & Gilbert 2016), especially because many of these same features are being modified by biological invasions and restoration practices.

Second, null models are imperfect but remain one of the most useful tools to differentiate among processes creating spatial patterns of diversity (Chase & Myers 2011). However, inferences regarding particular assembly mechanisms (e.g. biotic interactions, dispersal, environmental filtering and ecological drift) are not always straightforward (Gotelli & Ulrich 2012; Tucker *et al.* 2016). In addition, some have challenged the ability to compare null-model results across regions (Bennett & Gilbert 2015). We minimised these potential issues using two separate null models in conjunction with experimental manipulations, but urge conservatism in interpreting such results. To help facilitate deeper insights into underlying mechanisms, future studies should: (1) ensure that species abundances are measured in ways that allow quantification of changes in community size (Vellend *et al.* 2014), dominance (Avolio *et al.* 2015) and relative abundances in the species pool; (2) quantify ecophysiological and dispersal traits (Myers & Harms 2009a; Lowe & McPeck 2014) that determine how species respond to environmental change and (3) extend temporal replication to reveal mechanisms that are better detected with time-series (e.g. priority effects).

Finally, meta-analyses are vital to understanding the extent to which patterns and processes are general or context dependent, but can be complicated by the numerous uncontrolled factors that vary across studies. Standardised experimental networks, such as the Nutrient Network ([www.nutnet.umn.edu](http://www.nutnet.umn.edu)), can effectively control many of these elements. Furthermore, the current distribution of experiments that factorially manipulate disturbance and dispersal are biased to temperate and high-latitude ecosystems, with few exceptions. Although we expect our primary finding—that dispersal and neutral sampling effects mediate the influence of disturbance on community assembly—to be common, we emphasise the need for more empirical studies and future meta-analyses that span a broader range of ecosystems (e.g. arid and marine ecosystems) and organisms (e.g. animal and bacterial communities). Standardised experiments replicated across ecosystems, biogeographic regions and climatic gradients will be increasingly useful for understanding the generalities and idiosyncrasies of global change impacts on biodiversity.

## CONCLUSION

Our meta-analysis has broad implications for understanding the patterns, causes and consequences of biodiversity loss and homogenisation. Human activities are not only changing the frequency and intensity of natural disturbances, they are also influencing dispersal rates via habitat fragmentation, restoration practices involving species introductions, and biological invasions. If our current ability to anticipate the consequences of altered disturbance regimes is dependent on stationary

dispersal dynamics, then environmental change that simultaneously alters both disturbance and dispersal could undermine our predictive capacities. Moreover, spatial patterns of biodiversity play an important role in stabilising ecosystem functions (Wang & Loreau 2016). Comprehensive studies that explicitly consider how ecological disturbances interact with the dispersal traits of species will shed new light on the causes and consequences of biotic homogenisation and ecosystem responses to global change.

## ACKNOWLEDGEMENTS

We thank the > 40 authors who contributed data for this meta-analysis. This meta-analysis would not have been possible without their hard work and generosity. We also thank Mark Vellend, Marko Spasojevic, Sebastián Tello, Joseph LaManna, Laura Bhatti Catano, Dilys Vela Díaz, Ashley Knudson, Emma Moran, Vincent Fasanello and four anonymous reviewers for providing feedback that improved the manuscript. We thank Tyson Research Center (Graduate Research Award to CPC) and the National Science Foundation (DEB 1256788 and DEB 1557094 to JAM) for financial support.

## AUTHORSHIP

All authors conceived the study, CPC executed the statistical analyses and wrote the first draft of the manuscript, JAM and TLD contributed data, and all authors contributed to revisions.

## DATA ACCESSIBILITY STATEMENT

Should the manuscript be accepted, the data supporting the results will be archived in the Dryad public repository and the data DOI will be included at the end of the article.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

Editor, Marcel Rejmanek

Manuscript received 24 August 2016

First decision made 3 October 2016

Second decision made 30 November 2016

Manuscript accepted 8 December 2016