Evidence for niche-based community assembly in a deciduous forest understory plant community

Jason A. Sircely,[1] William S. F. Schuster,[2] and Shahid Naeem[1]

[1]Department of Ecology, Evolution and Environmental Biology, Columbia University, 10th Floor, Schermerhorn Extension, MC 5557, 1200 Amsterdam Avenue, New York, New York 10027

[2]Black Rock Forest, 129 Continental Road, Cornwall, New York 12518

Abstract

Niche theory and neutral theory provide alternative perspectives on the drivers of species distributions and community composition. Dispersal assembly has modest influence on plant community composition, and its importance is greater at larger spatial scales. Niche theory predicts that environmental variation is associated with niche-based assembly, which explains more variance in composition than dispersal. However, the relative strength of dispersal and niche-based processes on fine-scale assembly has not been assessed in plant communities, partially when distance and environmental variation are confounded. The study site at Black Rock Forest, Cornwall, New York is an oak-dominated forest supporting 120 vascular understory plant species. To infer the importance of dispersal versus niche-based assembly, we examined fine- to meso-scale (50-400 m) relationships between composition, distance, and environmental conditions in the understory plant community. Distance showed no detectable association with composition, providing no evidence for dispersal assembly. In contrast, environmental conditions were consistently correlated with composition, supporting niche-based community assembly.

Introduction

• Niche theory and neutral theory are the pre-eminent theoretical foundations for explaining patterns of community composition and the distribution and abundance of species in nature.

• Limits to species dispersal distance result in dispersal assembly of plant communities. Dispersal assembly, as predicted by neutral theory (Hubbell 1979; Hubbell 2001), has modest influence on plant community composition, especially at large- to meso- spatial scales (Terborgh *et al.* 1996; Pitman *et al.* 2001; Pitman *et al.* 2002; Tuomisto *et al.* 2003).

• Niche theory predicts that environmental variation is associated with niche-based assembly processes such as habitat specialization and interspecific competition (Colwell & Fuentes 1975; Liebold, 1995). Niche-based assembly explains more variance in plant community composition than dispersal assembly (Terborgh *et al.* 1996; Pitman *et al.* 2001; Pitman *et al.* 2002; Tuomisto *et al.* 2003; Gilbert & Lechowicz 2004; Karst *et al.* 2005).

• While the importance of dispersal assembly increases with the spatial scale of analysis, dispersal limitation should influence composition at all scales for which dispersal limitation is probable; even fine-scale (< 150 m) composition.

• The relative strength of dispersal and niche-based processes on fine- and meso-scale assembly has not been sufficiently investigated in plant communities, partially due to correlation between distance and environmental variation (Gilbert & Lechowicz 2004; Karst *et al.* 2005).

• Observational study of the relationships between community composition, spatial distance, and environmental conditions should provide a window into the respective importance of dispersal assembly and niche-based assembly at fine- to meso-scales.

Study Objective:

• To test whether temperate deciduous forest understory plant community composition is influenced more strongly by niche-based assembly (as measured by environmental differences among sites) or dispersal assembly (as measured by differences in distance among sites).

Methods

• *Study site:* The study was conducted on the north slope of Black Rock Mountain in Black Rock Forest, Cornwall, Orange County, New York. The site supports mature forest dominated by red (*Quercus rubra*) and chestnut oak (*Q. prinus*), with an elevation gradient from 140 to 200 m that is associated with declining soil moisture, soil depth and seep area, and with increasing exposure, temperature fluctuation, and soil rock content. Virtually all of the nearly 120 vascular plant species present are native to the region.

• *Sampling protocol:* Sixteen 25 x 25 m plots 50 m apart in a systematic grid were sampled in July and August 2005. The entire study area is 300 x 450 m vertically and horizontally, respectively. Cover of understory vegetation < 1.5 m in height was measured by releve, and each species was assigned the median value of its category.

• *Environmental distance:* A Sorensen (or Bray-Curtis) environmental distance metric was calculated from elevation and seep area (area with permanent surface ground water seepage), the only two variables that were significant predictors ($p < 0.05$) of multivariate community composition in a multiple regression analysis (Systat Software, Richmond, CA). To minimize confounding correlation between environmental differences and spatial distance, 5 to 6 plots were placed into each of three elevation classes (140-160 m; 165-175 m; and 180-200 m). Although environmental conditions vary greatly across elevation (i.e. vertically), plot scores in a principal components analysis (not presented) on several environmental variables did not correlate significantly with spatial distance within elevation (horizontally).

• *Understory plant community composition:* Plant community composition was quantified in the form of two metrics – Sorensen distance, and ordination via non-metric multidimensional scaling (MDS) based on a Sorensen distance matrix (PCOrd, MJM Software, Gleneden Beach, OR).

• *Statistical analysis:* We used Mantel tests (PCOrd, MJM Software, Gleneden Beach, OR) based on 1000 iterations of Monte Carlo randomization to investigate the significance of correlations between understory plant community composition, spatial distance, and Sorensen environmental distance.

Results

MDS Ordination:

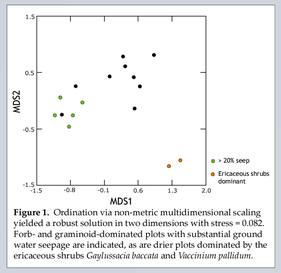

Figure 1. Ordination via non-metric multidimensional scaling yielded a robust solution in two dimensions with stress = 0.082. Forb- and graminoid-dominated plots with substantial ground water seepage are indicated, as are drier plots dominated by the ericaceous shrubs *Gaylussacia baccata* and *Vaccinium pallidum*.

Table 1. Summary statistics for 1000 iterations of Mantel Monte Carlo randomization tests. Environmental and vegetation distances are Sorensen distance. MDS differences are differences along MDS axis 1 or MDS axis 2 (Figure 1).

Matrix 1	Matrix 2 distance	Mantel r	Observed Z	Average Z (Var(Z))	P
Within and across elevation					
MDS1 difference	**Spatial**	0.293	44477.70	39856.80 ($2.31x10^6$)	**0.009**
MDS1 difference	**Environmental**	0.503	27.46	22.79 (0.96)	**0.001**
MDS2 difference	**Spatial**	0.054	27259.30	26639.30 ($1.84x10^6$)	0.303
MDS2 difference	**Environmental**	0.052	15.55	15.23 (0.74)	0.328
Vegetation distance	**Spatial**	0.214	27927.10	27114.30 ($1.43x10^6$)	**0.041**
Vegetation distance	**Environmental**	0.371	16.31	15.48 (0.06)	**0.003**
Within elevation					
MDS1 difference	**Spatial**	0.219	9733.48	8960.99 ($3.57x10^5$)	0.113
MDS1 difference	**Environmental**	0.339	4.52	3.95 (0.08)	**0.030**
MDS2 difference	**Spatial**	0.048	7528.44	7368.07 ($3.05x10^5$)	0.387
MDS2 difference	**Environmental**	-0.101	3.06	3.23 (0.08)	0.286
Vegetation distance	**Spatial**	0.058	7168.63	7105.07 ($3.73x10^5$)	0.375
Vegetation distance	**Environmental**	0.017	3.13	3.11 (0.01)	0.468

Within and across elevation (all plot comparisons):

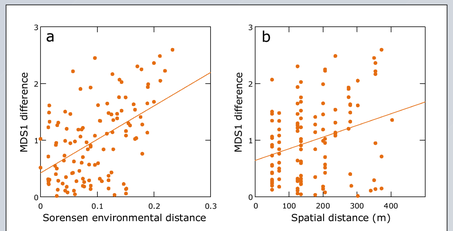

Figure 2. Difference in community composition, gauged as difference along MDS axis 1 (MDS1 difference) was significantly correlated with both **a)** environmental distance (based on elevation and percent seep), and **b)** spatial distance, yet environmental distance remains correlated with spatial distance, precluding a clear interpretation. Mantel test statistics are reported in Table 1.

• Correlation between environmental conditions and distance precludes a clear interpretation of the significant correlations Sorensen environmental distance (Figure 2a; Table 1) and spatial distance (Figure 2b; Table 1) exhibited with composition differences (MDS1 difference).

• The same concern applies to the significant correlations between Sorensen vegetation distance and both environmental and spatial distances (Table 1).

• No correlation was observed for MDS2 difference with either distance metric (Table 1), suggesting that MDS2 may be capturing stochastic influences on community composition.

• To effectively test for dispersal and niche-based assembly, it is necessary to reduce the degree of correlation between environment and spatial distance.

Within elevation (reduced environmental variation):

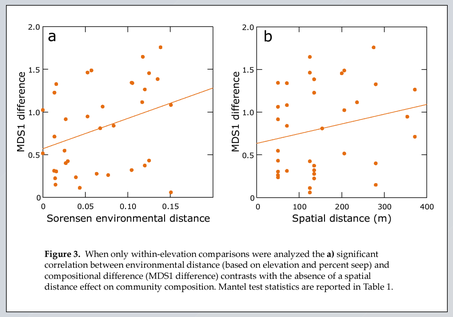

Figure 3. When only within-elevation comparisons were analyzed the **a)** significant correlation between environmental distance (based on elevation and percent seep) and compositional difference (MDS1 difference) contrasts with the absence of a spatial distance effect on community composition. Mantel test statistics are reported in Table 1.

• MDS1 yielded the only observed environmental influence on composition (MDS1 difference) within elevation (Figure 3a; Table 1), while MDS2 and Sorensen vegetation distance did not support either assembly mechanism (Table 1).

•The significant correlation between compositional and environmental differences supports the operation of niche-related assembly processes, even more strikingly on account of the minimal degree of environmental variation among plots at similar elevations.

• Dispersal assembly exerted no detectable influence on composition, because spatial distance did not correlate with compositional difference when controlling for environmental variation (Figure 3b; Table 1).

Discussion

• To adequately gauge the respective roles of dispersal and niche-based assembly, it was necessary to hold environmental conditions as constant as possible over various spatial distances.

Dispersal assembly

•There was no evidence that variation in community composition could be attributed to spatial distance when environmental variables were held to a minimum of variability. Dispersal assembly therefore has no detectable influence on understory community composition at the fine- to meso- spatial scales of the study.

Niche-based assembly

• The absence of support for dispersal assembly contrasts with the correlation between community composition and environmental conditions – even the minimal variation that can be found among plots at similar elevation. The relationship also suggests that the correlations among composition, environmental differences and spatial distance for all plot comparisons within and across elevation (Figure 2) may be largely attributable to niche-based processes. Environmental influence on composition is not surprising given the substantial Pearson correlations for MDS1 with seep area (r = -0.644) and elevation (r = 0.773).

Spatial scale

• While this study provides evidence for a significant role of niche-processes in community assembly, some caution is in order, as the spatial scale of inquiry may be too small for dispersal limitation to occur. However, at least 6 genera present are myrmecochorous, gravity-dispersing, or reproduce vegetatively (all 16 *Carex* species are probably in one of these groups). It is not likely that the spatial scale is trivial for such species.

• These findings are in agreement with those of Gilbert and Lechowicz (2004) and Karst *et al.* (2003), yet the current study combines evidence for niche-based assembly at fine spatial scales with a lower likelihood that the conclusions are affected by confounding spatial distance with environmental variation. Neutral explanations of community composition appear to hold little sway at this scale, while environmental variation is clearly coupled with community composition, as niche oriented explanations posit.

Literature cited

Colwell, R. K. & Fuentes, E. R. (1975). Experimental studies of the niche. *Annual Review of Ecology and Systematics*, 6, 281-310.

Gilbert, B., & Lechowicz, M.J. (2004). Neutrality, niches, and dispersal in a temperate forest understory. *Proceedings of the National Academy of Sciences*, 101, 7651-7656.

Hubbell, S.P. (1979). Tree dispersion, abundance and diversity in a tropical dry forest. *Science*, 203, 1299-1309.

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

Karst, J, Gilbert, B., & Lechowicz, M.J. (2005). Fern community assembly: the roles of chance and the environment at local and intermediate scales. *Ecology*, 86, 2473-2486.

Liebold, M. A. (1995). The niche concept revisited: mechanistic models and community context. *Ecology* 76, 1371-1382.

Pitman, N.C.A, Terborgh, J.W, Silman, M.R., Nunez V., P., Neill, D.A., Ceron, C.A., Palacios, W.A., & Aulestia, M. (2001). Dominance and distribution of tree species in upper Amazonian terra firme forests. *Ecology*, 82, 2101-2117.

Pitman, N.C.A, Terborgh, J.W, Silman, M.R., Nunez V., P., Neill, D.A., Ceron, C.A., Palacios, W.A., & Aulestia, M. (2002). A comparison of tree species diversity in two upper Amazonian forests. *Ecology*, 83, 3210–3224.

Terborgh, J. W., Foster, R.B., & Nunez V., P. (1996). Tropical tree communities: a test of the nonequilibrium hypothesis. *Ecology*, 77, 561-567.

Tuomisto, H., Ruokolainen, K., & Yli-Halla, M. (2003). Dispersal, environment, and floristic variation of western Amazonian forests. *Science*, 299, 241-244.

Acknowledgements

The authors would like to thank the Naeem Lab for helpful comments on the study, the Black Rock Forest staff for field assistance, and G. Moore and the Brooklyn Botanic Garden for assistance in identifying plant specimens. J. Sircely is especially grateful to Black Rock Forest for financial assistance.