



Isolation-driven functional assembly of plant communities on islands

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The physical and biotic environment is often considered the primary driver of functional variation in plant communities. Here, we examine the hypothesis that spatial isolation may also be an important driver of functional variation in plant communities where disturbance and dispersal limitation may prevent species from occupying all suitable habitats. To test this hypothesis, we surveyed the vascular plant composition of 30 islands in the Gulf of Maine, USA, and used available functional trait and growth form data to quantify the functional composition of these islands. We categorized species based on dispersal mode and used a landscape metric of isolation to assess the potential role of dispersal limitation as a mechanism of isolation-driven assembly. We tested for island and species level effects on functional composition using a hierarchical Bayesian framework to better assess the causal link between isolation and functional variation. Growth form composition and the community mean value of functional traits related to growth rate, stress tolerance, and nutrient use varied significantly with island isolation. Functional traits and growth forms were significantly associated with dispersal mode, and spatial isolation was the strongest driver of primary trait variation, while island properties associated with environmental drivers in our system were not strong predictors of trait variation. Despite the species-level association of dispersal mode and functional traits, dispersal mode only accounted for a small proportion of the overall isolation effect on community-level trait variation. Our study suggests that spatial isolation can be a key driver of functional assembly in plant communities on islands, though the role of particular dispersal processes remains unclear.

One of the goals in ecology is to better understand how biotic communities influence the way ecosystems function (Hooper et al. 2005, Chapin et al. 2011). Plants play an especially important role in the functioning of terrestrial ecosystems, and their functional traits – the morphological, physiological, and phenological characteristics that affect their growth, survival, and reproduction – are a principal means by which species affect their environment (Díaz and Cabido 2001, Lavorel and Garnier 2002, Díaz et al. 2004, Cornwell et al. 2008). The composition of functional traits in a community is driven in part by the physical and biotic environment, which selects for traits conferring high fitness in a given habitat (habitat selection) (Díaz et al. 1998, Cornwell et al. 2006, Ackerly and Cornwell 2007). However, non-environmental factors such as spatial isolation may also drive community composition by selecting for traits associated with better dispersal ability (immigrant selection; Lomolino 1984), particularly in systems such as islands and habitat fragments (Nilsson and Nilsson 1978, Voort et al. 1979, Kadmon and Pulliam 1993, Willson and Traveset 2000, Flinn and Vellend 2005, Aparicio et al. 2008, Fukami 2010, Schleicher et al. 2011, Marteinsdottir and Eriksson 2013).

The role of spatial isolation in community assembly may be especially apparent if the communities are in strong disequilibrium, where a recent disturbance or change in habitat quality prevents species from occupying all suitable habitats (Kadmon and Pulliam 1995, Whittaker et al. 1997, Svenning and Sandel 2013). Such reduction in the strength of species–environment associations increases the relative role of dispersal processes, and community composition becomes more closely associated with species' dispersal abilities. Differences in dispersal ability between species may thus lead to differences in composition across spatial isolation. For example, Kadmon and Pulliam (1995) found that spatial isolation increased the proportion of species with adaptations for wind dispersal on recently clear-cut lake islands. Whittaker et al. (1997) found that the early stages of plant colonization in recently cleared volcanic islands could be predicted based on dispersal traits. These and other studies increasingly recognize that dispersal-driven disequilibrium dynamics are not uncommon, often due to the ubiquity and strength of human disturbance (Drezner et al. 2001, Löfgren and Jerling 2002, Flinn and Vellend 2005, Nowacki and Abrams 2015), and will only become more prevalent in a changing climate (Svenning and Sandel 2013). This makes a strong case for

better understanding the role of dispersal in community assembly and, in turn, ecosystem function.

Several experimental studies have shown that reducing dispersal barriers can alter ecosystem functioning by changing community properties (Zobel et al. 2006). For example, seed additions can affect productivity, light capture, root biomass, and root carbon storage in old-field plant communities (Foster et al. 2007, Stein et al. 2008). Some of these effects may be attributed to the role of dispersal in maintaining species diversity, and links between diversity and ecosystem functioning (Loreau and Mouquet 1999, Mouquet and Loreau 2003, Gonzalez et al. 2009). Dispersal limitation may also have functional consequences if functional trait values are non-randomly associated with their dispersal ability (Zobel et al. 2006). For example, if species with rapid life histories, such as annuals, show adaptations toward both fast growth and high dispersal capacity, then isolated plant communities may contain a functionally biased subset of species from the regional species pool. Competition-colonization and tolerance-fecundity tradeoff theories suggest a link between dispersal ability and functional characteristics (Tilman 1990, 1994, Muller-Landau 2010). Many empirical studies have also demonstrated associations between functional characteristics and dispersal capacities of plants (Howe and Smallwood 1982, Hughes et al. 1994, Tilman 1994, Westoby et al. 1996, Díaz and Cabido 1997, Turnbull et al. 1999, Ozinga et al. 2005, Pärtel and Zobel 2007, Boedeltje et al. 2008, Gallagher and Leishman 2012), though we are not aware of any studies that test whether these associations generate patterns of functional variation in communities along gradients of spatial isolation.

Here, we test the hypothesis that spatial isolation is an important driver of functional trait variation in plant communities (functional assembly), and attempt to assess the role of dispersal in driving this relationship. We examined this hypothesis using the plant communities of 30 uninhabited continental islands in the Gulf of Maine, USA, coupled with island properties and species-level trait data. Following glacial retreat, the majority of islands in the Gulf of Maine were connected to the mainland about 11 thousand years ago, and their current form was generated from rising sea levels over the following eight thousand years (Barnhardt et al. 1995). At least since European establishment in the 17th and 18th centuries, islands in the Gulf of Maine have had rich history of human use, involving forest clearing, subsequent sheep grazing, followed by abandonment over this last century (McLane 1989, Conkling 2011). The earliest reports by European colonists suggest that the vast majority of islands in the Gulf of Maine were originally forested, but many islands remain unforested even after multiple decades of abandonment (Conkling 2011). These observations suggest that islands in the Gulf of Maine are, in the absence of further large disturbances, likely to transition to forests but at a rate strongly dependent on dispersal processes. We quantified the functional composition of each island using available trait data on vegetative height, specific leaf area, leaf dry matter content, and leaf nitrogen since these are among the key traits important for predicting species effects on ecosystem properties (Weiher et al. 1999, Lavorel and Garnier 2002, Díaz et al. 2004, Poorter et al. 2009), community dynamics (Gaudet and Keddy 1988, Wardle et al. 1998),

and plant resource use strategies (Reich et al. 2003, Wright et al. 2004, Reich 2014). We categorized the dispersal mode of each species based on propagule morphology, and used the richness of each dispersal mode on islands to quantify the composition of these dispersal traits. Similarly, we classified species into growth forms and used the richness of each growth form on islands to quantify the relative composition of these whole-plant functional characteristics (Leishman and Westoby 1992, Díaz and Cabido 1997).

We tested the effect of spatial isolation on functional composition and assessed the role of dispersal by testing the following predictions.

1) Functional traits related to growth rate, stress tolerance, and nutrient use will be significantly associated with particular modes of dispersal. Support for this prediction would be in line with empirical and theoretical findings on the association between functional characteristics, especially those related to competitive interactions and stress tolerance, and dispersal potential. Support for this prediction would also suggest a direct link by which dispersal processes can drive patterns of community functional variation.

2) The composition of dispersal modes will vary significantly with island isolation and drive the effect of isolation on functional composition. Because dispersal mode is an important predictor of dispersal potential (Tamme et al. 2014), support for this prediction would provide evidence for the importance of immigrant selection across our gradient of spatial isolation.

3) Functional assembly will be primarily driven by environmental drivers associated with island area and maximum elevation. Proximity and exposure to the ocean are known drivers of environmental variation on islands (Oosting 1945, Boyce 1954), so strong support for this alternative prediction would suggest evidence that spatial isolation is not the key driver of functional variation. Environmental variation offers an alternative hypothesis to explain patterns of functional trait variation across islands.

Material and methods

Species composition

We surveyed the vascular plants of 30 uninhabited islands in the Gulf of Maine, USA (43°43'N, 70°3'W to 44°29'N, 67°39'W; WGS 84) between 1992 and 2010. The 30 islands span 207 km along the coast of Maine and range from 1.1 to 66.9 ha in size (Table 1). We conducted non-systematic searches for vascular plants in all habitats, and survey effort was approximately proportional to island area. To increase the probability that all vascular plants present on each island would be documented, we made at least four monthly visits to each island throughout the growing season from June through September. The only exceptions were at Bar Island (59–265), Big Roberts Island, Little Roberts Island, Trumpet Island, and Matinicus Rock where fewer surveys were conducted because of access issues or nesting seabirds, but these islands were either relatively small in area (< 5 ha) and/or surveys were supplemented with previously existing lists (Supplementary material Appendix 1, Spreadsheet A1 for species lists and details on the year surveyed and number of visits made to each island).

Table 1. Islands in this study off the coast of Maine (USA; $n = 30$) and their associated biotic and geographic characteristics. 2000 m landscape measure of isolation (LMI, %) refers to the percent land cover within a 2000 m buffer around each island.

Island ID	Species richness	Area (ha)	Elevation max (m)	2000 m LMI (%)	UTM Zone 19T, datum = WGS 84	
					East	North
Baker	201	66.91	30	1.42	563989	4899020
Bald Porcupine	139	12.54	54	18.12	565191	4915220
Bar (59–194)	181	28.06	50	31.21	563151	4916440
Bar (59–265)	93	2.79	16	68.74	553960	4911620
Big Roberts	104	4.85	20	1.73	515561	4873240
Crane	117	4.07	6	4.16	469256	4860680
Eastern	74	1.67	7	11.6	584690	4917300
Egg Rock	56	3.43	10	0.03	568669	4911530
Franklin	115	4.27	10	2.99	469950	4859900
Hart	94	4.91	5	7.55	478665	4861310
Heron	115	20.8	7	2.08	542106	4883180
Inner Sand	125	7.3	15	3.73	605440	4925130
Johns	115	16.96	21	0.39	547600	4884240
Jordans Delight	121	10.01	27	4.54	593631	4921830
Little Duck	144	35.11	27	1.84	560387	4891500
Little Moose	169	20.31	16	25.16	575770	4909430
Little Roberts	48	1.047	8	2.06	515213	4873060
Little Spoon	88	8.98	19	1.4	534301	4876260
Little Thrumcap	81	2.5	8	2.72	455689	4851760
Matinicus Rock	67	8.88	15	0.02	511734	4848020
Outer White	137	4.28	25	2.55	453820	4848500
Ram	97	2.07	13	12.24	422337	4844250
Schoodic	136	26.05	13	8.71	577144	4909180
Seal	119	34.78	20	0	520809	4859330
Sheep Porcupine	140	8.9	38	13.03	564195	4916640
The Hop	139	3.02	17	7.72	567208	4918010
Trumpet	75	1.94	6	1.44	544506	4898950
Upper Flag	160	13.63	18	5.63	415848	4841820
West Pond	132	3.47	7	40.86	574129	4910335
Western Ear	106	8.14	28	13.18	527655	4872450

During each visit, we surveyed the perimeter of the island on foot, and searched portions of each habitat in the interior of the island. Extra time was spent in each unique habitat to ensure a complete inventory. All specimens not identified in the field were collected and identified in the lab with a dissecting microscope and key (Haines 2011). All vascular plants were identified to the species level. Intraspecific taxa were not considered in the analyses of this study because trait data were not available at the intraspecific level. All vascular plant nomenclature follows Haines (2011).

Trait data

We queried the TRY Plant Trait Database (Kattge et al. 2011) for values of the following functional traits for the 550 vascular plant species recorded across the 30 islands: specific leaf area ($\text{mm}^2 \text{mg}^{-1}$, SLA), leaf nitrogen per unit dry mass (mg g^{-1} , $[N_L]$), vegetative height (m, VH), and leaf dry matter content per leaf water-saturated mass (g g^{-1} , LDMC). Trait values were available for a total of 402 species (73%) (see Supplementary material Appendix 2, Table A2 for more details). Although trait values were missing for some species, we do not expect these missing values to be biased relative to community composition across our gradient of island isolation. The percent of species with unavailable trait values on islands ranged from 15–27% and was unrelated to our island isolation metric ($F_{1,28} = 0.0003$, $p > 0.5$). All available mean

and single measure trait values were averaged within species and log-transformed for analyses. Species composition was used to generate a pool of trait values specific to each island, and then values were averaged to generate an island-mean value for each trait. Island-mean trait values were not weighted by species abundances since islands were only surveyed to generate species lists.

We categorized the dispersal mode of all 550 species based on the visual morphology of their propagules. Spores or fruits with a pappus or wings are adaptations that aid in wind dispersal and those species were categorized as wind-dispersed. Fruits with a fleshy mesocarp or adhesive barbs are adaptations that aid with vertebrate dispersal and those species were categorized as animal-dispersed. Species without clear morphological adaptations for long-distance dispersal, including ant-dispersed fruits with elaiosomes, ballistic seed pods, and dehiscent seed pods, were categorized as unassisted. We recognize that these species are not truly unassisted since ant and ballistic dispersal are forms of assistance. However, we label these species as ‘unassisted’ in the context of this study since they are unassisted in traversing the distances of ocean required to reach our study islands from neighboring land masses. We were not able to evaluate adaptations for water dispersal since these are difficult to assess visually, but may include some of the species categorized as unassisted. While species are known to adopt multiple modes of dispersal, including ones for which they lack adaptations (Higgins et al. 2003, Ozinga et al. 2004), our general assignment of

dispersal mode allows an unbiased categorization of species based on traits strongly related to dispersal potential (Howe and Smallwood 1982, Tamme et al. 2014). Species were also categorized into growth forms based on broad morphological characteristics – trees, shrubs, forbs, and graminoids. Forb-like species with woody bases (e.g. *Aralia nudicaulis*) were categorized as forbs, short trees that are uncommon in canopies higher than 3 m (e.g. *Rhus* spp. and some *Amelanchier* spp.) were categorized as shrubs, and one species of woody vine (*Celastrus orbiculatus*) was categorized as a shrub.

Island properties

We used ArcGIS ver. 10.1 (ESRI 2013) to generate spatial data for each island using basemaps compiled from the Maine Office of GIS website (MOG, accessed Oct. 2012, <www.maine.gov/megis>). Polygons were drawn around the perimeter of each island to calculate island areas in hectares using 2011 orthoimagery obtained by the National Agricultural Imagery Program. Area was log-transformed for the remainder of the analysis. Island maximum elevation was obtained from 30 m resolution digital elevation models and rounded to the nearest meter. We calculated island isolation using several metrics: 1) the closest distance between an island’s perimeter and the mainland coastline, and 2) a landscape measure of isolation (LMI) (Diver 2008), calculated as the percent of land area within buffers of 100, 250, 500, 1000, 1500, 2000, 5000, and 10 000 m from each island perimeter. All isolation metrics were log-transformed for analyses. We subtracted each log-transformed LMI value from the maximum value, allowing larger values to correspond to greater island isolation.

Statistical analysis

All statistical analyses were performed in R 3.1.0 (R Development Core Team). We used ordinary least squares (OLS) regression to determine the relationship between log-transformed island area and species richness – the island species–area relationship (ISAR) (Supplementary material Appendix 3, Fig. A3). The residuals from this regression were used to test the effect of isolation on species richness in order to account for the effect of island area (Lomolino 1982, Diver 2008). We used the Akaike information criterion with correction for small sample size (AIC_c) to find the best isolation metric of our candidate models (Hurvich and Tsai 1989). Model probabilities (AIC_c wt) were calculated using the change in AIC_c between models, and we chose the metric of isolation that had the greatest probability for predicting variation in ISAR residuals (Wagenmakers and Farrell 2004). The resulting metric was regressed against island area and maximum elevation to ensure independence (Supplementary material Appendix 5, Fig. A5). The explanatory power of isolation metrics was also examined against species composition by calculating a non-metric multidimensional scaling

(NMDS) ordination with 999 iterations using the Bray–Curtis dissimilarity index. Isolation metrics were regressed on the ordination surface using permutation tests to assess the association between isolation and species composition. P-values and R^2 values were generated using 999 permutations of each isolation metric as a function of the primary two axes of the multivariate ordination.

To quantify associations between isolation, dispersal mode, functional traits, and growth forms, the isolation metric that had the greatest probability for predicting variation in ISAR residuals was used as the independent variable in OLS regressions of island-mean SLA, $[N_L]$, VH, LDMC, and the richness of growth forms (trees, shrubs, forbs, graminoids) and dispersal modes (animal, wind, or unassisted) on each island. Since the functional traits used in this study are known to be associated due to physiological and evolutionary tradeoffs (Wright et al. 2004), we combined the traits into a principal components analysis (PCA) to reduce redundant trait variation and evaluate the integrated functional phenotype of each species. A correlation matrix was used and traits were standardized by standard deviation. Missing values were replaced with the overall mean of each trait in the data, allowing for species with some but not all trait values to be included in the analysis without adding bias or variation to the data. Species were color-coded in PCA ordination plots based on growth form and species mean isolation to aid with visual interpretation of associations between these characteristics and multivariate trait axes. Species mean isolation was calculated by averaging the isolation value of all islands where the species was found. Isolation values were split into ‘high’ and ‘low’ bins based on the median value.

Correlations between dispersal mode, and functional traits and growth forms were analyzed in two ways. First, we used the non-parametric Wilcoxon rank sum pairwise test to contrast the effect of dispersal mode on SLA, $[N_L]$, VH, and LDMC, corrected for multiple testing by adjusting p-values using the Hochberg method (Hochberg 1988). Second, we used a chi-square test of independence with a Monte-Carlo generated p-value using 2000 replicates to test if growth forms were independent from dispersal adaptations.

Finally, we used a hierarchical Bayesian (HB) framework to test for the effect of island properties and dispersal mode on the primary axes of functional variation on islands. This method allowed us to: 1) simultaneously partition the influence of island (area, isolation, and elevation) and species characteristics (dispersal mode) on trait values; 2) account for random effects at the species and island level; and 3) provide direct statements on the probability and relative effect size of island and species characteristics. We built separate models for the primary two axes of trait variation (PCA1 and PCA2) and assumed the PCA scores for each species (s) were normally distributed across islands (i):

$$PCA\ axis_{s,i} \sim N(\mu_{s,i}, \sigma^2_{trait}).$$

We compared two models for each PCA axis:

$$\text{Island model: } \mu_{s,i} = \alpha + \beta_1 \times \log(\text{area})_i + \beta_2 \times \log(\text{isolation})_i + \beta_3 \times \log(\text{elevation})_i + N(0, \sigma^2_{species}) + N(0, \sigma^2_{island})$$

$$\text{Dispersal model: } \mu_{s,i} = \alpha + \beta_1 \times \log(\text{area})_i + \beta_2 \times \log(\text{isolation})_i + \beta_3 \times \log(\text{elevation})_i + \beta_4 \times \text{animal dispersed}_i + \beta_5 \times \text{wind dispersed}_i + N(0, \sigma^2_{species}) + N(0, \sigma^2_{island})$$

where α is the intercept and β is the slope of the explanatory variables, and $\sigma^2_{species}$ and σ^2_{island} denote random intercept terms accounting for particular species and islands. Continuous variables (area, isolation, elevation) were standardized by subtracting their mean and dividing by twice their standard deviation to make posterior coefficients (β) interpretable as relative effect sizes. Comparing the fitted isolation coefficient (β_2) between the two models allowed us to assess the unique contribution of dispersal mode on the isolation effect.

We parameterized HB models using a Markov chain Monte Carlo (MCMC) method implemented in JAGS (Plummer 2003), using the 'R2jags' package (Su and Yajima 2014). Three parallel MCMC chains were run for 20 000 iterations after a 5000 iteration burn-in and chains were visually inspected to ensure convergence. We assigned non-informative priors for all parameter distributions, including normal priors for fixed effect α and β coefficients (mean = 0, variance = 0.00001). The precision of species and island random effect priors were uniformly distributed between 0 and 100. R code specifying these models is available in Supplementary material Appendix 4.

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.cg7d4>> (Negoita et al. 2015).

Results

Species richness, growth forms, and dispersal modes

The total floristic dataset included 550 vascular plant species, with island richness ranging from 48 to 201 species. Of the 550 species, 334 were forbs, 101 were graminoids, 86 were shrubs, and 29 were trees (Table 2). Furthermore, 105 species exhibited propagule morphology consistent with vertebrate dispersal, that of 127 species consistent with wind dispersal, and 318 species had no apparent long-distance dispersal adaptation (unassisted) (Table 2).

Isolation metric

Of the isolation metrics tested, log-transformed percent land area within 2000 m around the perimeter of each island explained the most variation in species composition and had the best AIC support for explaining ISAR residuals (Table 3). This 2000 m LMI was used as the measure of isolation for the remainder of analyses and we henceforth use 'isolation' to refer to this measure. In addition, log-transformed area and log-transformed maximum elevation

Table 2. Contingency table of dispersal mode and growth form. Chi-square test of independence with a Monte-Carlo generated p-value suggests non-independence between growth forms and dispersal adaptations ($\chi^2(6, n = 550) = 324.86; p < 0.001$).

	Animal	Unassisted	Wind
Forbs	33	200	101
Graminoids	0	101	0
Shrubs	66	15	5
Trees	6	2	21

Table 3. Delta AIC_c (ΔAIC_c) and model probabilities (AIC_c wt) of isolation models for predicting island species-area relationship (ISAR) residuals and the explained variance (R^2) of models fitted to a non-metric multidimensional scaling ordination of species composition.

Isolation models	Species composition R^2	ISAR residuals	
		ΔAIC_c	AIC _c wt
Log (% land 2000 m buffer)	0.547***	—	0.480
Log (% land 1500 m buffer)	0.493**	0.757	0.329
Log (% land 1000 m buffer)	0.274**	3.679	0.076
Log (% land 10000 m buffer)	0.213*	4.192	0.059
Log (mainland distance)	0.126	5.026	0.039
Log (% land 500 m buffer)	0.185	8.073	0.008
Log (% land 5000 m buffer)	0.276*	9.339	0.005
Log (% land 250 m buffer)	0.148	10.880	0.002
Log (% land 100 m buffer)	0.165	11.941	0.001

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

were not significantly associated with the 2000 m isolation measure ($F_{1,28} = 0.45, p > 0.5$; $F_{1,28} = 0.51, p > 0.1$), allowing for the effects of isolation and area or elevation on island trait composition to be studied independently (Supplementary material Appendix 5, Fig. A5).

Functional-dispersal associations

Dispersal mode explained significant differences between the community mean functional trait values of species in our system (Fig. 1). Species with adaptations for animal dispersal had significantly lower SLA than wind-dispersed (mean untransformed difference = 4.63; $p < 0.01$) and unassisted species (mean untransformed difference = 5.57; $p < 0.001$). Species with adaptations for animal dispersal also had significantly higher LDMC than wind-dispersed (mean untransformed difference = 0.096; $p < 0.05$) and unassisted species (mean untransformed difference = 0.113; $p < 0.01$). Unassisted species had significantly higher $[N_L]$ than wind-dispersed (mean untransformed difference = 3.64; $p < 0.05$) and animal-dispersed species (mean untransformed difference = 4.30; $p < 0.01$) as well as significantly lower VH than wind-dispersed (mean untransformed difference = 4.98; $p < 0.0001$) and animal-dispersed species (mean untransformed difference = 2.43; $p < 0.0001$).

Growth forms and dispersal mode were not independent (Table 2). Shrubs were more likely to be animal dispersed (77%), all graminoids had no apparent dispersal mode, and forbs were more likely to be wind dispersed (30%) or lacked an apparent dispersal mode (60%). Trees were more likely to be wind dispersed (72%).

Functional traits and growth forms across the isolation gradient

Island-mean values of the functional traits in this study were significantly associated with island isolation (Fig. 2). SLA and $[N_L]$ increased with island isolation ($F_{1,28} = 12.8, p < 0.01$; $F_{1,28} = 20.62, p < 0.001$, respectively), while LDMC and VH decreased with island isolation ($F_{1,28} = 13.8, p < 0.001$;

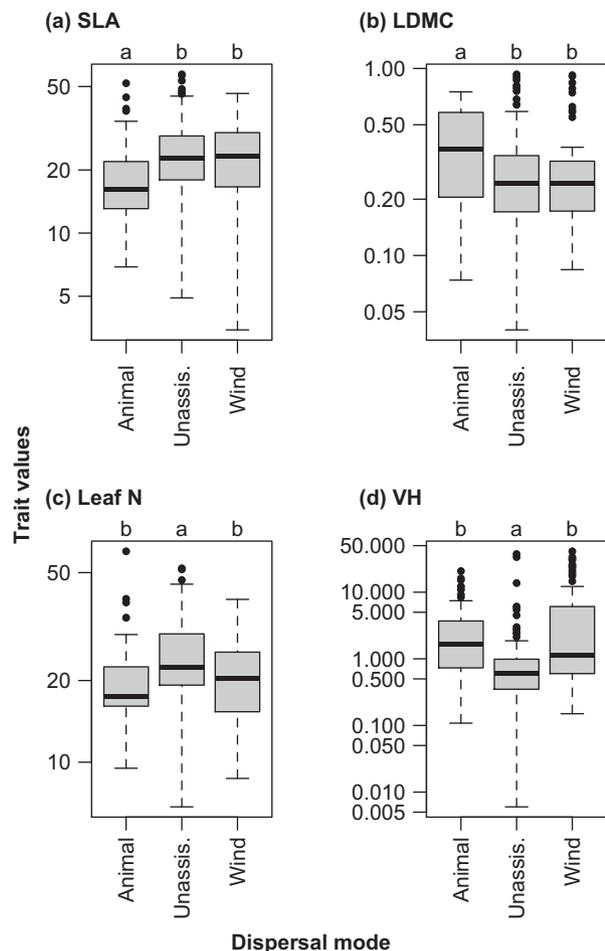


Figure 1. Associations of functional traits and dispersal modes. (a) Specific leaf area ($\text{mm}^2 \text{mg}^{-1}$, SLA); (b) leaf dry matter content (g g^{-1} , LDMC); (c) leaf nitrogen (mg g^{-1} , $[\text{N}_1]$); (d) vegetative height (m, VH). Animal, wind, and unassisted (unassis.) dispersal modes are based on propagule morphology. Axes are log-scaled. Differences between mean trait values ($\alpha = 0.05$).

$F_{1,28} = 21.58$, $p < 0.0001$, respectively) (Fig. 2). The richness of trees and shrubs significantly decreased with isolation ($F_{1,28} = 15.25$, $p < 0.001$ and $F_{1,28} = 13.01$, $p < 0.01$, respectively) (Fig. 3). There was no significant association between the richness of forbs and graminoids and isolation (Fig. 3). The richness of species adapted to wind and animal dispersal also significantly decreased with isolation ($F_{1,28} = 5.59$, $p < 0.05$ and $F_{1,28} = 10.66$, $p < 0.01$) (Fig. 4). The richness of species without an apparent mode of dispersal showed no significant change with isolation (Fig. 4). The primary axes of variation in the PCA of functional traits explained 67% of trait variation (PC1, 42%; PC2, 25%). Visual inspection suggested a grouping between species mean isolation bins and growth forms, especially along PCA axis 1 (Fig. 5).

The fitted HB island model of PC1 yielded a much greater effect of isolation than area and elevation (Fig. 6). Including dispersal mode in this model reduced the relative effect size of isolation slightly (compare gray and black credible intervals in Fig. 6). This suggests that dispersal mode may partly account for the effect of isolation on the primary

axis of functional variation, though the effect is minimal. The fitted HB island model of PC2 yielded no effect of area and isolation, but a small effect of elevation. Dispersal mode overall had the largest effect size in both dispersal models of functional variation, but about a two-fold greater effect in the model of PC1 (Fig. 6).

Discussion

The distribution of plant functional traits and growth forms across Maine islands supports our prediction that spatial isolation is a key driver of functional trait variation in island plant communities. Island area and maximum elevation had only a small effect on functional variation compared with spatial isolation, making a strong case for the role of spatial processes in this system. Despite the species-level association of functional traits with dispersal mode and the community-level association of dispersal mode with isolation, dispersal mode only accounted for a small proportion of the overall isolation effect on community-level trait variation. This suggests that dispersal processes in this system may extend beyond the role of dispersal mode, or that other unmeasured environmental covariates are also important.

Immigrant selection may be an important driver of isolation-driven assembly, but the role of dispersal mode per se is not so clear. Though dispersal mode composition was associated with island isolation, our results were not always consistent with predicted dispersal potential (Tamme et al. 2014). Morphological adaptations such as fleshy or winged fruits are predicted to increase the dispersal capacity of a species (Howe and Smallwood 1982, Willson 1993, Willson and Traveset 2000, Tamme et al. 2014), but the diversity of these species decreased with isolation compared with unassisted species. This may be due to the context-dependence of dispersal vectors, dispersal by nonstandard vectors, and other unmeasured trait associations. For example, bird dispersal of fleshy fruits is contingent on bird behavior and the lack of perching trees on more distant islands may pose a significant dispersal barrier to animal dispersed species in our system (Willson 1991, 1993, Sasal and Morales 2013), consistent with other island studies (Nilsson and Nilsson 1978, Kadmon and Pulliam 1995, Drezner et al. 2001, but see Burns 2005). Water may be an important but unaccounted vector for the dispersal of unassisted species, especially given the high diversity of these species around island shorelines (Mittelhauser and Negoita unpubl.). Some amount of error should also be attributed to nonstandard dispersal vectors, i.e. some of these species may disperse using vectors other than those for which their morphology suggests they are adapted (Westoby et al. 1996, Higgins et al. 2003, Ozinga et al. 2004). For example, the forb genus *Bidens* spp. was often found growing on the shoreline as if dispersed by water even though these species have barbs that aid with dispersal by clinging to fur or feathers (Mittelhauser unpubl.). The complexity of dispersal potential may not always be elucidated using a simple categorization of dispersal mode and future work should aim to directly measure dispersal potential and its role in driving functional assembly.

Vegetative height, specific leaf area, leaf dry matter content, and leaf nitrogen are key traits for predicting species

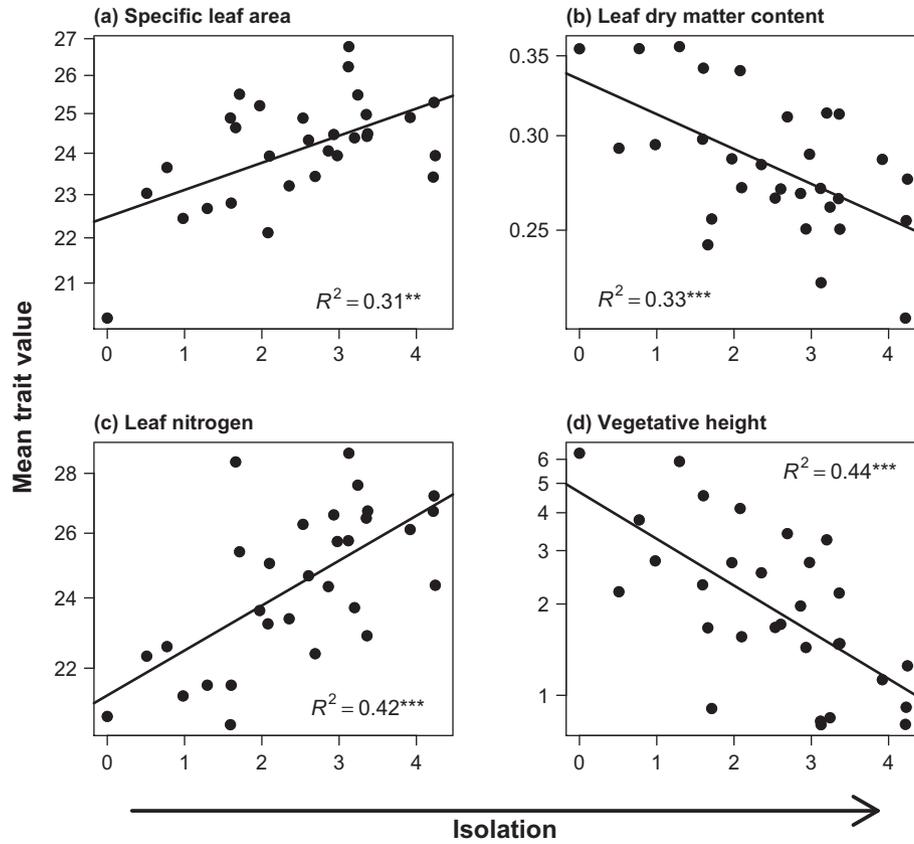


Figure 2. Island mean trait values for (a) specific leaf area ($\text{mm}^2 \text{mg}^{-1}$, SLA), (b) leaf dry matter content (g g^{-1} , LDMC), (c) leaf nitrogen (mg g^{-1} , $[\text{N}]_L$), and (d) vegetative height (m, VH) across island isolation. Trait axes are log-scaled. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

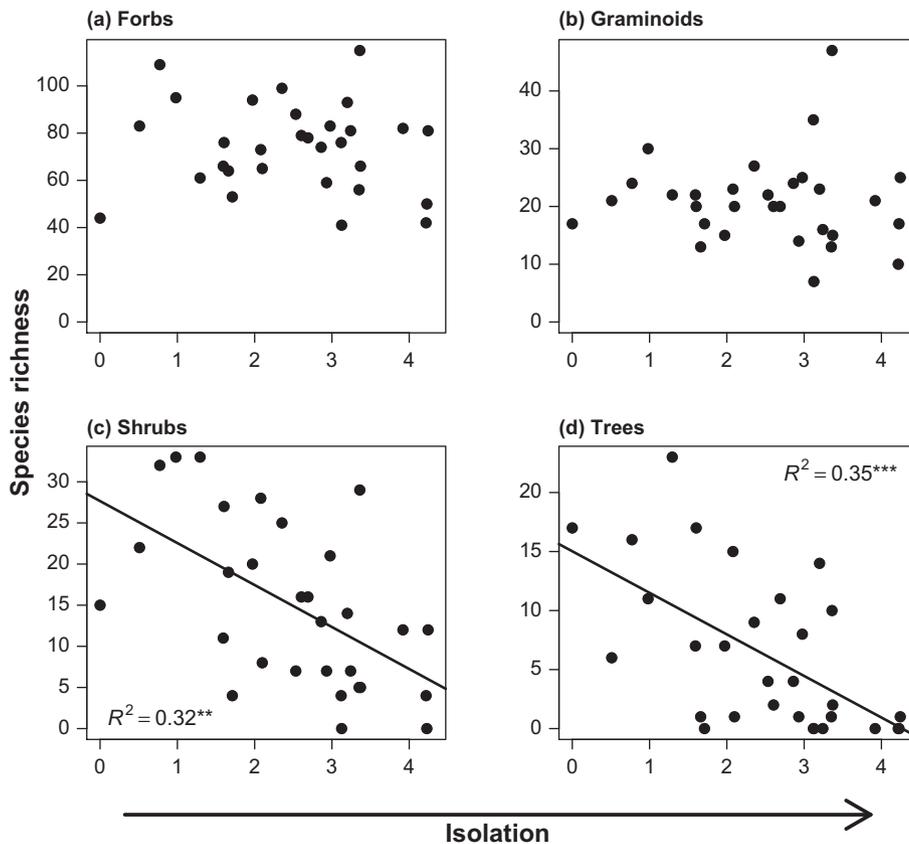


Figure 3. Richness of (a) forbs, (b) graminoids, (c) shrubs, and (d) trees across island isolation. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

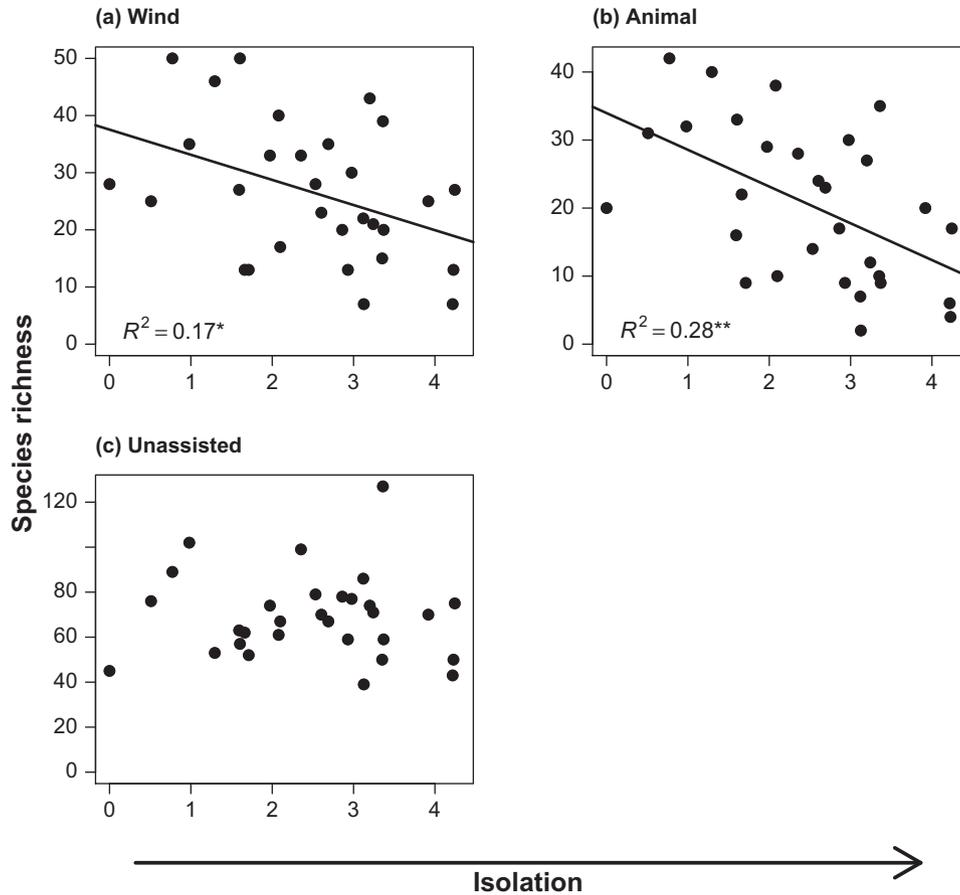


Figure 4. Richness of species adapted for (a) wind dispersal, (b) animal dispersal, or (c) no apparent adaptation for dispersal (unassisted) across island isolation. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

effects on ecosystem and community properties (Gaudet and Keddy 1988, Wardle et al. 1998, Weiher et al. 1999, Lavorel and Garnier 2002, Reich et al. 2003, Díaz et al. 2004, Wright et al. 2004, Poorter et al. 2009, Reich 2014).

For example, the taller species on less isolated islands could affect the light environment and competitive interactions, driving local species distribution patterns (Givnish 1982, Gaudet and Keddy 1988). Higher leaf nitrogen and

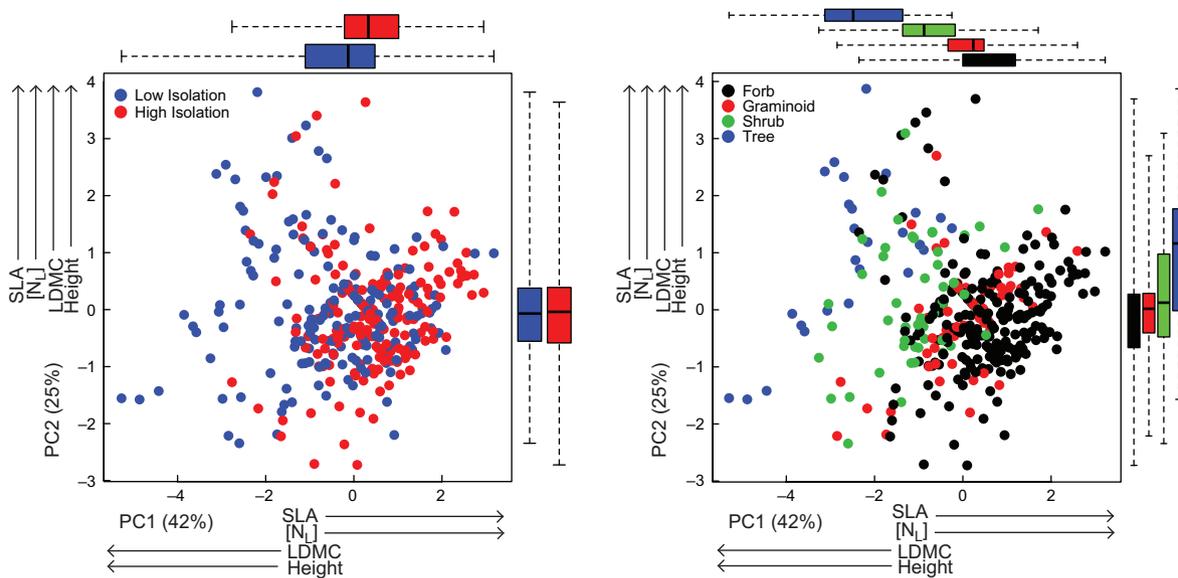


Figure 5. Principal components analysis of functional trait variation across the 402 species found on 30 islands for which functional trait data were available. Axis labels indicate significant eigenvector scores for the first two principal components. Island isolation refers to the mean isolation of islands where a species occurs. Distinction between 'high' and 'low' isolation bins is based on median isolation value.

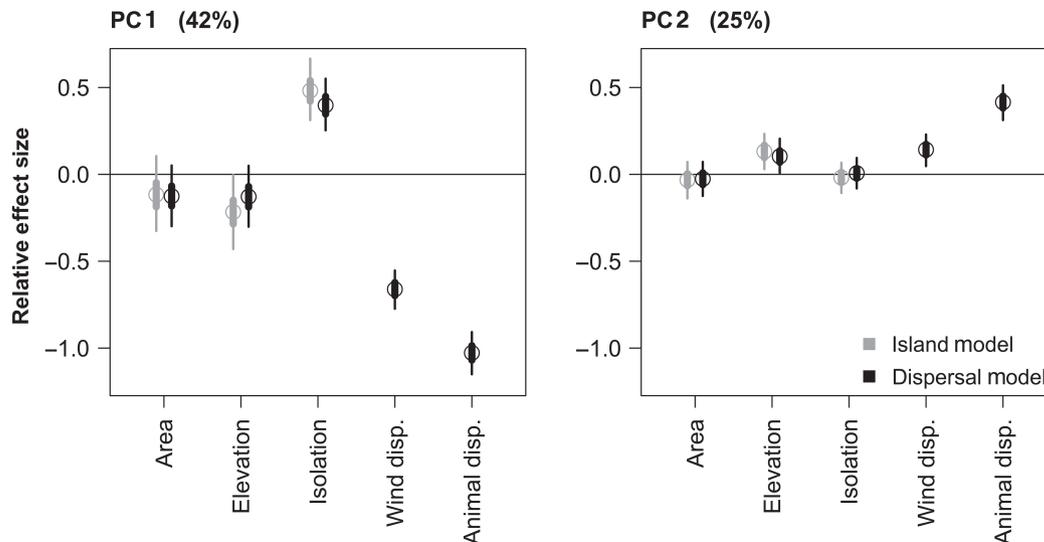


Figure 6. Relative effect size (posterior distributions) of island and dispersal mode parameters on the primary axes (PC1 and PC2) of functional variation. Thin lines indicate 95% credible intervals (CI), thick lines indicate 50% CI, and circles mark the mean.

specific leaf area, and lower leaf dry matter content on more isolated islands could indicate greater net primary productivity and more rapid leaf litter turnover on these islands, leading to higher rates of nitrogen mineralization, positive feedbacks on productivity, and other effects on ecosystem-level properties (Nilsson et al. 1999, Chapin 2003, Chapin et al. 2011). Growth form composition is also a useful way to gauge potential ecosystem-level processes due to the functional traits associated with particular functional groups such as woody species, forbs, and graminoids (Leishman and Westoby 1992, Díaz and Cabido 1997, Shachak et al. 2008). For example, differences in the composition and richness of trees has been shown to correlate with understory species richness on islands (Diver 2010). Additionally, the larger biomass of growth forms such as trees can often exert a disproportionate influence on ecosystem-level processes (Grime 1998). Our results provide compelling evidence on the role of spatial isolation as a driver of functional trait variation, though future studies should aim to directly test how these trait distributions affect the ecosystem properties of isolated communities. Finally, it is important to acknowledge a limitation of using species-mean trait data from a global database. Plasticity or local adaptation could yield convergence in trait variation within species and reduce the isolation signal we found. Future work should quantify intraspecific trait variation across gradients of isolation to test the importance of scale-dependence in trait variation in island plant communities.

Environmental and anthropogenic drivers of functional variation

Environmental features associated with continental archipelagoes could affect the functional variation among our study islands (Díaz et al. 1998, Cornwell et al. 2006). For example, salt spray, wave action, and wind are key

environmental features of these exposed coastal communities (Oosting 1945, Boyce 1954), and may be important in structuring some aspects of the island shoreline communities. However, we do not believe these factors had a strong confounding effect on island-mean trait values or the relative richness of growth forms in our system. Maximum island elevation and island area are important determinants of island exposure to salt spray, wave action, and wind. However, both area and maximum elevation were unassociated with isolation and had a consistently low relative effect on the primary axis of functional trait variation compared with isolation. Moreover, several genera of common trees and shrubs in this archipelago (*Picea* spp., *Morella* spp., and *Rubus* spp.) were not recorded on the most isolated islands yet can be found near the intertidal zone of salt spray on islands where they do occur (Negoita unpubl.). Nonetheless, we cannot completely disentangle other unmeasured environmental covariates associated with isolation. Some of the patterns in functional trait variation on our study islands may also be attributed to the environmental conditions generated by the dominant woody species (Anderson et al. 1969, Hobbie 1992, Grime 1998, Shachak et al. 2008), suggesting that functional variation may be an indirect effect of isolation on the trees occupying these islands.

The human-use history of these islands is an important factor to consider in the Gulf of Maine (Conkling 2011), and some of the variation in functional trait and growth form composition may be attributable to the unique anthropogenic history of each island. The sequence of clear cutting and sheep grazing, followed by abandonment, is common to most Maine islands (McLane 1989, Conkling 2011), as it is for much of New England (Foster 1992), and has likely had a strong influence on the successional state of island communities (Kadmon and Pulliam 1995, Drezner et al. 2001, Löfgren and Jerling 2002). However, it is unclear what legacy effects these patterns in functional assembly may have on the future of these island ecosystems.

Conclusions

Our study suggests that spatial isolation can be a key driver of functional variation in island plant communities. While we did not find strong support for the role of dispersal mode in our system, the close association of functional traits and dispersal mode suggests a viable mechanism by which immigrant selection may shape the functional assembly of isolated communities. Our study provides a baseline of functional trait variation in the context of island biogeography – an important step for integrating functional ecology and biogeography (Ricklefs and Jenkins 2011, Violle et al. 2014, Whittaker et al. 2014), incorporating a species-specific approach to island biogeography (Lomolino 2000), and studying the role of immigrant selection in plants (Lomolino 1984, Lomolino et al. 2006, Gaston et al. 2008). This is one of the few studies to quantify the ecogeographical patterns of functional trait variation across islands (but see Whittaker et al. 2014), and the first, of our knowledge, to quantify these traits across a gradient of island isolation. Additional insights will come by studying these patterns in other archipelagoes (Lomolino et al. 2006), incorporating species abundances (Grime 1998), and measuring ecosystem-level properties of islands or other isolated communities (Wardle 2002). Future work should explicitly incorporate the associations between functional traits and dispersal ability into experiments that directly test the role of dispersal on ecosystem function (Zobel et al. 2006).

Acknowledgements – We thank Andrew Siefert, Mark Lesser, Vigdis Vandvik, and Benjamin Blonder for insightful comments on earlier drafts of this manuscript. We are also grateful for field assistance with island surveys from Jill Weber, Sally Rooney, Matthew Dickinson, Jordan Chalfant, and the Maine Natural History Observatory, Gouldsboro, Maine. This material is based upon work supported by the National Science Foundation Graduate Research Fellowship under Grant no. (DRG 0750965). The study has been supported by the TRY initiative on plant traits (<www.try-db.org>). The TRY initiative and database is hosted, developed and maintained by J. Kattge and G. Bönnisch (Max-Planck-Inst. for Biogeochemistry, Jena, Germany). TRY is/has been supported by DIVERSITAS, IGBP, the Global Land Project, the UK Natural Environment Research Council (NERC) through its program QUEST (Quantifying and Understanding the Earth System), the French Foundation for Biodiversity Research (FRB), and GIS ‘Climat, Environnement et Société’ France.

References

- Ackerly, D. D. and Cornwell, W. K. 2007. A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. – *Ecol. Lett.* 10: 135–145.
- Anderson, R. et al. 1969. Herbaceous response to canopy cover, light intensity, and throughfall precipitation in coniferous forests. – *Ecology* 50: 255–263.
- Aparicio, A. et al. 2008. Dispersal potentials determine responses of woody plant species richness to environmental factors in fragmented Mediterranean landscapes. – *For. Ecol. Manage.* 255: 2894–2906.
- Barnhardt, W. A. et al. 1995. Late Quaternary relative sea-level change in the western Gulf of Maine: evidence for a migrating glacial forebulge. – *Geology* 23: 317–320.
- Boedeltje, G. et al. 2008. The trade-off between vegetative and generative reproduction among angiosperms influences regional hydrochorous propagule pressure. – *Global Ecol. Biogeogr.* 17: 50–58.
- Boyce, S. G. 1954. The salt spray community. – *Ecol. Monogr.* 24: 29–67.
- Burns, K. 2005. A multi-scale test for dispersal filters in an island plant community. – *Ecography* 28: 552–560.
- Chapin, F. S. 2003. Effects of plant traits on ecosystem and regional processes: a conceptual framework for predicting the consequences of global change. – *Ann. Bot.* 91: 455–463.
- Chapin, F. S. et al. 2011. Principles of terrestrial ecosystem ecology. – Springer.
- Conkling, P. 2011. Islands in time: a natural and cultural history of islands in the gulf of maine. – Island Inst.
- Cornwell, W. K. et al. 2006. A trait-based test for habitat filtering: convex hull volume. – *Ecology* 87: 1465–1471.
- Cornwell, W. K. et al. 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. – *Ecol. Lett.* 11: 1065–1071.
- Díaz, S. and Cabido, M. 1997. Plant functional types and ecosystem function in relation to global change. – *J. Veg. Sci.* 463–474.
- Díaz, S. and Cabido, M. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. – *Trends Ecol. Evol.* 16: 646–655.
- Díaz, S. et al. 1998. Plant functional traits and environmental filters at a regional scale. – *J. Veg. Sci.* 9: 113–122.
- Díaz, S. et al. 2004. The plant traits that drive ecosystems: evidence from three continents. – *J. Veg. Sci.* 15: 295.
- Diver, K. C. 2008. Not as the crow flies: assessing effective isolation for island biogeographical analysis. – *J. Biogeogr.* 35: 1040–1048.
- Diver, K. C. 2010. Beyond area and isolation: forest dynamics and change in plant species richness patterns on islands. – *Ann. Assoc. Am. Geogr.* 100: 1110–1127.
- Drezner, T. D. et al. 2001. Plant distribution and dispersal mechanisms at the Hassayampa River Preserve, Arizona, USA. – *Global Ecol. Biogeogr.* 10: 205–217.
- ESRI 2013. ArcGIS Desktop 10.1 – Environmental Systems Research Inst.
- Flinn, K. and Vellend, M. 2005. Recovery of forest plant communities in post-agricultural landscapes. – *Front. Ecol. Environ.* 3: 243–250.
- Foster, B. L. et al. 2007. Restoration of prairie community structure and ecosystem function in an abandoned hayfield: a sowing experiment. – *Restor. Ecol.* 15: 652–661.
- Foster, D. 1992. Land-use history (1730–1990) and vegetation dynamics in central New England, USA. – *J. Ecol.* 80: 753–771.
- Fukami, T. 2010. Community assembly dynamics in space. – In: Verhoef, H. A. and Morin, P. J. (eds), *Community ecology: processes, models, and applications*. Oxford Univ. Press, pp. 45–54.
- Gallagher, R. V. and Leishman, M. R. 2012. A global analysis of trait variation and evolution in climbing plants. – *J. Biogeogr.* 39: 1757–1771.
- Gaston, K. J. et al. 2008. Ecogeographical rules: elements of a synthesis. – *J. Biogeogr.* 35: 483–500.
- Gaudet, C. and Keddy, P. 1988. A comparative approach to predicting competitive ability from plant traits. – *Nature* 334: 242–243.
- Givnish, T. 1982. On the adaptive significance of leaf height in forest herbs. – *Am. Nat.* 120: 353–381.
- Gonzalez, A. et al. 2009. Biodiversity as spatial insurance: the effects of habitat fragmentation and dispersal on ecosystem functioning. – In: Naeem, S. et al. (eds), *Biodiversity, ecosystem functioning, and human wellbeing: an ecological and economic perspective*. Oxford Univ. Press, pp. 134–146.

- Grime, J. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. – *J. Ecol.* 86: 902–910.
- Haines, A. 2011. *Flora Novae Angliae: a manual for the identification of native and naturalized higher vascular plants of New England.* – Yale Univ. Press.
- Higgins, S. et al. 2003. Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? – *Ecology* 84: 1945–1956.
- Hobbie, S. E. 1992. Effects of plant species on nutrient cycling. – *Trends Ecol. Evol.* 7: 336–339.
- Hochberg, Y. 1988. A sharper bonferroni procedure for multiple tests of significance. – *Biometrika* 75: 800–802.
- Hooper, D. et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. – *Ecol. Monogr.* 75: 3–35.
- Howe, H. E. and Smallwood, J. 1982. Ecology of seed dispersal. – *Annu. Rev. Ecol. Syst.* 13: 201–228.
- Hughes, L. et al. 1994. Predicting dispersal spectra: a minimal set of hypotheses based on plant attributes. – *J. Ecol.* 82: 933–950.
- Hurvich, C. M. and Tsai, C.-L. 1989. Regression and time series model selection in small samples. – *Biometrika* 76: 297–307.
- Kadmon, R. and Pulliam, H. 1993. Island biogeography: effect of geographical isolation on species composition. – *Ecology* 74: 977–981.
- Kadmon, R. and Pulliam, H. 1995. Effects of isolation, logging and dispersal on woody-species richness of islands. – *Plant Ecol.* 116: 63–68.
- Kattge, J. et al. 2011. TRY – a global database of plant traits. – *Global Change Biol.* 17: 2905–2935.
- Lavorel, S. and Garnier, E. 2002. Predicting changes in composition and ecosystem functioning from plant traits: revisiting the Holy Grail. – *Funct. Ecol.* 16: 545–556.
- Leishman, M. R. and Westoby, M. 1992. Classifying plants into groups on the basis of associations of individual traits – evidence from Australian semi-arid woodlands. – *J. Ecol.* 80: 417–424.
- Löfgren, A. and Jerling, L. 2002. Species richness, extinction and immigration rates of vascular plants on islands in the Stockholm archipelago, Sweden, during a century of ceasing management. – *Folia Geobot.* 37: 297–308.
- Lomolino, M. V. 1982. Species-area and species-distance relationships of terrestrial mammals in the thousand island region. – *Oecologia* 54: 72–75.
- Lomolino, M. V. 1984. Immigrant selection, predation, and the distributions of *Microtus pennsylvanicus* and *Blarina brevicauda* on islands. – *Am. Nat.* 123: 468–483.
- Lomolino, M. V. 2000. A call for a new paradigm of island biogeography. – *Global Ecol. Biogeogr.* 9: 1–6.
- Lomolino, M. V. et al. 2006. The island rule and a research agenda for studying ecogeographical patterns. – *J. Biogeogr.* 33: 1503–1510.
- Loreau, M. and Mouquet, N. 1999. Immigration and the maintenance of local species diversity. – *Am. Nat.* 154: 427–440.
- Marteinsdottir, B. and Eriksson, O. 2013. Trait-based filtering from the regional species pool into local grassland communities. – *J. Plant Ecol.* 7: 347–355.
- McLane, C. B. 1989. *Islands of the mid-Maine coast, vol. 2: Mount Desert to Machias Bay.* – The Kennebec River Press.
- Mouquet, N. and Loreau, M. 2003. Community patterns in source-sink metacommunities. – *Am. Nat.* 162: 544–557.
- Muller-Landau, H. C. 2010. The tolerance-fecundity trade-off and the maintenance of diversity in seed size. – *Proc. Natl Acad. Sci. USA* 107: 4242–4247.
- Negoita, L. et al. 2015. Data from: Isolation-driven functional assembly of plant communities on islands. – Dryad Digital Repository, <<http://dx.doi.org/10.5061/dryad.cg7d4>>.
- Nilsson, M. et al. 1999. Effects of plant litter species composition and diversity on the boreal forest plant-soil system. – *Oikos* 86: 16–26.
- Nilsson, S. and Nilsson, I. 1978. Species richness and dispersal of vascular plants to islands in Lake Möckeln, southern Sweden. – *Ecology* 59: 473–480.
- Nowacki, G. J. and Abrams, M. D. 2015. Is climate an important driver of post-European vegetation change in the eastern United States? – *Global Change Biol.* 21: 314–334.
- Oosting, H. J. 1945. Tolerance to salt spary of plants of coastal dunes. – *Ecology* 26: 85–89.
- Ozinga, W. et al. 2004. Dispersal potential in plant communities depends on environmental conditions. – *J. Ecol.* 92: 767–777.
- Ozinga, W. et al. 2005. Assessing the relative importance of dispersal in plant communities using an ecoinformatics approach. – *Folia Geobot.* 40: 53–67.
- Pärtel, M. and Zobel, M. 2007. Dispersal limitation may result in the unimodal productivity–diversity relationship: a new explanation for a general pattern. – *J. Ecol.* 95: 90–94.
- Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. – DSC Working Papers.
- Poorter, H. et al. 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. – *New Phytol.* 182: 565–588.
- Reich, P. B. 2014. The world-wide “fast-slow” plant economics spectrum: a traits manifesto – *J. Ecol.* 102: 275–301.
- Reich, P. B. et al. 2003. The evolution of plant functional variation: traits, spectra, and strategies. – *Int. J. Plant Sci.* 164: S143–S164.
- Ricklefs, R. E. and Jenkins, D. G. 2011. Biogeography and ecology: towards the integration of two disciplines. – *Phil. Trans. R. Soc. B* 366: 2438–2448.
- Sasal, Y. and Morales, J. M. 2013. Linking frugivore behavior to plant population dynamics. – *Oikos* 122: 95–103.
- Schleicher, A. et al. 2011. Dispersal traits determine plant response to habitat connectivity in an urban landscape. – *Landscape Ecol.* 26: 529–540.
- Shachak, M. et al. 2008. Woody species as landscape modulators and their effect on biodiversity patterns. – *Bioscience* 58: 209–221.
- Stein, C. et al. 2008. Dispersal and seed limitation affect diversity and productivity of montane grasslands. – *Oikos* 117: 1469–1478.
- Su, Y.-S. and Yajima, M. 2014. R2jags: a package for running jags from R. – R package ver. 0.04-03, <<http://CRAN.R-project.org/package=R2jags>>.
- Svenning, J.-C. and Sandel, B. 2013. Disequilibrium vegetation dynamics under future climate change. – *Am. J. Bot.* 100: 1266–1286.
- Tamme, R. et al. 2014. Predicting species’ maximum dispersal distances from simple plant traits. – *Ecology* 95: 505–513.
- Tilman, D. 1990. Constraints and tradeoffs: toward a predictive theory of competition and succession. – *Oikos* 58: 3–15.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. – *Ecology* 75: 2–16.
- Turnbull, L. et al. 1999. Seed mass and the competition/colonization trade-off: a sowing experiment. – *J. Ecol.* 87: 899–912.
- Violle, C. et al. 2014. The emergence and promise of functional biogeography. – *Proc. Natl Acad. Sci. USA* 111: 13690–13696.
- Voort, J. N.-V. der et al. 1979. Immigration rates of plant species in three Dutch polders. – *J. Biogeogr.* 6: 301–308.
- Wagenmakers, E.-J. and Farrell, S. 2004. AIC model selection using Akaike weights. – *Psychon. Bull. Rev.* 11: 192–196.
- Wardle, D. 2002. Islands as model systems for understanding how species affect ecosystem properties. – *J. Biogeogr.* 29: 583–591.
- Wardle, D. et al. 1998. Can comparative approaches based on plant ecophysiological traits predict the nature of biotic interactions

- and individual plant species effects in ecosystems? – *J. Ecol.* 86: 405–420.
- Weihner, E. et al. 1999. Challenging theophrastus: a common core list of plant traits for functional ecology. – *J. Veg. Sci.* 10: 609–620.
- Westoby, M. et al. 1996. Comparative ecology of seed size and dispersal. – *Phil. Trans. R. Soc. B* 351: 1309–1318.
- Whittaker, R. J. et al. 1997. The rebuilding of an isolated rain forest assemblage: how disharmonic is the flora of Krakatau? – *Biodivers. Conserv.* 6: 1671–1696.
- Whittaker, R. J. et al. 2014. Functional biogeography of oceanic islands and the scaling of functional diversity in the Azores. – *Proc. Natl Acad. Sci. USA* 111: 13709–13714.
- Willson, M. 1991. Dispersal of seeds by frugivorous animals in temperate forests. – *Rev. Chil. Hist. Nat.* 64: 537–554.
- Willson, M. 1993. Dispersal mode, seed shadows, and colonization patterns. – *Vegetatio* 107: 260–280.
- Willson, M. and Traveset, A. 2000. The ecology of seed dispersal. – In: Fenner, M. (ed.), *Seeds: the ecology of regeneration in plant communities*. CAB International, pp. 85–110.
- Wright, I. J. et al. 2004. The worldwide leaf economics spectrum. – *Nature* 428: 821–827.
- Zobel, M. et al. 2006. Biodiversity and ecosystem functioning: it is time for dispersal experiments. – *J. Veg. Sci.* 17: 543–547.

Supplementary material (Appendix ECOG-01551 at <www.ecogeography.org/appendix/ecog-01551>). Appendix 1–5.