Dispersal mode mediates the effect of patch size and patch connectivity on metacommunity diversity

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Summary

1. Metacommunity theory predicts that increasing patch size and patch connectivity can alter local species diversity by affecting either colonization rates, extinction rates or both. Although species' dispersal abilities or 'dispersal mode' (e.g. gravity-, wind- or animal-dispersed seeds) can mediate the effects of patch size and connectivity on diversity, these important factors are frequently overlooked in empirical metacommunity work.

2. We use a natural metacommunity of aspen stands within a grassland matrix to determine whether dispersal mode alters the influence of stand size and connectivity on understorey plant diversity. We sampled the same area in each patch, controlled for the presence of matrix species in aspen stands, and tested for the effects of size, connectivity and dispersal mode on metacommunity richness. Because dispersal groups responded differently to patch size and connectivity, we created a null model and assessed ungulate activity to explore whether competitive dynamics or herbivory were driving diversity patterns.

3. Animal-dispersed species and species with no dispersal aid had higher diversity per unit area in larger stands, likely because large stands can both support larger populations that are less prone to extinction and may also attract seed-dispersing animals such as birds and small mammals that are sensitive to edge effects. Consistent with other empirical work, we found a positive relationship between diversity and connectivity for wind-dispersed species. However, we detected a negative effect of stand connectivity on the diversity of species with no dispersal aid, possibly due to the presence of other highly competitive species groups dominating well-connected patches, as our null model results suggest. We found no evidence for higher ungulate activity in highly connected patches, suggesting that herbivory may not be driving the decline in diversity of plants with no dispersal aid.

4. *Synthesis.* Overall, we see a positive effect of stand area on diversity for most groups despite sampling equal area in all stands, which is a prediction of metacommunity theory that is normally overlooked. Our results demonstrate the importance of considering variation in the dispersal modes of focal species for explaining the diversity patterns of natural metacommunities.

Key-words: animal-dispersed seeds, aspen stands, connectivity, diffuse boundaries, dispersal syndrome, metapopulation, plant diversity, species richness

Introduction

Biological communities rarely occur in complete isolation, but instead often exist as part of a 'metacommunity' of local patches connected by dispersal (Wilson 1992). Island and pond systems are classic examples of metacommunities (Simberloff & Wilson 1970), as are other distinct assemblages of organisms that occur in patchily distributed habitats. The metacommunity paradigm, based on concepts from metapopulation and island biogeography theories, was developed to understand the mechanisms that maintain species diversity in patchy landscapes (Leibold *et al.* 2004). Several classes of metacommunity dynamics have been identified, all of which recognize the importance of extinction and colonization dynamics of species within and among patches for explaining local and regional diversity patterns (Leibold *et al.* 2004).

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Recent theoretical and empirical work has focused on determining how factors that alter the extinction and colonization rates of species within metacommunities scale up to alter local and regional diversity (Altermatt, Schreiber & Holyoak 2011; Haegeman & Loreau 2014; LeCraw, Srivastava & Romero 2014).

Patch size and connectivity (inter-patch distance) both affect colonization and extinction dynamics and are predicted to be important drivers of diversity patterns in metacommunities (Holyoak, Leibold & Holt 2005). Larger patches can support a greater number of species per unit area, as higher colonization rates combined with larger population sizes that are less vulnerable to extinction result in an increase in the ratio of colonization to extinction rate (MacArthur & Wilson 1967; Holt 1993; Leibold *et al.* 2004). Similarly, by influencing the rate at which species move between patches, patch connectivity can strongly affect local diversity; this phenomenon has recently been demonstrated in both theoretical models (Pillai, Gonzalez & Loreau 2011; Gilbert 2012; Haegeman & Loreau 2014) and empirical studies (Howeth & Leibold 2010; Matthiessen, Mielke & Sommer 2010; Chisholm, Lindo & Gonzalez 2011). In metacommunities with poorly connected patches, local diversity tends to be low because dispersal-limited species cannot reach suitable patches (Cadotte 2006a) or priority effects exclude subsequent colonizers (Levins & Culver 1971). As patch connectivity increases, local diversity increases as incoming colonists rescue small populations from extinction (Brown & Kodric-Brown 1977). Finally, when dispersal rates are high, diversity can decline whether competitively dominant species or generalist predators are able to reach all patches and drive other species locally extinct (Mouquet & Loreau 2003). Empirical studies have detected a variety of relationships between dispersal and diversity; reported relationships are often positive (Warren 1996; Gilbert, Gonzalez & Evans-Freke 1998; Cadotte 2006b; Chase, Burgett & Biro 2010) or hump-shaped (Kneitel & Miller 2003; Matthiessen & Hillebrand 2006; Howeth & Leibold 2010; Vanschoenwinkel, Buschke & Brendonck 2013), but negative relationships have also been detected (Matthiessen, Mielke & Sommer 2010). However, it is difficult to interpret these patterns and draw broader conclusions about the ecological processes shaping natural systems, in part because of the difficulties associated with capturing a biologically relevant range of dispersal rates when dispersal is manipulated experimentally.

One of the most fundamental predictions of metacommunity theory is that interspecific differences in dispersal affect coexistence and diversity (Leibold *et al.* 2004; Holyoak, Leibold & Holt 2005). Although co-occurring species often differ greatly in dispersal ability (Howe & Smallwood 1982), these differences are often overlooked in experimental studies. For example, most studies manipulate dispersal by transferring a set proportion of a community among patches, thereby removing natural variation in species' dispersal abilities (Kneitel & Miller 2003; Cadotte, Fortner & Fukami 2006; Howeth & Leibold 2010; Declerck *et al.* 2013; but see Cadotte 2006a; Limberger & Wickham 2011; Vanschoenwinkel,

Buschke & Brendonck 2013; Guelzow, Dirks & Hillebrand 2014). Similarly, seed addition experiments used to test dispersal–diversity relationships often remove dispersal differences among species (Cadotte 2006b). Although these studies have made important advances in testing some aspects of metacommunity theory, the higher tractability associated with homogenizing dispersal rates across species comes at the expense of understanding how natural variation in dispersal abilities can affect the persistence of coexisting species within a metacommunity. Studies that allow differential dispersal rates are underrepresented in the literature (Logue *et al.* 2011) and are currently biased towards small passively dispersed organisms inhabiting freshwater ponds (e.g. protists, algae and zooplankton; Louette & De Meester 2005; Vanschoenwinkel, Buschke & Brendonck 2013).

The manner in which patch size and patch connectivity affect the colonization rates of coexisting species and subsequently shape diversity will depend on species' traits that affect dispersal. In plants, dispersal differences can manifest through morphological adaptations in seeds, with the seed representing the primary dispersive stage of a plant's life cycle. These adaptations can be categorized into different dispersal modes or syndromes, reflecting how (and how far) seeds move across the landscape. For example, common dispersal modes in plants include gravitropic dispersal *via* passive release from the parent plant, dispersal *via* insects such as ants (myrmecochory), wind dispersal *via* the presence of a feathery pappus, and vertebrate dispersal *via* fleshy fruited seeds or burs that are carried by birds or mammals (Howe & Smallwood 1982). Focusing on patterns of diversity separately for species with different dispersal modes can reveal unique relationships between patch size or connectivity and diversity (Vanschoenwinkel, Buschke & Brendonck 2013). For example, species that have no dispersal aid rarely disperse long distances and may be more strongly affected by patch connectivity than animal- or wind-dispersed species that can easily reach all sites (Vanschoenwinkel, Buschke & Brendonck 2013). Similarly, habitat selection by animals that move seeds could alter the relationship between patch size and diversity if animal vectors prefer larger patches (Levey *et al.* 2005; Nathan *et al.* 2008; Evans *et al.* 2012). Despite the recognized importance of dispersal for metacommunity dynamics (Mouquet & Loreau 2003; Cadotte 2006a) and the ubiquity of variation in dispersal abilities among co-occurring species (Nathan & Muller-Landau 2000; Muller-Landau 2003; Gilbert, Turkington & Srivastava 2009), the implications of these dispersal differences on metacommunity diversity are only beginning to be tested in natural systems (Löbel, Snäll & Rydin 2009; Hájek *et al.* 2011; De Bie *et al.* 2012; Vanschoenwinkel, Buschke & Brendonck 2013).

In this paper, we investigate how patch size and connectivity affects understorey plant diversity in a naturally patchy landscape of aspen stands. Aspen (*Populus sp.*) are common tree species in Northern climates, frequently occurring in grassland habitats where they form clonal forest stands with clear boundaries. These stands are naturally patchy and support a distinct plant community compared to the surrounding

grassland matrix, indicating that aspen-associated understorey species function as a metacommunity. However, unlike pond or island patches, aspen stands have diffuse boundaries, meaning that important spatial dynamics may be swamped out by the presence of species that are not constrained to habitat patches in the metacommunity (e.g. generalists; Harrison 1999). How influential the presence of these species on our ability to resolve the dynamics of diffuse metacommunities remains an open question (Leibold *et al.* 2004).

In Lac Du Bois Provincial Park, British Columbia, Canada, we sampled understorey plant communities in aspen stands that varied in size and connectivity (Fig. 1). We sampled the same total area in all stands to remove the confounding effects of species–area relationships in our assessment of species diversity. Species were then categorized into three dispersal syndrome groups based on seed morphology: no dispersal aid, wind dispersed and animal dispersed. We used these data to address four questions: (i) Does stand size and/ or connectivity affect understorey plant diversity and species composition? (ii) Does dispersal mode mediate these relationships? (iii) Are the observed diversity patterns consistent with common ecological processes such as competition or herbivory? (iv) How sensitive are our results to the inclusion of generalist and matrix-associated species, a common feature of metacommunities with diffuse boundaries?
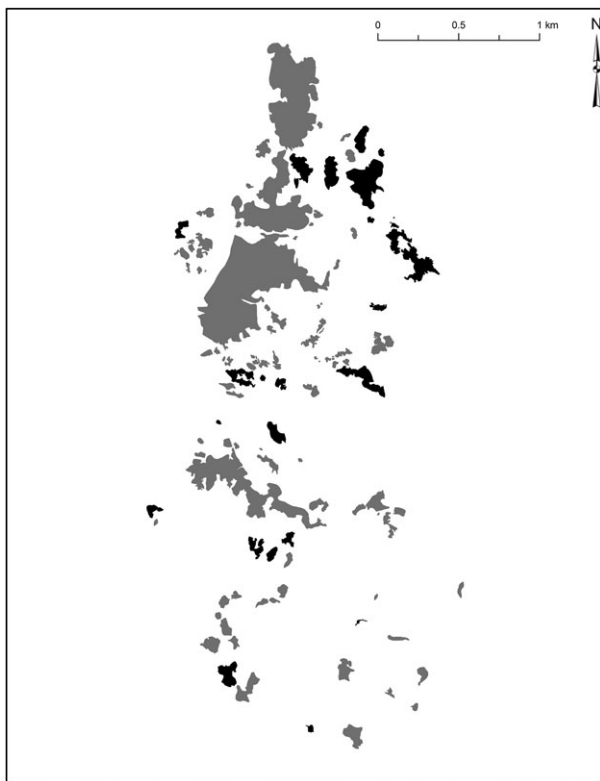
Fig. 1. Map of sampled (black; $n = 24$) and unsampled (grey; $n = 86$) aspen stands at the Lac Du Bois Provincial Park in the southern interior of British Columbia, Canada (latitude = 50.7007, longitude = −120.4603); both sampled and unsampled stands were included in our calculations of stand connectivity. The matrix habitat was primarily grassland.

Materials and methods

STUDY SITE AND SPECIES SAMPLING

This study was conducted in the high-elevation grasslands of Lac Du Bois Provincial Park in the southern interior of British Columbia, Canada (latitude = 50.7007, longitude = −120.4603). The region is semi-arid, with hot dry summers and little annual precipitation (279 mm), 27% of which falls as snow (Environment Canada 2014). Aspen (*Populus tremuloides*) cover ~100-ha of the park and occur primarily on moist, north-facing slopes (Dickinson 1998). They form clonal stands that support a unique flora of understorey plant species compared to the surrounding grassland matrix (Fig. S1 in Supporting Information). These stands are relatively undisturbed by humans, and range in age from approximately 24 to 148 years old.

In the summer of 2007, we randomly selected 24 of a total of 110 aspen stands in the park (Fig. 1), excluding any stands located within 50 metres of a road. The stands ranged from 658 m² to 37 622 m² in size. We established a single 10×25 m plot in the centre of each stand and recorded the occurrences of all identifiable understorey vascular plant species. This large plot size was selected to capture species diversity at a scale that incorporates a reasonable level of microsite heterogeneity. By using the same plot size in all stands, we standardized sampling intensity and were thus able to assess species richness per unit area to avoid the confounding influence of species–area relationships on our diversity measurements. Although edge effects may be confounded with the size of the patch in our study (and in most naturally patchy ecosystems), we believe that these effects are negligible for two reasons. First, even the smallest stands were over four times the size of the plot, and secondly, the abundance of matrix species was generally low (Fig. S2).

To confirm that aspen stands support a unique flora and to identify aspen- and matrix-associated species, we also sampled plant diversity in the adjacent grassland matrix. The grassland sampling followed the same sampling protocol as in the aspen stands, with at least one plot placed 25 to 50 m outside of each of the sampled aspen stands ($n = 24$ total; May & Baldwin 2011). See *Data analyses* for methods on statistically delineating grassland- and aspen-associated species. Concurrent with the plant survey, we recorded the amount of ungulate scat within our plots, ranked from 0 (none) to 3 (abundant), as a proxy for large herbivore activity (Bailey & Putman 1981; Heinze *et al.* 2011). Our surveys were conducted in a single year, and thus, could not be used to track colonization and extinction as they happened. However, island biogeography theory predicts that the outcome of colonization/extinction dynamics can be inferred, rather than observed directly, from the equilibrium species richness of habitat patches. There was no relationship between species richness and the age of the stands ($t_{1,23} = 0.31$, $P = 0.763$) suggesting that the patterns observed were not driven by differences in time to accumulate species.

We classified all aspen-associated species into three dispersal mode categories based on seed morphology: (i) no dispersal aid (gravitropic, ballistic or ant dispersal; $n = 32$), (ii) wind dispersed (anemochorous; $n = 17$), indicated by the presence of a pappus and (iii) animal dispersed (bird or large mammal dispersal; $n = 18$), indicated by the presence of burs or fleshy fruit. We grouped ant-dispersed species into the 'no dispersal aid' group because ants move seeds at a spatial scale comparable to passive gravitropically or ballistically dispersed seeds (Thomson *et al.* 2011). Only two of the 32 species in this dispersal mode category are known to be dispersed by ants.

DATA ANALYSES

A presence–absence matrix was created for all species in the 24 sampled aspen stands and 24 grassland plots. We conducted a principal coordinates analysis (PCoA) using the Jaccard dissimilarity coefficient to identify compositional differences between aspen stands and the surrounding grassland matrix (Fig. S1). To identify and remove all species that were not strongly aspen associated, we calculated the proportion of aspen to grassland plots that each species occurred in and removed generalist and grassland specialist species that did not occur in aspen stands at least 66% of the time ($n = 103$ species; Table S1). We removed generalists and grassland specialists because only species that occur in favourable focal habitat patches imbedded in a matrix of unfavourable habitat constitute a metacommunity (Cook et al. 2002). We repeated our analyses using less stringent cut-offs (an analysis using all species and another requiring 50% of occurrences to be in aspen stands), and a more stringent cut-off (requiring 75% of occurrences to be in aspen stands). We found that including all species obscured patterns, but that our results were qualitatively similar (Table S2) at all other indicator cut-off levels; we therefore report the results generated using the 66% cut-off, which identified 67 aspen-associated species (Table 1) but also discuss the sensitivity of our results to the cut-off level that was used.

To calculate stand size and distances among stands, all sampled and unsampled aspen stands were digitized from online basemaps streamed through ArcGIS 10.1 (ESRI.com). The digitized stand locations and shapes were compared with field notes to confirm accuracy. We calculated the area of each stand and then created a matrix of pairwise Euclidian distances between all stands based on edge-to-edge distances, which were then used in the connectivity function described below.

Our model for incorporating stand size and connectivity came from a plant metapopulation model where the expected occupancy per species increases monotonically with the ratio of colonization (C) to extinction (E) rates. When summed across weakly interacting species, this relationship predicts that species richness per unit area (S) in stand i increases with this ratio: $S \sim C_i/E_i$. Using a logarithmic transformation, this equation becomes: $\log(S_i) \sim \log(C_i) - \log(E_i)$. The second of these terms, the probability of extinction (E) in stand i, is a decreasing function of stand area and is often modelled as inversely related to area. The other term, colonization (C), is an increasing function of stand connectivity. We used a metapopulation approach (Hanski 1994; Gilbert & Levine 2013) for calculating the connectivity of a stand that incorporates the distance between stand i and all other j stands, and combined this with extinction to predict species richness per unit area:

$$\log(S_i) = \text{intercept} + b_1 \log \sum_{j \neq i}^{n} \left(e^{-d_{ij}/\alpha} \right) + b_2 \log(\text{Area}_i) + \varepsilon_i, \qquad (1)$$

where S is the species richness per unit area at site i, and ε is a normally distributed error term. The variable d is the distance between any two sites; the summation incorporates distances from all other sites. Our connectivity measure (the summation term in eqn 1) uses the standard assumption of an exponential dispersal curve with a mean dispersal distance, α. As a result, connectivity between site i and j decreases at greater distances (d_{ij}) and increases with greater dispersal ability (α). This model has a similar functional form as Hanski's incidence function (equation 4 in Hanski 1994), but differs in that α represents the mean dispersal distance of seeds, as it is commonly presented in plant dispersal literature (Hanski 1994; Muller-Landau et al. 2008). Here, we consider α identical for all species within a dispersal mode group, and fit eqn (1) separately for each group. To fit eqn (1), we first used published estimates of mean dispersal distance for our dispersal mode groups (Thomson et al. 2011) and fitted the other parameters (intercept, b_1 and b_2) using linear regressions. We also fitted all parameters (α, intercept, b_1 and b_2) using maximum likelihood; because the results predicted qualitatively similar effects of connectivity on species richness, we report the second approach in the Supporting Information (Table S3). Specific details on the model fitting for both methods of estimating α are further explained in the Supporting Information.

When fitting eqn (1), we noted that stand area and connectivity were often weakly correlated ($r = 0.36$, $P = 0.086$ when all species are included in the analysis). To account for this, we report our results for species richness from analyses with both stand size and connectivity included (Table 1) and also analyses with each factor tested separately (Table S4). This is important in interpreting our results because a significant effect of one stand characteristic could obscure meaningful relationships of the other stand characteristic, purely because the stand characteristics themselves are correlated.

Although our analyses of species richness allowed us to test whether the dispersal mode groups responded to stand size and connectivity, we could not conclude with certainty that differences in

Table 1. Effects of stand size and connectivity on log-transformed species richness. 'All species' includes all aspen-associated species from the three dispersal mode groups

Dispersal mode	# species	α estimate	log Stand size			log Stand connectivity		
			b	$t_{1,23}$	P	b	$t_{1,23}$	P
All species	67	88.5	0.34	4.89	**< 0.001**	−0.19	−1.85	0.078
No dispersal aid	32	5*	0.40	4.25	**< 0.001**	−0.02	−2.18	**0.041**[†]
Wind-dispersed	17	8.5	0.07	0.68	0.507	0.03	1.68	0.107[‡]
Animal-dispersed	18	254.5[§]	0.29	4.35	**< 0.001**	−0.05	−0.30	0.768

Significant effects are bolded; all df = 24. b is the slope of the relationship.

*Using an α estimate of 2.43 m, the average for species with no dispersal aid from Thomson et al. (2011), provided qualitatively equivalent model fit for this group (log (Stand size) $P < 0.001$; log (Stand connectivity) $P = 0.04$; see Supporting Information).

[†]Was only significant when stand size was included in the model ($t_{1,23} = -0.002$, $P = 0.998$; Table S4).

[‡]Was significant when stand size was not included in the model ($t_{1,23} = 2.41$, $P = 0.025$; Table S4).

[§]Thomson et al. 2011 separated animal dispersal into ingestion ($n = 116$), attachment ($n = 4$) and seed-caching ($n = 26$). We calculated a weighted mean based on the number of species in each category.

responses between groups were statistically different because they were tested in separate linear models. To confirm that they were statistically different, we used a multivariate approach to test whether the relative number of species belonging to any particular dispersal mode groups shifted with stand size and connectivity. To do this, we created a distance matrix of Bray–Curtis dissimilarity coefficients for all pairwise combinations of the 24 stands. Bray–Curtis dissimilarity is typically used to compare sites based on the abundances of multiple species; our analysis is analogous, in that we use 'dispersal mode groups' and 'species richness' rather than 'species' and 'abundances', respectively. We then ran a PCoA on the distance matrix, and used linear models to test the effects of log(stand size) and log(connectivity) on the first and second axes scores of the PCoA. Because sites with similar axis scores are compositionally similar in terms of dispersal modes, the presence of significant relationships would indicate that the dispersal mode groupings capture meaningful variation in how species are distributed across the landscape. For this analysis, the α used to calculate connectivity was the average α value of the three groups.

Because we observed a negative relationship between species richness and connectivity for one of the dispersal mode groups (Table 1; Fig. 2), we tested two additional hypotheses for the negative species richness–connectivity relationship that can occur at intermediate to high connectivity (i.e. the backend of a hump-shaped relationship). First, it is possible that increased connectivity allows the establishment of highly competitive species that exclude inferior competitors (Mouquet & Loreau 2003; Cadotte 2006b). We tested this hypothesis using a null model designed to identify negative relationships among dispersal mode groups, after accounting for environmental covariance. The model used was Schluter's covariance test (Schluter 1984) tested against a randomized null expectation calculated with row and column sums held constant (the most conservative null model; Ulrich & Gotelli 2010). Secondly, the movement of large herbivores might be restricted by stand connectedness. We tested this possibility using a linear model looking at the effects of log(stand size) and log(connectivity) on the amount of ungulate scat found per stand during the understorey sampling period.

We also used a multivariate approach to look at turnover in species composition across stands within the dispersal mode groups to identify variation that is not accounted for by grouping by dispersal mode. Specifically, we created three distance matrices, one for each dispersal mode group, by calculating the Jaccard dissimilarity coefficient on the presence/absence data for all pairwise combinations of the 24 stands. The Jaccard dissimilarity coefficient is a resemblance measure that accounts for increased variation in species richness as species richness increases as expected with random sampling (e.g. MacArthur & Wilson 1967). We then performed PCoAs on the three distance matrices and used the first and second axis scores as response variables in linear models testing the effects of log(stand size) and log(connectivity). The presence of significant relationships would indicate that, within the dispersal mode groups, some species are more likely than others to encounter and persist in stands of varying size and connectivity.

Results

We found a significant effect of stand size ($P < 0.001$) and a marginally significant effect of connectivity ($P = 0.078$) on overall species richness, with higher richness observed in larger, less connected stands (Table 1; Fig. 2). However, when species were broken down by dispersal mode, the importance of these two stand characteristics varied markedly (Table 1).

Specifically, we found a positive effect of stand size ($P < 0.001$) and a negative effect of connectivity ($P = 0.041$) on the species richness of the no dispersal aid group, whereas the number of animal-dispersed species increased with increasing stand size ($P < 0.001$) but was unaffected by stand connectivity ($P = 0.768$). The number of wind-dispersed species was not affected by stand size ($P = 0.507$) or connectivity ($P = 0.107$) when both factors were included in the model. However, when we considered each factor separately, species richness of wind-dispersed species increased with greater connectivity ($P = 0.025$; Table S4). In comparing among groups, there was a significant effect of stand size (axis 1; $P < 0.001$) and connectivity (axis 2; $P = 0.0122$) on the relative number of species represented by each group (Fig. 3). Together, these results support our hypothesis that both patch size and connectivity affect metacommunity diversity, and that these effects vary with species' dispersal mode.

We found additional variation within the dispersal mode groups in how species responded to the stand size and stand connectivity (Table 2). Specifically, the composition of species with no dispersal aid changed with stand size (axis 2, $P = 0.024$), and animal-dispersed species changed with both stand size (axis 1; $P = 0.002$) and stand connectivity (axis 1; $P = 0.012$). We could not calculate compositional turnover for species in the wind-dispersed group, as a low frequency of joint presences precluded analysis with Jaccard similarity.

Because we found a negative relationship between species richness and stand connectivity for plants that lack a dispersal aid, we tested the possibility that competition or herbivory could be mediating this relationship (Fig. 4). Our null model revealed that, overall, the species richnesses of the dispersal groups negatively covaried across stands ($P = 0.033$). This means that, after accounting for and removing the common effects of stand size or connectivity among dispersal mode groups, the diversity of the different groups was negatively associated. We found no evidence to suggest that ungulates, common herbivores at the study site, were more active in highly connected stands ($t_{1,20} = -0.803$, $P = 0.432$).

Our results on the effects of stand size and connectivity on species richness were qualitatively similar among analyses that used different cut-off values for identifying aspen-associated species (i.e. species occurring in aspen stands 50, 66 and 75% of the time; Table S2). In all three analyses, species with no dispersal aid were affected by stand size (all $P < 0.001$) and connectivity (all $P \leq 0.002$), animal-dispersed species were affected by stand size only (all $P < 0.001$), and wind-dispersed species were not affected by either stand characteristic (all $P \geq 0.099$). It was only when all species (i.e. generalists and grassland specialists) were included that we failed to detect any trends, except for the effect of stand size on the species richness of animal-dispersed species because animal-dispersed species did not occur in the grassland matrix.

Discussion

Our study highlights the importance of considering variation in species' dispersal modes in metacommunity studies. When
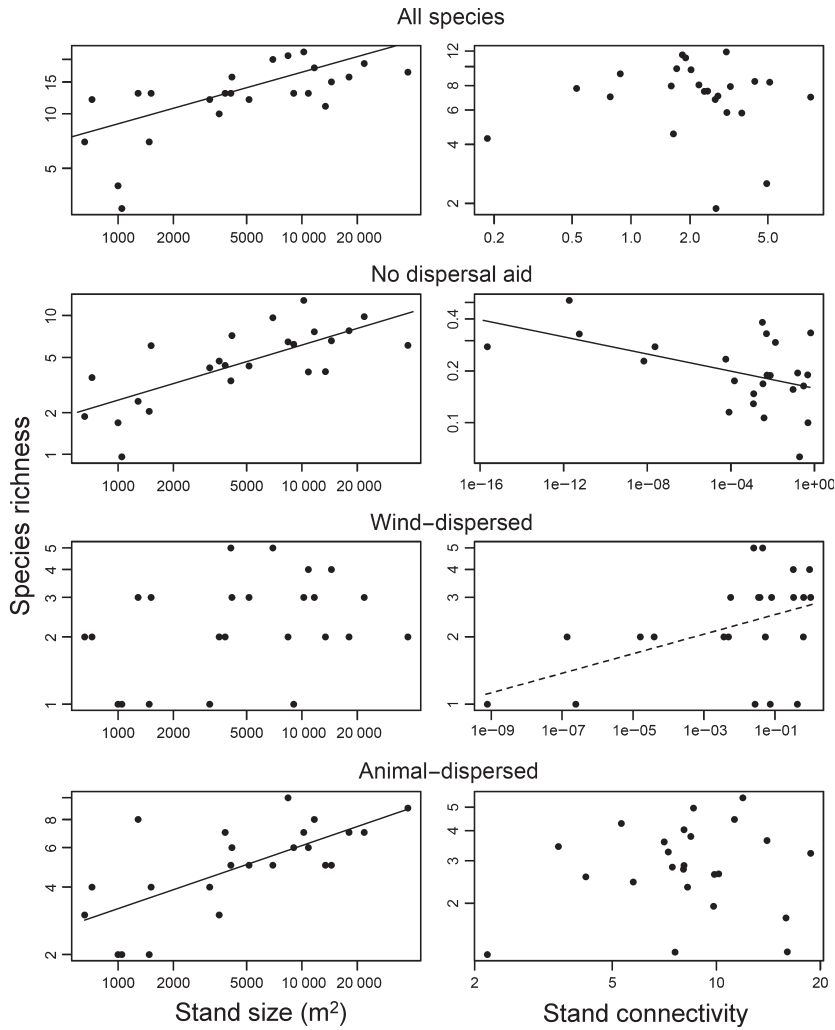
Fig. 2. The effect of stand size and stand connectivity on species richness when all aspen-associated species are grouped together (top panels) and for each dispersal group considered separately. Species richness values were adjusted to account for the other factor in the model (size or connectivity) whenever that factor was significant. Fitted lines indicate when a factor was significant at $P < 0.05$ in a model with both factors (solid line) or only the significant factor (dashed line) included. All variables are log-transformed but shown on the original scale.
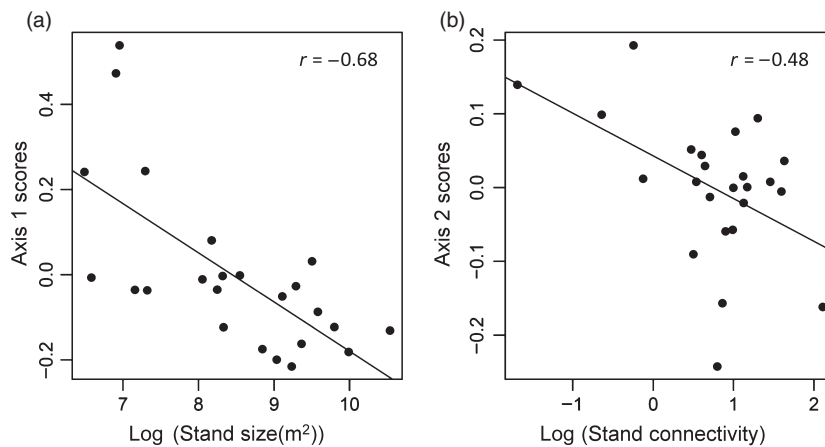
Fig. 3. The effect of (a) stand size and (b) connectivity on the relative representation of species belonging to each dispersal mode group from a PCoA using the Bray–Curtis coefficient. We only display the stand characteristic-axis score combinations that were significantly correlated. Each axis was delineated by changes in group representation: axis 1 primarily summarized variation in wind and animal-dispersed species richness ($r_{wind} = -0.35$, $r_{animal} = 0.35$) but not the richness of species with no dispersal aid ($r_{no\ aid} = -0.08$). Axis 2 summarized variation in the richness of species with no dispersal aid ($r_{no\ aid} = 0.91$), as well as wind ($r_{wind} = -0.63$) and animal ($r_{animal} = -0.51$) dispersed species.

dispersal mode was ignored and all aspen-associated species were grouped together, species richness per unit area was positivity associated with stand size only (Table 1; Fig. 2), which

has been observed in some (Holt, Robinson & Gaines 1995; Harvey & MacDougall 2014) but not all (Holt, Robinson & Gaines 1995) metacommunities. Our approach of separating

Table 2. Effects of stand size and stand connectivity on species composition (axis 1 and 2 scores of PCoA using Jaccard dissimilarity coefficient) by dispersal mode

Axis #	Dispersal mode	# species	α estimate	log Stand size			log Stand connectivity		
				b	$t_{1,23}$	P	b	$t_{1,23}$	P
1	All species	67	88.5	−0.11	−3.13	**0.005**	0.14	2.57	**0.018**
	No dispersal aid	32	5*	−0.02	−0.34	0.736	0.01	0.84	0.411
	Wind-dispersed	17	8.5	NA	NA	NA	NA	NA	NA
	Animal-dispersed	18	254.5	−0.15	−3.44	**0.002**	0.28	2.74	**0.012**
2	All species	67	88.5	0.12	3.32	**0.003**	−0.07	−1.38	0.183
	No dispersal aid	32	5*	0.12	2.44	**0.024**	−0.01	−0.98	0.341
	Wind-dispersed	17	8.5	NA	NA	NA	NA	NA	NA
	Animal-dispersed	18	254.5	−0.0650	−1.25	0.224	0.05	0.40	0.694

Significant effects are bolded; all df = 24. b is the slope of the relationship. We could not calculate Jaccard dissimilarity for plots in the wind-dispersed species group, because had many species had single occurrences.
*α estimates ranging from 2 to 5 m provided qualitatively equivalent model fit for this group.
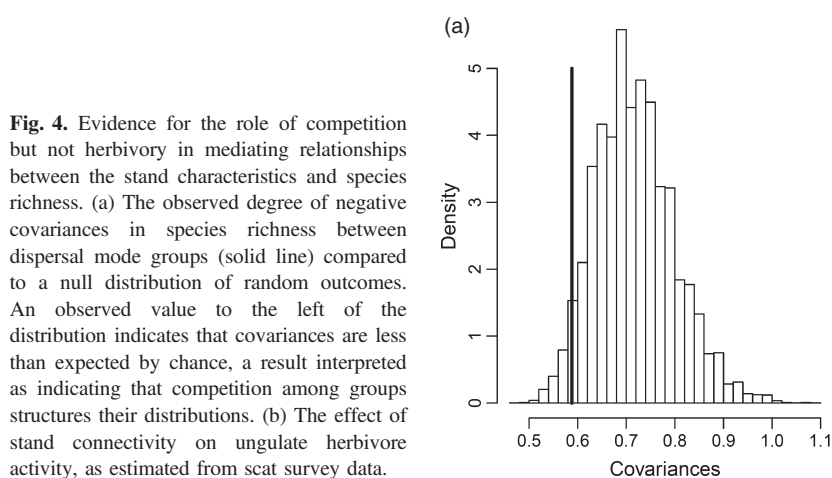
Fig. 4. Evidence for the role of competition but not herbivory in mediating relationships between the stand characteristics and species richness. (a) The observed degree of negative covariances in species richness between dispersal mode groups (solid line) compared to a null distribution of random outcomes. An observed value to the left of the distribution indicates that covariances are less than expected by chance, a result interpreted as indicating that competition among groups structures their distributions. (b) The effect of stand connectivity on ungulate herbivore activity, as estimated from scat survey data.

species by fruit type, a life-history characteristic that affects how seeds are dispersed across landscapes, clarified how relationships between stand size, connectivity and diversity differ among species' with different dispersal modes (Table 1; Fig. 2).

Larger stands contained more animal-dispersed species and species with no dispersal aid, a pattern consistent with classic theory in which bigger patches support larger populations that are less prone to extinction. However, animal-dispersed species' responses to stand size might also be explained by habitat selection by seed-dispersing animals. If animals preferentially select larger patches, animal-dispersed species might be underrepresented in small patches simply because their dispersal agents do not transport them there. Although we did not quantify animal abundances within the aspen patches, previous work has documented that many bird and large mammal species prefer larger stands (Johns 1993; Oaten & Larsen 2008) and are thus more likely to deposit seeds in these stands. Interestingly, the diversity of wind-dispersed species was unaffected by stand size. Although we cannot isolate the specific mechanism driving this pattern, many of the wind-dispersed species found in our study, such as the *Antennaria*,

Cirsium and *Lactuca*, are considered ruderal species; therefore, their persistence should be more generally limited by disturbance events (which in this system likely occur at low levels among all patches) than factors such as stand size.

Although the range of relationships between connectivity and diversity presented by previous empirical work precludes a single prediction, we expected to see a positive or hump-shaped relationship, as these have most commonly been found in other studies (Kneitel & Miller 2003; Matthiessen & Hillebrand 2006; Chase, Burgett & Biro 2010; Howeth & Leibold 2010; Vanschoenwinkel, Buschke & Brendonck 2013). Consistent with these studies, we found evidence that connectivity had a positive effect on the richness of wind-dispersed species (Fig. 2, Table S4), indicating that colonization rates in this group are limited by connectivity; the most distant, least connected site had only a single wind-dispersed species. Although wind-dispersed species may access all stands via infrequent long-distance dispersal events (e.g. in wind storms; Soons, Nathan & Katul 2004), colonization events would be rare compared to extinctions, thus creating this gradient in diversity.

We also detected a negative relationship between connectivity and richness for species with no dispersal aid, which may be

suggestive of the declining half of a hump-shaped curve. The most widely accepted explanation for a decline in richness in highly connected patches is that competitively dominant or generalist predator species that are poor dispersers can dominate highly connected patches and drive other species locally extinct (Forbes & Chase 2002; Kneitel & Miller 2003; Cadotte 2006b; Chase, Burgett & Biro 2010; Matthiessen, Mielke & Sommer 2010; Vanschoenwinkel, Buschke & Brendonck 2013). If this were the case, we would expect to see either negative relationships between dispersal mode groups (competitor hypothesis), increased herbivore activity in highly connected patches (predator hypothesis) or both. Although our observational data set does not allow us to discriminate definitively among the mechanisms underlying observed patterns, estimates of competition and herbivory were used to determine whether observed patterns were consistent with either of these mechanisms. We found some evidence in support of the competitor hypothesis only: the null model revealed negative covariance among dispersal mode groups ($P = 0.038$; Fig. 4a). This suggests that species with no dispersal aid might be competitively suppressed by the other dispersal mode groups in highly connected stands. We note, however, that theory predicts that the no dispersal aid group should be competitively dominant, and our results suggest the opposite. Our results are nonetheless consistent with experimental work in aspen stands in the boreal forest (Gilbert, Turkington & Srivastava 2009) and raises questions about persistence of weak dispersers when they are also weak competitors.

Our investigation of turnover in species composition among dispersal mode groups suggests that these groupings capture meaningful variation in how species in our aspen metacommunity move across the landscape (Fig. 3). Interestingly, our analyses also indicate that there is additional variation within groups in how species are responding to stand size and connectivity (Table 2). For example, both Rocky Mountain juniper (*Juniperus scopulorum*) and prickly wild rose (*Rosa acicularis*) are animal dispersed, but differ in their association with large or small stands. This variation would not likely be fully accounted for by incorporating information on species-specific dispersal abilities, because species also varied in their responses to stand size. This result could reflect interspecific variation in sensitivity to local extinction, or different animal vectors (i.e. bird, rodent, deer) for animal-dispersed species. Overall, our findings indicate that while including dispersal mode is important for understanding metacommunity dynamics, investigation of interspecific differences in dispersal within modes may further clarify how spatial dynamics structure diversity in this ecosystem.

Early metacommunity theory posited that species richness will increase per unit area in highly connected patches when communities are comprised of weakly interacting species (Holt 1993). This prediction is often overlooked, with many metacommunity studies estimating diversity across a patch size gradient and confounding patch size with the area sampled by increasing sampling effort proportionally with patch size. Other researchers have recognized this problem and subsequently accounted for unequal sampling *post hoc* through rarefaction or by randomly selecting a subset of patches (e.g.

Meynard *et al.* 2013). Although our approach is unlikely to capture the total diversity across all aspen stands, it is more consistent with metacommunity predictions than approaches that attempt to standardize sampling effort *post hoc*. Standardizing area in metacommunity sampling has long been advocated (Holt 1993) because this method directly tests species' responses to patch size by eliminating the confounding effects on species richness of increased sampling effort and habitat heterogeneity in larger patches.

Unlike more classic examples of metacommunities, such as ponds or islands, the boundaries of aspen stands are diffuse to some species that also occur in the surrounding grassland matrix. For example, matrix-associated species may be present in the aspen stands if they are generalists that persist in both habitat types, or if they are grassland specialists experiencing source-sink dynamics whereby populations in aspen stands are supplemented with incoming colonists from the matrix. In either case, these species' pose a conceptual and methodological challenge for how the metacommunity is defined, given that the matrix may be inhospitable to some species but not others (Delong & Gibson 2012). In our study, we used a paired plot design consisting of one grassland-matrix plot surveyed adjacent to each aspen stand. This method allowed us to identify and exclude species that were highly associated with the grassland matrix and that were therefore not likely to be constrained by the boundaries of the aspen metacommunity. Of the 170 species observed in our paired plot surveys, 66 and 44 species were found primarily ($\geq$66% of the time) or exclusively in aspen stands, respectively, with 36 species occurring only in grassland plots. This means that, of the 110 total species found in the aspen stand plots, 66 experience the grassland matrix as inhospitable, and thus adhere to classic metacommunity definitions (Leibold *et al.* 2004). Our data revealed effects of patch size and connectivity on diversity that were robust to the choice of cut-off that was used (i.e. species occurring in aspen stands at least 50, 66 and 75% of the time; Table S2). It was only when all species (i.e. generalists and grassland specialists) were included that we failed to detect these trends. The paired plot design used here could be implemented in future work in similarly diffuse habitat-patch networks (e.g. coral reefs, serpentine hummocks), a recognized class of metacommunities that dominates many landscapes (Leibold *et al.* 2004).

Our assessment of the effects of stand size and connectivity on diversity is one of the first to use a naturally patchy metacommunity to test how differences in species dispersal modes influence local diversity. In doing so, we show that dispersal mode mediates the effects of stand size and connectivity on metacommunity diversity in ways that would be obscured if all species were grouped together. Our results also raise the intriguing possibility that life-history traits that affect dispersal may also alter distributions of these groups through differences in competitive ability, habitat-specific movement of animal vectors and different local extinction rates. Our approach to studying the effects of dispersal and patch characteristics on metacommunity diversity has provided new insights into the complex relationship between patch characteristics and metacommunity diversity.

Acknowledgements

Data accessibility

Species information: uploaded as Table S1. Data deposited in the Dryad repository: http://dx.doi.org/10.5061/dryad.9mb00 (Jones *et al.* 2015).

References

Altermatt, F., Schreiber, S. & Holyoak, M. (2011) Interactive effects of disturbance and dispersal directionality on species richness and composition in metacommunities. *Ecology*, **92**, 859–870.

Bailey, R. & Putman, R. (1981) Estimation of fallow deer (Dama dama) populations from faecal accumulation. *Journal of Applied Ecology*, **18**, 697–702.

Brown, J.H. & Kodric-Brown, A. (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology*, **58**, 445.

Cadotte, M.W. (2006a) Metacommunity influences on community richness at multiple spatial scales: a microcosm experiment. *Ecology*, **87**, 1008–1016.

Cadotte, M.W. (2006b) Dispersal and species diversity: a meta-analysis. *The American Naturalist*, **167**, 913–924.

Cadotte, M.W., Fortner, A.M. & Fukami, T. (2006) The effects of resource enrichment, dispersal, and predation on local and metacommunity structure. *Oecologia*, **149**, 150–157.

Chase, J.M., Burgett, A.A. & Biro, E.G. (2010) Habitat isolation moderates the strength of top-down control in experimental pond food webs. *Ecology*, **91**, 637–643.

Chisholm, C., Lindo, Z. & Gonzalez, A. (2011) Metacommunity diversity depends on connectivity and patch arrangement in heterogeneous habitat networks. *Ecography*, **34**, 415–424.

Cook, W.M., Lane, K.T., Foster, B.L. & Holt, R.D. (2002) Island theory, matrix effects and species richness patterns in habitat fragments. *Ecology Letters*, **5**, 619–623.

De Bie, T., Meester, L., Brendonck, L., Martens, K., Goddeeris, B., Ercken, D. *et al.* (2012) Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. *Ecology Letters*, **15**, 740–747.

Declerck, S.A.J., Winter, C., Shurin, J.B., Suttle, C.A. & Matthews, B. (2013) Effects of patch connectivity and heterogeneity on metacommunity structure of planktonic bacteria and viruses. *The ISME journal*, **7**, 533–542.

Delong, M.K. & Gibson, D.J. (2012) What determines "suitable habitat" for metapopulation studies? An analysis of environmental gradients and species assemblages in xeric forest openings. *American Journal of Botany*, **99**, 46–54.

Dickinson, T. (1998) *Lac Du Bois Provincial Park Management Plan*. BC Parks, Kamloops, B.C..

Environment Canada. (2014) *Canadian Climate Normals 1971–2000 for Kamloops, British Columbia*. National Climate Data and Information Archive. http://climate.weather.gc.ca/climate_normals/index_e.html (accessed 10 November 2014).

Evans, D.M.E., Turley, N.E., Levey, D.J. & Tewksbury, J.J. (2012) Habitat patch shape, not corridors, determines herbivory and fruit production of an annual plant. *Ecology*, **93**, 1016–1025.

Forbes, A.E. & Chase, J.M. (2002) The role of habitat connectivity and landscape geometry in experimental zooplankton metacommunities. *Oikos*, **96**, 433–440.

Gilbert, B. (2012) Joint consequences of dispersal and niche overlap on local diversity and resource use. *Journal of Ecology*, **100**, 287–296.

Gilbert, F., Gonzalez, A. & Evans-Freke, I. (1998) Corridors maintain species richness in the fragmented landscapes of a microecosystem. *Proceedings of the Royal Society B: Biological Sciences*, **265**, 577–582.

Gilbert, B. & Levine, J.M. (2013) Plant invasions and extinction debts. *Proceedings of the National Academy of Sciences of the United States of America*, **110**, 1744–1749.

Gilbert, B., Turkington, R. & Srivastava, D.S. (2009) Dominant species and diversity: linking relative abundance to controls of species establishment. *The American Naturalist*, **174**, 850–862.

Guelzow, N., Dirks, M. & Hillebrand, H. (2014) Effect of (a)synchronous light fluctuation on diversity, functional and structural stability of a marine phytoplankton metacommunity. *Oecologia*, **176**, 497–510.

Haegeman, B. & Loreau, M. (2014) General relationships between consumer dispersal, resource dispersal and metacommunity diversity. *Ecology letters*, **17**, 175–184.

Hájek, M., Roleček, J., Cottenie, K., Kintrová, K., Horsák, M., Poulíčková, A., Hájková, P., Fránková, M. & Dítě, D. (2011) Environmental and spatial controls of biotic assemblages in a discrete semi-terrestrial habitat: comparison of organisms with different dispersal abilities sampled in the same plots. *Journal of Biogeography*, **38**, 1683–1693.

Hanski, I. (1994) A practical model of metapopulation dynamics. *The Journal of Animal Ecology*, **63**, 151–162.

Harrison, S. (1999) Local and regional diversity in a patchy landscape: native, alien, and endemic herbs on serpentine. *Ecology*, **80**, 70–80.

Harvey, E. & MacDougall, A.S. (2014) Trophic island biogeography drives spatial divergence of community establishment. *Ecology*, **95**, 2870–2878.

Heinze, E., Boch, S., Fischer, M., Hessenmöller, D., Klenk, B., Müller, J., Prati, D., Schulze, E.-D., Seele, C., Socher, S. & Halle, S. (2011) Habitat use of large ungulates in northeastern Germany in relation to forest management. *Forest Ecology and Management*, **261**, 288–296.

Holt, R.D. (1993) Ecology at the Mesoscale: the influence of regional processes on local communities. *Species Diversity in Ecological Communities* (eds R.E. Ricklefs & D. Schluter), pp. 77–88. University of Chicago Press, Chicago, IL.

Holt, R.D., Robinson, G.R. & Gaines, M.S. (1995) Vegetation dynamics in an experimentally fragmented landscape. *Ecology*, **76**, 1610–1624.

Holyoak, M., Leibold, M.A. & Holt, R.D. (eds) (2005) *Metacommunities: Spatial Dynamics and Ecological Communities*. The University of Chicago Press, Chicago, IL.

Howe, H.F. & Smallwood, J. (1982) Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, **13**, 201–228.

Howeth, J.G. & Leibold, M.A. (2010) Species dispersal rates alter diversity and ecosystem stability in pond metacommunities. *Ecology*, **91**, 2727–2741.

Johns, B.W. (1993) The influence of grove size on bird species richness in aspen parklands. *Wilson Bulletin*, **105**, 256–264.

Jones, N.T., Germain, R.M., Grainger, T.N., Hall, A.M., Baldwin, L. & Gilbert, B. (2015) Data from: Dispersal mode mediates the effect of patch size and patch connectivity on metacommunity diversity. *Journal of Ecology*, http://dx.doi.org/10.5061/dryad.9mb00

Kneitel, J.M. & Miller, T.E. (2003) Dispersal rates affect species composition in metacommunities of Sarracenia purpurea inquilines. *The American Naturalist*, **162**, 165–171.

LeCraw, R.M., Srivastava, D.S. & Romero, G.Q. (2014) Metacommunity size influences aquatic community composition in a natural mesocosm landscape. *Oikos*, **123**, 903–911.

Leibold, M.a., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M. & Gonzalez, A. (2004) The metacommunity concept: a framework for multiscale community ecology. *Ecology Letters*, **7**, 601–613.

Levey, D.J., Bolker, B.M., Tewksbury, J.J., Sargent, S. & Haddad, N.M. (2005) Effects of landscape corridors on seed dispersal by birds. *Science*, **309**, 146–148.

Levins, R. & Culver, D. (1971) Regional coexistence of species and competition between rare species. *Proceedings of the National Academy of Sciences of the United States of America*, **68**, 1246–1248.

Limberger, R. & Wickham, S.A. (2011) Predator dispersal determines the effect of connectivity on prey diversity. *PLoS ONE*, **6**, e29071.

Löbel, S., Snäll, T. & Rydin, H. (2009) Mating system, reproduction mode and diaspore size affect metacommunity diversity. *Journal of Ecology*, **97**, 176–185.

Logue, J.B., Mouquet, N., Peter, H. & Hillebrand, H. (2011) Empirical approaches to metacommunities: a review and comparison with theory. *Trends in Ecology & Evolution*, **26**, 482–491.

Louette, G. & De Meester, L. (2005) High dispersal capacity of cladoceran zooplankton in newly founded communities. *Ecology*, **86**, 353–359.

MacArthur, R.H. & Wilson, E.O. (1967) Chapter 2: area and number of species. *The Theory of Island Biogeography* (ed. R.H. MacArthur), pp. 8–18. Princeton University Press, Princeton, NJ.

Matthiessen, B. & Hillebrand, H. (2006) Dispersal frequency affects local biomass production by controlling local diversity. *Ecology Letters*, **9**, 652–662.

Matthiessen, B., Mielke, E. & Sommer, U. (2010) Dispersal decreases diversity in heterogeneous metacommunities by enhancing regional competition. *Ecology*, **91**, 2022–2033.

May, L. & Baldwin, L.K. (2011) Linking field based studies with greenhouse experiments: the impact of Centaurea stoebe (=C. maculosa) in British Columbia grasslands. *Biological Invasions*, **13**, 919–931.

Meynard, C.N., Lavergne, S., Boulangeat, I., Garraud, L., Van Es, J., Mouquet, N. & Thuiller, W. (2013) Disentangling the drivers of metacommunity structure across spatial scales. *Journal of Biogeography*, **40**, 1560–1571.

Mouquet, N. & Loreau, M. (2003) Community patterns in source-sink meta-communities. *The American Naturalist*, **162**, 544–557.

Muller-Landau, H.C. (2003) Seeds of understanding of plant diversity. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 1469–1471.

Muller-Landau, H.C., Wright, S.J., Calderón, O., Condit, R. & Hubbell, S.P. (2008) Interspecific variation in primary seed dispersal in a tropical forest. *Journal of Ecology*, **96**, 653–667.

Nathan, R. & Muller-Landau, H. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution*, **15**, 278–285.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. & Smouse, P.E. (2008) A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 19052–19059.

Oaten, D.K. & Larsen, K.W. (2008) Stand characteristics of three forest types within the dry interior forests of British Columbia, Canada: implications for biodiversity. *Forest Ecology and Management*, **256**, 114–120.

Pillai, P., Gonzalez, A. & Loreau, M. (2011) Metacommunity theory explains the emergence of food web complexity. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 19293–19298.

Schluter, D. (1984) A variance test for detecting species associations, with some example applications. *Ecology*, **65**, 998–1005.

Simberloff, D.S. & Wilson, E.O. (1970) Experimental zoogeography of islands: a two-year record of colonization. *Ecology*, **51**, 934–937.

Soons, M.B., Nathan, R. & Katul, G.G. (2004) Human effects on long-distance wind dispersal and colonization by grassland plants. *Ecology*, **85**, 3069–3079.

Thomson, F.J., Moles, A.T., Auld, T.D. & Kingsford, R.T. (2011) Seed dispersal distance is more strongly correlated with plant height than with seed mass. *Journal of Ecology*, **99**, 1299–1307.

Ulrich, W. & Gotelli, N.J. (2010) Null model analysis of species associations using abundance data. *Ecology*, **91**, 3384–3397.

Vanschoenwinkel, B., Buschke, F. & Brendonck, L. (2013) Disturbance regime alters the impact of dispersal on alpha and beta diversity in a natural metacommunity. *Ecology*, **94**, 2547–2557.

Warren, P.H. (1996) The effects of between-habitat dispersal rate on protist communities and metacommunities in microcosms at two spatial scales. *Oecologia*, **105**, 132–140.

Wilson, D. (1992) Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. *Ecology*, **73**, 1984–2000.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Species list from aspen stands and grassland plots in Lac Du Bois Provincial Park, British Columbia, Canada (see main text for sampling protocol).

Table S2. The sensitivity of the effects of log stand size and log stand connectivity on log species richness by dispersal mode to three alternative criteria to determine aspen-association, with percentages specifying the percent of occurrences that had to be within aspen stands in order for a species to be included in the analysis.

Table S3. The results of the effects of log stand size and log stand connectivity on log species richness by dispersal mode when estimating the average dispersal distances (α) using our maximum likelihood function.

Table S4. Effects of stand size and stand connectivity on log-transformed species richness by dispersal mode, with each factor analyzed in separate linear models.

Table S5. Effects of stand size and stand connectivity on log-transformed species richness by dispersal mode with a connectivity function that incorporates the size of the surrounding sites.

Figure S1. Principal coordinates analysis (PCoA) with Jaccard's coefficient confirming that aspen stands differ in species composition from the surrounding grassland matrix.

Figure S2. Rank abundance curve comparing the abundance of matrix-associated plants to aspen–associated and generalist species' in the understory of 24 aspen stands.

Data S1. Model Fitting.