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The role of dispersal in shaping plant community composition of wetlands within an old-growth forest

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Summary

1. Dispersal ability can influence the importance of dispersal relative to other processes organizing metacommunities, such as species sorting among habitats along environmental gradients.

2. We compare plants with different dispersal modes and habitat affinities, evaluating the roles of environmental and spatial controls on plant community composition in 128 wetlands within 10 km^2 of old-growth maple–beech forest in southern Québec, Canada.

3. We address two hypotheses. First, we ask whether species with short-distance dispersal mechanisms are more dispersal-limited than species with adaptations for long-distance dispersal. Second, because wetland habitats are more fragmented than upland habitats in this forested area, we test the hypothesis that wetland species are more dispersal-limited than upland species growing in the same wetlands (e.g. on hummocks within a swamp).

4. Variation partitioning based on constrained ordinations showed that the distributions of species with short-distance dispersal mechanisms related more strongly to spatial factors than the distributions of long-distance dispersers, supporting the interpretation that these species are more dispersal-limited. The distributions of short-distance dispersers also showed finer-scale spatial patterns than the distributions of long-distance dispersers.

5. Distributions of wetland species related more strongly to environmental conditions than the distributions of upland species growing in the same wetlands, suggesting that wetland species are actually less dispersal-limited than upland species. Wetland and upland species had similar patterns of spatial variation in community composition.

6. *Synthesis*. The processes of dispersal limitation and species sorting along environmental gradients have differential importance to plants that grow within the same communities, but differ in dispersal ability and habitat affinity. This result emphasizes the impact of dispersal ability on the organization of metacommunities.

Key-words: determinants of plant community diversity and structure, dispersal, metacommunity, ordination, principal coordinates of neighbour matrices, redundancy analysis, spatial structure, species sorting, variation partitioning, wetland

Introduction

Dispersal plays a key role in structuring the distributions of species across a range of spatial scales. At larger scales, dispersal determines the contribution from a regional pool of species to a local landscape (Ricklefs, Qian & White 2004). Within a local landscape, dispersal can affect patterns of species composition by linking sets of communities into metacommunities (Leibold *et al.* 2004; Cottenie 2005). While only dispersal can account for the movement of species among isolated habitats, local processes such as environmental sorting and biotic interactions may then determine their persistence. The degree to which dispersal actually influences community composition relative to other processes remains an open question.

One way to address this question is to assess the extent to which variation in community composition relates to environmental conditions vs. spatial patterns; spatial patterns in species distributions are often attributed primarily to dispersal

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limitation (e.g. Duivenvoorden, Svenning & Wright 2002; Tuomisto, Ruokolainen & Yli-Halla 2003; Gilbert & Lechowicz 2004; Cottenie 2005). Comparing the relative strengths of environmental and spatial effects on community composition across organisms and habitats can yield general insights into where each process should predominate (Cottenie 2005). For example, spatial scale and the range of environmental variation may affect the balance of environmental and spatial control (Karst, Gilbert & Lechowicz 2005; Jones *et al.* 2006; van der Gucht *et al.* 2007). Greater habitat connectivity should reduce dispersal limitation and allow more effective species sorting, producing metacommunities structured primarily by local processes (Driscoll & Lindenmayer 2009). Better-dispersed species would also be expected to track environmental gradients more closely (Beisner *et al.* 2006; van de Meutter, de Meester & Stoks 2007; Vanschoenwinkel *et al.* 2007).

Comparing different sets of species within the same communities allows for particularly effective tests of how environmental and spatial controls vary with species traits. Such comparisons can control not only for landscape structure, but also for the number and quality of environmental and spatial variables (Jones *et al.* 2008). Although several studies have compared environmental and spatial effects on the distributions of aquatic organisms with different dispersal strategies (Beisner *et al.* 2006; van de Meutter, de Meester & Stoks 2007; Vanschoenwinkel *et al.* 2007), to our knowledge this study is the first to address the role of dispersal in regulating environmental and spatial controls on plant community composition.

Specifically, we compare plants with different dispersal modes and habitat affinities, assessing the relative strength of environmental and spatial controls on the distributions of each set of species across small wetlands within an old-growth forest in southern Québec, Canada. We test two specific hypotheses. First, we test whether species with short-distance dispersal mechanisms (by ants, explosion, splash or gravity) are more dispersal-limited than species with adaptations for long-distance dispersal (by vertebrates, water or wind). Second, because wetland habitats are more fragmented than upland habitats in this forested landscape, we test the hypothesis that wetland species are more dispersal-limited than upland species. This hypothesis assumes that upland species, which can establish and persist in upland habitats, should be better able to migrate through the forested landscape than wetland species because the upland forests surrounding the wetland habitats represent a dispersal barrier of differential penetrability to species with different habitat affinities. Note that we do not compare upland and wetland habitats, but upland and wetland species growing within the same wetland habitats, where upland species may occur, for example, on hummocks within swamps. Thus, we can compare the distribution of species with different dispersal traits across the same spatial configuration of habitats.

We test each hypothesis in two ways. First, we compare the amount of variance in community composition explained by environmental and spatial variables, assuming that the distributions of more dispersal-limited species should relate more strongly to spatial patterns, and less dispersal-limited species should better track environmental gradients. Second, we compare the amount of variance in community composition explained by spatial variables at different scales, assuming that the distributions of more dispersal-limited species should show spatial patterns at finer scales, and the distributions of less dispersal-limited species should relate more strongly to broader spatial scales. If species with short-distance dispersal mechanisms and/or wetland species meet these expectations for greater dispersal limitation, it would indicate that dispersal indeed constrains species' distributions across this landscape and that the degree of constraint depends on species' traits.

Materials and methods

We conducted this study in the Gault Nature Reserve, a 10-km^2 tract of old-growth forest on Mont Saint-Hilaire, in southern Québec, Canada (45°32′N, 73°8′W). Upland forests dominated by *Acer saccharum*, *Fagus grandifolia* and *Quercus rubra* cover most of the reserve (Arii, Hamel & Lechowicz 2005), but there also are a variety of wetland habitats, including lakeshores, permanent and seasonal ponds, swamps, glades and streamsides (Flinn, Lechowicz & Waterway 2008). We sampled 128 sites ranging in area from 80 to 5755 m^2 that represent the full range of wetlands within the reserve (map in Flinn, Lechowicz & Waterway 2008). The reserve consists of a central, 32-ha lake surrounded by seven hills, with wet areas around the lakeshores and along stream drainages. Other wet areas include a 5-ha swamp on peat deposits, small ponds and other depressions, and seeps and springs. Flinn, Lechowicz & Waterway (2008) describe in detail the plant species diversity and community composition of these sites.

We sampled plant community composition by estimating the percentage cover of all vascular plant species in each site, using the classes 0 to < 1, 1 to < 5, 5 to < 25, 25 to < 75 and 75 to 100. Each site was thoroughly searched twice at different times in the growing season. For analyses of community composition, we excluded species present at only one site and genera that could not be reliably identified to species in vegetative condition, such as *Impatiens* and *Viola*. Abundances were Hellinger-transformed (Legendre & Gallagher 2001; Peres-Neto *et al.* 2006). For comparisons, we classified species by dispersal mode (short-distance, vertebrate, water, wind) and habitat affinity (wetland, upland; see Appendix S1 in Supporting Information).

To characterize the local water regime, we described the topography of each site by its slope and curvature, using the mean of 5 × 5 m cells in a digital elevation model with decimetre resolution. Curvature represents the concavity or convexity of a land surface, calculated by comparing the elevation of each cell with its neighbouring cells in ArcGIS (Environmental Systems Research Institute, Redlands, CA, USA). To quantify soil properties at each site, we pooled soil samples collected 10 cm deep every 10 m along transects within each wetland and analysed NO_3^-, NH_4^+, P, K, Ca, Mg, pH (in water; Forest Pedology Laboratory, Laval University, Québec, QC, Canada) and organic matter (by loss-on-ignition). We combined NO_3^- and NH_4^+ into a measure of total N. At the same locations where we collected soil samples, we took hemispherical photographs from 1 m above the ground to quantify canopy openness. We used Gap Light Analyzer software (Frazer, Canham & Lertzman 1999) to analyse the percentage openness of the canopy in each photograph and calculated the mean for each site. For practical reasons, we did not take photographs in ten of the deepest ponds. Instead, we assigned these sites the maximum observed value for mean canopy openness (28%). To better detect unimodal relationships between species abundance

Fig. 1. Maps of the spatial structure of community composition at different spatial scales. Each panel shows a map of the study area, with *x*- and *y*-axes representing geographical coordinates in a Cartesian coordinate system, and symbols for each sampled site. For each group of species, the shading and size of the symbols in panel (a) show the sign and magnitude, respectively, of the first canonical axis from the redundancy analysis (RDA) of the species abundance data based on all forward-selected principal coordinates of neighbour matrices (PCNM) variables. This RDA was based on only spatial variables ([*S*]). Filled squares represent positive values, open squares represent negative values and the size of the squares is proportional to the value plotted. The percentage value indicates the amount of variation explained by all forward-selected PCNM variables. Thus, panel (a) shows spatial variation in plant community composition. Symbols in panels (b–e) show the sign and magnitude of the most significant PCNM variable at each spatial scale. The percentage value indicates the amount of variation explained by that PCNM variable. Thus, panels (b–e) show the strongest spatial pattern in plant community composition at each scale. Spatial scales for which no PCNM variable was forward-selected are undefined and thus not shown.

and the environment, we also centred and squared the 10 measured environmental variables (Declerck *et al.* 2005). Centring the unimodal distribution of an environmental variable about zero generates positive and negative values of that environmental variable. Squaring these centred environmental values transforms all negative values into positive values, thereby converting the original distribution of the environmental variable from unimodal to quasi-linear. Although this centring and squaring technique was used to generate the results presented here, our results are qualitatively equivalent to those obtained when using only the ten untransformed environmental variables. In analysing space–environment relationships for particular subsets of plants defined by dispersal mode or habitat affinity, we then applied forward selection to the 20 environmental variables (10 untransformed variables and 10 transformed by centring and squaring) to identify significant environmental correlates of their distribution (Blanchet *et al.* 2008). Depending on the particular subset of the sampled flora, forward selection using the adjusted coefficient of multiple determination calculated for all environmental variables and the alpha significance level as our stopping criteria retained 6–16 environmental variables (Appendix S2).

We used principal coordinate analysis of neighbour matrices (PCNM) to characterize spatial structure at multiple scales (Borcard & Legendre 2002; Dray, Legendre & Peres-Neto 2006). PCNM analysis can be used to describe both regular and irregular sampling designs. In sampling designs based on a regular grid, PCNM analysis yields a series of ordered orthogonal sinusoidal waves describing spatial variation in species abundance from the largest to the smallest scales (Borcard *et al.* 2004). In irregular sampling designs, such as ours where sample sites are not regularly spaced on a grid, the PCNM variables are not regular sinusoidal waves, but they remain orthogonal and can be ordered based on the spatial scales they represent (Borcard *et al.* 2004). Here, we decomposed the spatial patterns in our data into 67 orthogonal PCNM variables whose wavelengths range from the largest distance between first neighbours (500 m) to the full extent of the study area (*c.* 3000 m). For each species group, we performed forward selection on these PCNM variables using the previously described double stopping criteria (Blanchet *et al.* 2008) to select only those PCNM variables that explained a significant amount of the variation in species abundance. Depending on the species group, forward selection yielded full spatial models consisting of 9–14 PCNM variables. For each species group, we also generated four classes of spatial submodels by splitting the PCNM variables of the full spatial model according to the scale they represent. This yielded very broad- (PCNM 1-5), broad- (6–15), intermediate- (16–40) and fine-scale (41–67) spatial submodels for each species group.

For each group of species and each spatial model, we partitioned variation in community composition to identify the unique and joint contributions of environmental and spatial processes (Borcard, Legendre & Drapeau 1992). First, we performed three redundancy analyses (RDAs) to determine the proportions of variation in species' percentage cover values explained by environmental variables ([*E*]; Appendix S2), spatial variables ([*S*]; Fig. 1), and both sets of predictors together ($[\mathrm{E} + S]$). From these analyses, we divided the variation in community composition into four non-overlapping fractions: (i) the proportion explained by environment independent of space, $[E|S] = [E + S] - [S]$; (ii) the proportion explained by space independent of environment, $[S|E] = [E + S] - [E]$; (iii) the proportion shared by environment and space, $[E \cap S] = [E + S] - [\mathrm{E}\,|\mathrm{S}] - [S|E]$; and (iv) the proportion not explained by environment or space, $1 - [E + S]$. To evaluate the significance of the four fractions, we used Monte Carlo permutation tests with 1000 permutations under the reduced model (Anderson & Legendre 1999). We used the adjusted estimates developed by Peres-Neto *et al.* (2006) to account for the sample size and to correct for differences in the number of predictors. Analyses were conducted with the vegan package in R (http://cran.r-project.org/). We tested whether the fractions obtained for each subset differed significantly from random samples of the same size using randomization tests (Appendices S3 and S4).

Results

Environmental and spatial variables explained a total of 32% of the variation in plant community composition (Table 1). For all plant species, spatial variables alone and environmental variables alone each explained almost 10% of the variation in community composition. Joint environmental and spatial variation accounted for a greater share than either set of predictors independently. The strongest environmental predictors of plant community composition were soil organic matter, canopy openness and soil N, except for upland species, which related most strongly to soil Ca (Appendix S2).

Consistent with our first hypothesis, the distributions of species with short-distance dispersal mechanisms related more strongly to spatial variables than did long-distance dispersers, particularly wind- and vertebrate-dispersed species (Table 1). Short-distance dispersers also had a greater share of variation explained by joint environmental and spatial variation than the other groups. Plants with different dispersal modes had similar amounts of variation explained by the environment, except for wind-dispersed species, which related more strongly to environmental variables.

The comparison of species with different habitat affinities did not fit the hypothesis that wetland species should be more dispersal-limited in this landscape. Rather, spatial variables had a similar impact on upland and wetland species, while environmental variables had much more influence on wetland than on upland species. While fractions of explained variation differed among subsets, all fell within the confidence intervals for random subsets of the same size, except the proportion of upland species composition explained by environmental vari-

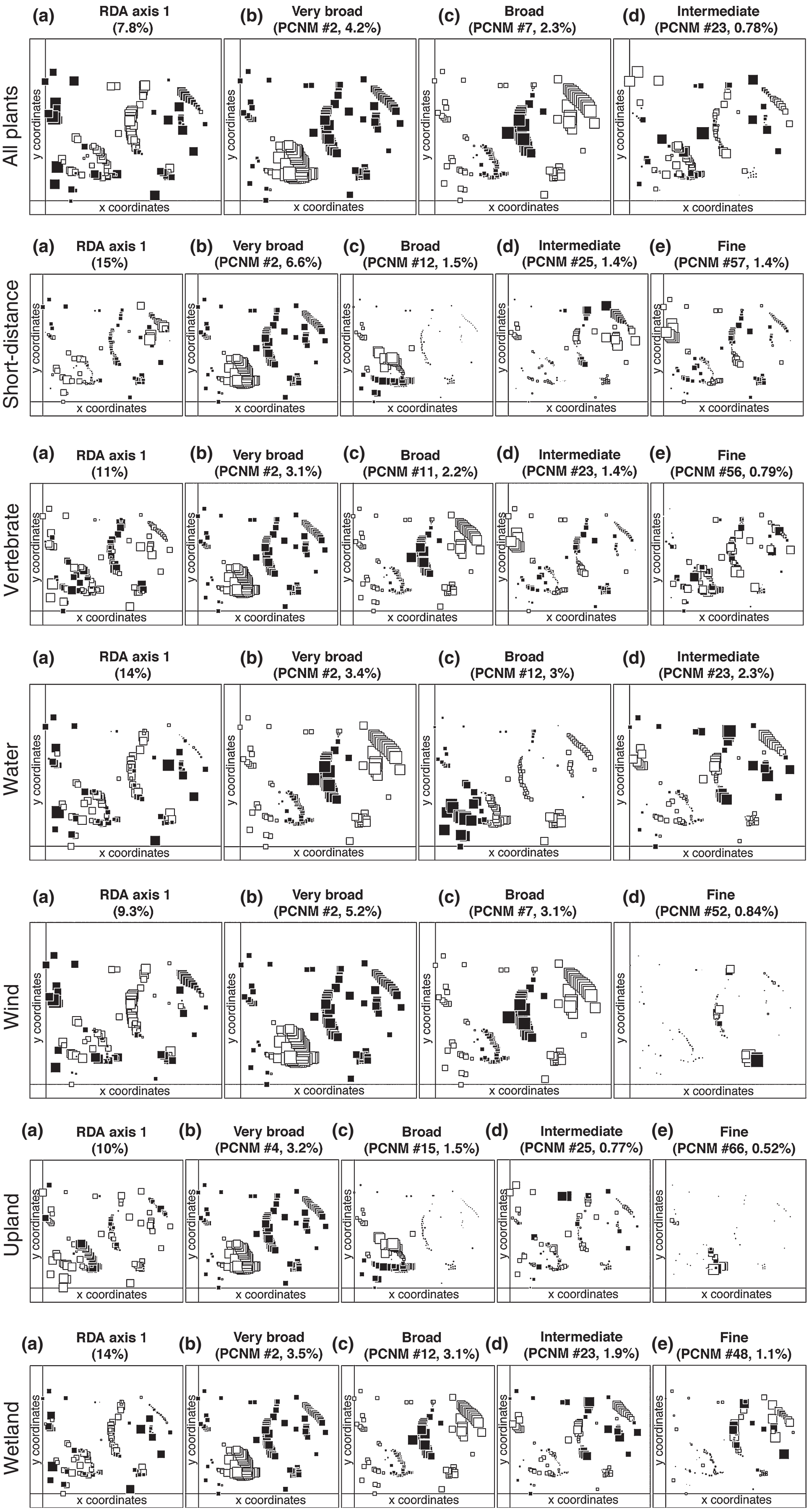
All plants
(a) RDA axis 1 (7.8%)
(b) Very broad (PCNM #2, 4.2%)
(c) Broad (PCNM #7, 2.3%)
(d) Intermediate (PCNM #23, 0.78%)
Short-distance
(a) RDA axis 1 (15%)
(b) Very broad (PCNM #2, 6.6%)
(c) Broad (PCNM #12, 1.5%)
(d) Intermediate (PCNM #25, 1.4%)
(e) Fine (PCNM #57, 1.4%)
Vertebrate
(a) RDA axis 1 (11%)
(b) Very broad (PCNM #2, 3.1%)
(c) Broad (PCNM #11, 2.2%)
(d) Intermediate (PCNM #23, 1.4%)
(e) Fine (PCNM #56, 0.79%)
Water
(a) RDA axis 1 (14%)
(b) Very broad (PCNM #2, 3.4%)
(c) Broad (PCNM #12, 3%)
(d) Intermediate (PCNM #23, 2.3%)
Wind
(a) RDA axis 1 (9.3%)
(b) Very broad (PCNM #2, 5.2%)
(c) Broad (PCNM #7, 3.1%)
(d) Fine (PCNM #52, 0.84%)
Upland
(a) RDA axis 1 (10%)
(b) Very broad (PCNM #4, 3.2%)
(c) Broad (PCNM #15, 1.5%)
(d) Intermediate (PCNM #25, 0.77%)
(e) Fine (PCNM #66, 0.52%)
Wetland
(a) RDA axis 1 (14%)
(b) Very broad (PCNM #2, 3.5%)
(c) Broad (PCNM #12, 3.1%)
(d) Intermediate (PCNM #23, 1.9%)
(e) Fine (PCNM #48, 1.1%)
y coordinates
x coordinates

Table 1. Redundancy analysis (RDA) variation partitioning of plant community composition into fractions explained by environmental and spatial variables

	Dispersal mode							
	All plants ($n = 228$)		Short-distance ($n = 28$)		Vertebrate ($n = 85$)		Water ($n = 49$)	
	Adjusted R^2	P	Adjusted R^2	P	Adjusted R^2	P	Adjusted R^2	P
$[E\|S]$	0.0966	0.0010	0.0722	0.0010	0.0727	0.0010	0.0899	0.0010
$[E\cap S]$	0.1335		0.1821		0.1380		0.1261	
$[S\|E]$	0.0909	0.0010	0.1286	0.0010	0.1070	0.0010	0.1222	0.0010
$1 - [E + S]$	0.6790		0.6171		0.6824		0.6619	
S:E	0.94		1.8		1.5		1.4	

	Habitat affinity					
	Wind ($n = 91$)		Upland ($n = 37$)		Wetland ($n = 49$)	
	Adjusted R^2	P	Adjusted R^2	P	Adjusted R^2	P
$[E\|S]$	0.1071	0.0010	0.0304	0.0010	0.0930	0.0010
$[E\cap S]$	0.1213		0.0617		0.1877	
$[S\|E]$	0.0959	0.0010	0.1196	0.0010	0.1092	0.0010
$1 - [E + S]$	0.6757		0.7883		0.6101	
S:E	0.9		3.9		1.2	

$[E|S]$, the proportion explained by environmental variables independent of space; $[S|E]$, the proportion explained by spatial variables independent of environment; $[E\cap S]$, the proportion explained by shared environmental and spatial variation; $1 - [E + S]$, the proportion not explained by either environmental or spatial variables; S : E is the ratio of spatial to environmental variation. Estimates are adjusted to account for the sample size and the number of predictors (Peres-Neto *et al.* 2006).

ables, which was significantly lower than for random subsets, and the proportion of wetland species composition explained by shared environmental and spatial variation, which was significantly higher (Appendix S3).

For all plant species considered together, spatial variation in community composition occurred primarily at broad and very broad scales, where joint spatial and environmental variation was also strongest (Fig. 1 and Table 2). Spatial variation at very broad and broad scales largely distinguished major creek drainages; the intermediate scale separated clusters of contiguous sites comprising a habitat patch (e.g. a 5-ha swamp); and the fine scale separated individual sites (Fig. 1).

Consistent with our hypothesis, the distributions of short-distance dispersers related more strongly to intermediate and fine scales than the distributions of long-distance dispersers, particularly water- and wind-dispersed species (Fig. 1 and Table 2). Wetland and upland species had similar patterns of spatial variation in community composition, in that wetland species distributions related to broad, intermediate and very broad scales, whereas spatial variation in upland species distributions was mostly at very broad and broad scales.

Discussion

Dispersal indeed appears to limit plant species' distributions in wetlands on this largely forested landscape, with the degree of limitation dependent on species' adaptations for dispersal. The distributions of species with adaptations for short-distance dispersal depend more strongly on spatial patterns, and on spatial patterns at finer scales, than the distributions of species with adaptations for long-distance dispersal. Long-distance dispersers track environmental gradients more effectively and show broader spatial patterns. Species' habitat affinities, however, did not predict their degree of dispersal limitation on this landscape. Wetland species' distributions, despite being restricted to more fragmented habitats, related more strongly to environmental conditions than the distributions of upland species growing in the same wetland habitats.

Although this is the first such comparison of plants with different dispersal modes, it corroborates similar results for aquatic organisms of varying motility (Beisner *et al.* 2006; van de Meutter, de Meester & Stoks 2007; Vanschoenwinkel *et al.* 2007). These comparisons suggest that, across a wide range of taxa, spatial patterns in species' distributions represent limited dispersal based on species traits. Among plants, species dispersed only by ants, explosion, splash or gravity contrasted with vertebrate-, water- and wind-dispersed species. Vertebrate-dispersed species, even though thought to be most efficiently dispersed (Vittoz & Engler 2007), showed slightly greater spatial effects and finer spatial patterning than wind-dispersed species. Wind-dispersed species also had stronger relationships with the environment than other plants. These results for wind-dispersed species, which include ferns and other seedless vascular plants, support many findings that environmental factors predominate over spatial patterns in explaining fern distributions (Tuomisto, Ruokolainen & Yli-Halla 2003; Gilbert & Lechowicz 2004; Karst, Gilbert & Lechowicz 2005; Jones *et al.* 2006, 2008).

Table 2. Redundancy analysis (RDA) variation partitioning of plant community composition into fractions explained by environmental and spatial variables at different spatial scales

	Very broad		Broad		Intermediate		Fine	
	Adjusted R^2	P	Adjusted R^2	P	Adjusted R^2	P	Adjusted R^2	P
All plant species (n = 228)								
$[E\|S]$	0.1989	0.0010	0.1482	0.0010	0.2315	0.0010		
$[E \cap S]$	0.0311		0.0819		0			
$[S\|E]$	0.0438	0.0010	0.0537	0.0010	0.0040	0.0130		
$1 - [E + S]$	0.7261		0.7162		0.7659			
S:E	0.2		0.4		0.02			
Short-distance dispersing species (n = 28)								
$[E\|S]$	0.0993	0.0010	0.2588	0.0010	0.2649	0.0010	0.2304	0.0010
$[E \cap S]$	0.1550		0		0		0.0240	
$[S\|E]$	0.0722	0.0010	0.0366	0.0010	0.0142	0.0090	0.0048	0.1449
$1 - [E + S]$	0.6735		0.7090		0.7315		0.7409	
S:E	0.7		0.1		0		0	
Vertebrate-dispersed species (n = 85)								
$[E\|S]$	0.1788	0.0010	0.1376	0.0010	0.2020	0.0010	0.2089	0.0010
$[E \cap S]$	0.0318		0.0730		0.0086		0.0017	
$[S\|E]$	0.0434	0.0010	0.0503	0.0010	0.0120	0.0160	0.0057	0.0410
$1 - [E + S]$	0.7459		0.7391		0.7773		0.7836	
S:E	0.2		0.4		0.1		0	
Water-dispersed species (n = 49)								
$[E\|S]$	0.1654	0.0010	0.1750	0.0010	0.1883	0.0010		
$[E \cap S]$	0.0506		0.0409		0.0276			
$[S\|E]$	0.0253	0.0040	0.0559	0.0010	0.0334	0.0010		
$1 - [E + S]$	0.7588		0.7282		0.7507			
S:E	0.2		0.3		0.2			
Wind-dispersed species (n = 91)								
$[E\|S]$	0.2099	0.0010	0.1395	0.0010			0.2297	0.0010
$[E \cap S]$	0.0185		0.0889				0	
$[S\|E]$	0.0383	0.0010	0.0570	0.0010			0.0067	0.0160
$1 - [E + S]$	0.7333		0.7146				0.7649	
S:E	0.2		0.4				0	
Upland species (n = 37)								
$[E\|S]$	0.0402	0.0010	0.0930	0.0010	0.0861	0.0010	0.0936	0.0010
$[E \cap S]$	0.0519		0		0.0060		0	
$[S\|E]$	0.0807	0.0010	0.0245	0.0010	0.0077	0.0130	0.0044	0.0879
$1 - [E + S]$	0.8272		0.8833		0.9002		0.9035	
S:E	2.0		0.3		0.1		0.1	
Wetland species (n = 49)								
$[E\|S]$	0.2164	0.0010	0.1844	0.0010	0.2624	0.0010	0.2803	0.0010
$[E \cap S]$	0.0643		0.0963		0.0183		0.0011	
$[S\|E]$	0.0232	0.0010	0.0449	0.0010	0.0240	0.0020	0.0062	0.0380
$1 - [\mathrm{E} + \mathrm{S}]$	0.6961		0.6744		0.6953		0.7131	
S:E	0.1		0.2		0.1		0	

$[E|S]$, the proportion explained by environmental variables independent of space; $[S|E]$, the proportion explained by spatial variables independent of environment; $[E \cap S]$, the proportion explained by shared environmental and spatial variation; and $1 - [E + S]$, the proportion not explained by either environmental or spatial variables. S:E is the ratio of spatial to environmental variation. Estimates are adjusted to account for the sample size and the number of predictors (Peres-Neto *et al.* 2006). Missing values indicate that none of the PCNM variables that define the spatial submodel were forward-selected.

Expecting upland forests to represent a dispersal barrier to wetland species, we also predicted that wetland species would show stronger spatial patterning in this forest reserve than upland species. For example, Freestone & Inouye (2006) found that serpentine-seep endemics were more sensitive to dispersal limitation than other plant species in a landscape where serpentine seeps were naturally patchy. At our site, however, the influence of spatial relative to environmental variables was much greater for upland than for wetland species. This result undercuts the idea that wetland species have more difficulty migrating through an upland landscape. This pattern might arise if upland species included more short-distance dispersers, but the two groups had similar proportions of species with short-distance dispersal mechanisms. Wetland species do, however, include more plants dispersed by water, and they may move efficiently through upland forests via streams (Johansson, Nilsson & Nilsson 1996). Wetland species also appear more prone than upland species to maintain seed banks in wetlands, which may allow them to better maintain populations through time (Hopfensberger 2007; unpublished data). The contrast between groups could also result if wetland species were more ecologically specialized than upland species along the environmental gradients we measured. This seems plausible, given that extensive vegetation sampling of Mont Saint-Hilaire (Gilbert & Lechowicz 2004; unpublished data) has rarely found wetland species in upland plots, whereas a number of upland species occurred in the wetlands. Upland plants may grow in these wetlands not because environmental conditions there particularly suit them, but because they happen to occur nearby, in the surrounding forest. Populations of upland species in wetlands might in fact represent sink populations maintained through ongoing dispersal rather than within-habitat reproduction (Pulliam 1988). Evidently, species with different habitat affinities depend on different processes to determine their distributions across these wetlands.

Among the environmental predictors, most species related most strongly to soil organic matter, canopy openness and soil N (Appendix S2). Soil organic matter probably represents not only an important measure of soil fertility, but also an index of soil saturation. Canopy openness, as a descriptor of vegetation structure and habitat type as well as light availability, also seems likely to explain a large share of variation in plant species composition. In addition, canopy openness could act as a surrogate for the presence and duration of standing water, because standing water excludes most trees. Soil organic matter and canopy openness were positively correlated (Appendix S5). The importance of soil organic matter and canopy openness suggests that direct measurements of soil moisture or hydrological regime may have explained a large share of plant community composition, had it been practical to measure these characteristics at so many sites over time. This study further confirmed that soil N forms a major gradient for floristic variation in wetlands as well as uplands across this landscape (Gilbert & Lechowicz 2004; Arii, Hamel & Lechowicz 2005; Karst, Gilbert & Lechowicz 2005). Only upland species related more strongly to soil Ca, revealing this as another important edaphic gradient shaping community composition through a particular subset of the flora. In summary, we found or confirmed meaningful, if relatively weak, relationships between environmental gradients and plant distributions in this old-growth forest reserve.

Overall, environmental and spatial factors contributed equally to variation in plant community composition across the landscape, with joint environmental and spatial variation explaining a somewhat greater share. We found a greater role for spatial relative to environmental processes than several studies in continuous forests, in which environmental influences related more strongly to plant community composition (Phillips *et al.* 2003; Jones *et al.* 2006). In particular, our results from wetlands contrast with Gilbert & Lechowicz's (2004) study of mostly upland forests within the same reserve, where environmental conditions had a relatively stronger impact on species distributions, explaining 2–20 times more variation than spatial location. While this contrast could arise from a number of differences between the two data sets, it supports the interpretation that the relatively greater spatial isolation of the wetland habitats leads to stronger dispersal limitation and weaker matching with the environment. Whatever the cause, colonization and extinction dynamics apparently continue to structure plant communities in these habitats within the reserve despite their relative permanence and proximity.

It is useful to note that the proportion of total variation explained by environmental and spatial variables was modest (32%), but comparable with many other studies using ordination to partition variation in community composition (e.g. Svenning *et al.* 2004; Beisner *et al.* 2006; Langenheder & Ragnarsson 2007; Jones *et al.* 2008; Carr *et al.* 2009). In fact, most unexplained variation in these analyses represents lack of fit to the model implicit in ordination methods, whereas relative comparisons of the fractions of explained variation remain valid (Legendre & Legendre 1998; Økland 1999). Measuring additional environmental variables might increase the share of explained variation, but we have already measured most principal environmental gradients relevant to plants. Absolute amounts of explained variation certainly depend on data quality and quantity (Jones *et al.* 2008); the qualitative trends reported in our comparisons among species groups are not affected by any limitation in the statistical analyses.

In this study, the overall importance of spatial factors and the differences among species with contrasting dispersal traits indicate that dispersal-driven processes generally dominate in determining community membership. However, our comparisons of plant groups also demonstrate that dispersal ability can alter the balance of processes structuring metacommunities. Species with different dispersal ability showed strikingly different relationships to environmental and spatial variables. Although community assembly by dispersal is often viewed as a neutral process (Hubbell 2001), this trait-based variation among species suggests a selective process of dispersal assembly that depends on key species characteristics (Vellend *et al.* 2007). In particular, dispersal limitation had differential importance to plant species depending on their adaptations for dispersal.

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Supporting Information

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

Appendix S1. Dispersal modes and habitat affinities of 228 plant species, with references.

Appendix S2. Environmental correlates of distribution for subsets of species.

Appendix S3. Randomization tests comparing species subsets to random samples of the same size.

Appendix S4. Matlab functions to perform randomization tests.

Appendix S5. Correlations among environmental variables.