



Habitat-Dependent Forest Structure and Species Distributions in Two Deciduous Broadleaved Forests

Zhigao Wang[†], Zhongxing Zhang, Renyan Duan and Ganlin Wu

School of Life Science, Anqing Normal University, the Province Key Laboratory of the Biodiversity and Ecological Conservation in Southwest Anhui, Anqing 246133, China

[†]Correspondence author: Zhigao Wang

Nat. Env. & Poll. Tech.
Website: www.neptjournal.com

Received: 03-12-2015
Accepted: 28-01-2016

Key Words:

Forest structure
Species distribution
Habitat associations
Niche-assembly
Dabieshan Mountain

ABSTRACT

Forest structure and species distribution patterns were compared among four topographic habitats in two fully mapped 1-ha plots, named Diaoguanjing and Anjiping, on Daieshan Mountain in China. In Diaoguanjing plot, mean DBH was lower and Fisher's alpha, stem density and the number of species was higher in large versus small habitats. While in Anjiping plot, mean DBH was lower and Fisher's alpha and stem density were higher from high to lower elevation communities. Only 20 out of 78 species were either positively or negatively associated with at least one habitat type in Diaoguanjing, while 33 of 82 species in Anjiping showed habitat associations. A Chi-squared test revealed a greater number of species-habitat associations in Anjiping versus Diaoguanjing ($P < 0.05$). Species-habitat associations were also relatively more frequent in mature forests of both plots ($P < 0.05$). These results suggest that habitat area and forest maturity should be considered in explaining the processes driving species-habitat associations.

INTRODUCTION

Classic niche-assembly theory explains species coexistence in communities via habitat specialization, the idea that different species are best suited to different habitats (Tilman 1982, Tilman & Pacala 1993), thus accounting for the maintenance of species diversity (Ashton 1969, Connell 1978, Leigh 1999, Silvertown 2004).

Variation in topographic factors such as aspect, elevation and slope may, either directly or indirectly, produce resource heterogeneity (John et al. 2007). There is some evidence that this heterogeneity causes particular species to become associated with specific topographical habitats (Harms et al. 2001, Valencia et al. 2004, Gunatilleke et al. 2006). Hence, the process of niche partitioning may play a role in structuring communities. However, patterns of species-habitat associations may also be caused by other, alternative processes, such as species interactions (Silvertown 2004) and habitat-related competitive superiority (Hubbell & Foster 1986). Species-specific effects on local diversity have been found at small scale in tropical forests (Wiegand et al. 2007). Species richness can vary with community successional stage (Schoonmaker et al. 1988, Bruelheide et al. 2008). For example, the community of a secondary forest differed from five other topographical habitats (Valencia et al. 2004). The relative importance of niche partitioning can also vary with habitat heterogeneity, with more significant species-habitat associations occurring in heterogeneous Sri

Lankan dipterocarp forests (Gunatilleke et al. 2006) than in the relatively more homogeneous Barro Colorado Island and Yasuni Forests (Harms et al. 2001, Valencia et al. 2004). The process of niche-assembly has been found to dominate in heterogeneous versus homogeneous environments (Sheng et al. 2013). More research is needed in order to better understand the processes driving species-habitat associations. Owing to spatial autocorrelation in plant population distributions, Harms et al. (2001) recommended the use of torus translation tests of species-habitat associations over ordination, canonical correspondence analysis or Komolgorov-Smirnov tests. This method has been used successfully to determine the contribution of niche partitioning among habitats to species diversity (Valencia et al. 2004, Gunatilleke et al. 2006, Dewalt et al. 2006, Comita et al. 2007).

In this study, four habitat types were assigned on the basis of topographic variables in two 1-ha study plots. The study goals were to compare forest structure and species-habitat association patterns between the two study plots and to explore the processes underlying any observed patterns.

MATERIALS AND METHODS

Study site: Two permanent subtropical forest plots (named Anjiping and Diaoguanjing) were created in Yaoluoping Nature Reserve on Dabieshan Mountain in Anhui province, China. Both 1-ha (100×100m) plots were divided into twenty-five 20×20 m quadrats and a permanent stake was

placed at the corners of each quadrat. The relative elevation of each corner was measured using a theodolite. All trees in the research plots with a DBH above 2cm were mapped, tagged using an aluminium plate with a unique number, and identified by species. Multiple stems were measured separately and all stems, with the exception of the largest, were defined as sprouting stems. Sprouting stems were excluded from the analysis.

Data Analysis

Categorization of quadrats by habitat:

Type 1: High-slope (HS) quadrats had slope $>26^\circ$ and elevation $>710\text{m}$

Type 2: High-gully (HG) quadrats had slope $<26^\circ$ and elevation $>710\text{m}$

Type 3: Low-slope (LS) quadrats had slope $>26^\circ$ and elevation $\leq 710\text{m}$

Type 4: Valley (V) quadrats had slope $<26^\circ$, elevation $>710\text{m}$

Tests of forest structure and species-habitat associations:

Chi-square tests were used to compare Fisher's alpha, stem density, basal area (per ha), species number (per ha) and mean DBH among habitat types. Torus-translation tests (Harms et al. 2011) were also used to determine the number of species-habitat associations.

RESULTS

Total abundance and forest structure: Anjiping plot contained 32 families, 50 genera, 70 species and 2586 stems (including 458 sprouting stems) with DBH ≥ 2 cm. The dominant family was Rosaceae (9 species). The dominant tree species was *Platycarya strobilacea*, a canopy species belonging to the Juglandaceae, with 146 individuals and a maximum DBH of 70 cm. The most abundant species was *Sorbus hemsleyi*, an understory species belonging to the Rosaceae family, with 412 individuals, which accounted for

20.3% of the total number of stems. There were 13 singleton species in the plot.

In Diaoguanjing plot, there were 32 families, 52 genera, 82 species and 6133 stems (including 855 sprouting stems) with DBH ≥ 2 cm. The dominant family was again Rosaceae (8 species and 4 genera). The dominant tree species was *Dalbergia hupeana*, a canopy species in the Papilionaceae family, with 206 individuals and a maximum DBH of 28 cm. The most abundant species was *Lindera chienii*, an understory species in the Lauraceae family, with 345 individuals, accounting for 25.4% of the total number of stems. There were 7 singleton species in the plot.

Habitat differences in forest diversity and structure:

In Diaoguanjing plot, Fisher's alphas, stem densities and numbers of species were higher in habitats encompassing a larger area (i.e. high-slope and valley patches), indicating that species diversity was area dependent. And also, larger area patches had the lower mean DBH than smaller one, revealed species diversity may related to forest maturity (larger mean DBH in mature habitat and lower mean DBH in immature habitat). In Anjiping plot, mean DBH decreased, while Fisher's alpha and stem density increased, with mean elevation increasing; thus diversity was elevation and maturity related, but area dependent was not clearly in this plot (Table 1).

A total of 74.4% and 59.8% of the species in Diaoguanjing and Anjiping plots, respectively, did not show any association with the four habitat types (Table 2). In Diaoguanjing plot, only 20 out of 78 species were either positively or negatively associated with at least one habitat type. In Anjiping plot, 40.2% of the species showed significant habitat associations ($P < 0.05$) (31.8% showed positive and 8.5% negative associations). A Chi-squared test revealed that more species showed habitat associations in Anjiping versus Diaoguanjing plot ($P < 0.05$). More species-habitat associations were found in habitats covering larger areas

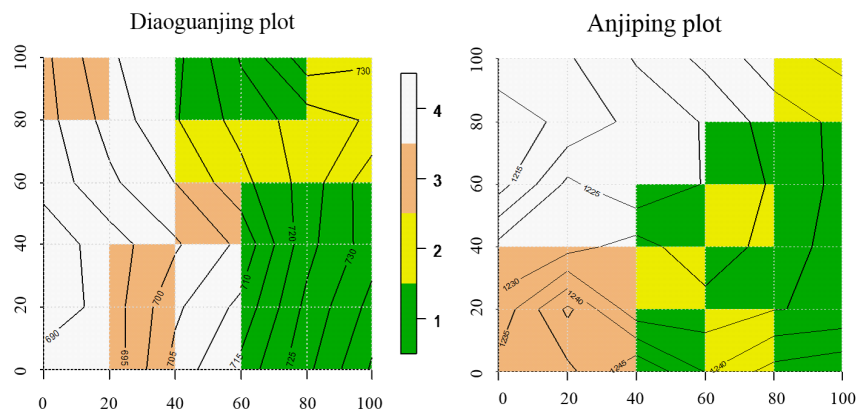


Fig. 1: Topographic maps and habitat assignments.

Table 1: Species diversity and basal area in Diaoguanjing and Anjiping plots.

	Area (ha)	Fisher's α	Stem density	Species number	Mean DBH	Total basal area per 1 ha
Diaoguanjing plot						
whole plot	1	16.94	2128	82	8.90	18931
high-slope	0.32	17.82	2328	63	8.74	20343
high-gully	0.16	14.51	1750	50	9.69	16590
low-slope	0.16	17.79	1693	51	9.35	21980
valley	0.36	17.94	2269	70	8.61	19537
Anjiping plot						
whole plot	1	15.89	2134	78	9.32	19895
high-slope	0.32	16.15	2463	60	8.76	21572
high-gully	0.16	16.63	2431	45	7.98	19403
low-slope	0.16	13.72	1694	40	10.35	17537
valley	0.36	15.75	1906	68	10.32	19672

Table 2: Species-habitat associations as found by the Torus test.

Habitat	Total number of species	Positive association	Negative association	No association
Diaoguanjing plot				
High slope	61	4	2	55
High gully	53	2	2	49
Low slope	47	1	1	45
Valley	59	6	2	51
Total	78	13	7	58
Anjiping plot				
High slope	67	2	3	62
High gully	47	7	0	38
Low slope	53	4	1	48
Valley	66	13	3	50
Total	82	26	7	49

and mature habitat in Diaoguanjing plot and in the lower elevation and mature habitats in Anjiping plot ($P < 0.05$).

DISCUSSION

In this study on Dabieshan Mountain in China, forest structure varied with topography and species-habitat associations were found in the two study plots. Forest structure and species diversity differed in mature versus immature habitat patches in Anjiping and Diaoguanjing plot, whereas mature habitat was found on larger habitat area in Diaoguanjing plot and on lower elevation in Anjiping plot. Furthermore, more habitat specialists were found in Anjiping than in Diaoguanjing, and specialists were most frequent in mature communities in the two plots.

The number of tree species and of individual trees increased with area in our study. This is a common finding in ecology as when individuals are distributed at random, larger samples thus contain more individuals and more species (Arrhenius 1921, Gleason 1922, Connor & McCoy 1979, Baldi 2008). Using both Fisher's alpha and stem density to correct for the effect of sample size, Diaoguanjing had area-dependent patterns of species diversity and forest structure,

but patterns were elevation-related in Anjiping plot. The Diaoguanjing plot was located on a west-facing slope and its topography was relatively uniform in comparison to that of Anjiping (Fig. 1). There were fewer species-habitat associations (25.6%) in Diaoguanjing than in Anjiping (45.2%), which may indicate a lesser role for niche partitioning in structuring Diaoguanjing communities.

The significantly greater number of species-habitat associations in the mature habitat patches of the two plots may be explained by complex plant-plant interactions in these communities (Silverton 2014). In tropical forests, forest structure has been found to differ between ridges and valleys, with valleys having more young trees and fewer individuals overall owing to moisture availability and other soil factors (Clark et al. 1999, Svenning 1999, Webb & Peart 2000, Valencia et al. 2004). In contrast to these results, in this study, mature forest occurred more frequently in lower elevation areas that had lower species diversity and stem densities as well as larger individuals in Anjiping. In plant communities, there may be some species which either facilitate or hinder other species (Wiegand et al. 2007), for example, larger trees in a forest can reduce the space avail-

able for other species, but may also provide habitat for some shade-adapted species. In this study, mature forests in lower elevation habitats in Anjiping showed the most species-habitat associations. Hence, forest structure and species diversity varied among habitats in Anjiping, with communities in lower elevation areas being the most mature.

The role of habitat differentiation in maintaining species diversity has been investigated at a local scale by ascertaining whether or not species show associations (or are specialized to) particular habitat types (Hubbell & Foster 1986, Svenning 1999, Harms et al. 2001, Valencia et al. 2004). Niche partitioning has been found overall to make a varying contribution to diversity maintenance and there may be other important mechanisms of species coexistence in species-rich communities (Svenning 1999, Harms et al. 2001, Valencia et al. 2004). Habitat associations may be dependent on plant size or life stage (Webb & Peart 2000). Habitat partitioning most likely acts during early life stages and therefore coexistence can be made possible through partitioning of the 'regeneration niche' (Grubb 1977). Habitat associations in large tree species typically do not form at early life stages and therefore multiple life stages should be included to detect developmental shifts in ecological preferences (Comita et al. 2007, PUNCHI-MANAGE et al. 2013). Niche partitioning alone cannot explain the high species richness found in tropical forests (Silvertown 2004, Hubbell 2005, 2006). Even strong habitat preferences may not necessarily produce large differences in population dynamics across habitats; the mechanisms that generate density differences across habitats remain to be unravelled (Yamada et al. 2007). In this study, species-habitat associations were found to correlate with either the area or maturity of a community.

ACKNOWLEDGEMENTS

The authors gratefully thank many individuals who contributed to field surveys of Diaoguanjing and Anjiping plots. We would also like to thank Emily Drummond at the University of British Columbia for her assistance with English language and grammatical editing of the manuscript. Financial support was provided by the Anhui Provincial Natural Science Foundation of China (1408085MC64), the Natural Science Foundation of the Anhui Higher Education Institution of China (KJ2010B087) and the National Natural Science Foundation of China (31570417).

REFERENCES

- Arrhenius, O. 1921. Species and area. *Journal of Ecology*, 9(1): 95-99.
- Ashton, P. 1969. Speciation among tropical forest trees: some deductions in light of recent evidence. *Biological Journal of the Linnean Society*, 1: 155-196.
- Báldi, A. 2008. Habitat heterogeneity overrides the species-area relationship. *Journal of Biogeography*, 35(4): 675-681.
- Bruehlheide, H., Bohnke, M., Both, S., Fang, T., Assmann, T., Baruffol, M. and Schmid, B. 2011. Community assembly during secondary forest succession in a Chinese subtropical forest. *Ecological Monograph*, 81(1): 25-41.
- Clark, D., Palmer, M. and Clark, D. 1999. Edaphic factors and the landscape-scale distributions of tropical rain forest trees. *Ecology*, 80: 2662-2675.
- Comita, L., Condit, R. and Hubbell, S. 2007. Developmental changes in habitat associations of tropical trees. *Journal Ecology*, 95(3): 482-492.
- Connell, J. 1978. Diversity in tropical rain forest and coral reefs. *Science*, 199:1302-1309.
- Connor, E. and McCoy, E. 1970. The statistics and biology of the species-area relationship. *American Naturalist*, 113: 791-833.
- Gleason, H. 1922. On the relation between species and area. *Ecology*, 3(2): 158-162.
- Grubb, P. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews*, 52(1): 107-145.
- Hubbell, S. and Foster, R. 1986. Biology, chance, and history and the structure of tropical rain forest tree communities. *Community Ecology* (eds Diamond J., Case T.), Harper and Row, New York, pp: 314-330.
- Hubbell, S. 2006. Neutral theory and the evolution of ecological equivalence. *Ecology*, 87(6): 1387-1398.
- Hubbell, S. 2005. Neutral theory in community ecology and the hypothesis of functional equivalence. *Functional Ecology*, 19(1): 166-172.
- John, R., Dalling, J., Harms, K., Yavitt, J., Stallard, R., Mirabello, M., Hubbell, S., Valencia, R., Navarrete, H., Vallejo, M. and Foster, R. 2007. Soil nutrients influence spatial distributions of tropical tree species. *Proceedings of the National Academy of Sciences*, 104(3): 864-869.
- Leigh, E. 1999. *Tropical Forest Ecology: A View from Barro Colorado Island*. Oxford University Press, Oxford, UK.
- Punchi-Manage, R., Getzin, S., Wiegand, T., Kanagaraj, R., Savitri Gunatilleke, C., Nimal Gunatilleke, I. and Huth, A. 2013. Effects of topography on structuring local species assemblages in a Sri Lankan mixed dipterocarp forest. *Journal of Ecology*, 101(1): 149-160.
- Schoonmaker, P. and McKee, A. 1988. Species composition and diversity during secondary succession of coniferous forests in the western Cascade Mountains of Oregon. *Forest Science*, 34(4): 960-979.
- Shen, G., He, F., Waagepetersen, R., Sun, L., Hao, Z., Chen, Z. and Yu, M. 2013. Quantifying effects of habitat heterogeneity and other clustering processes on spatial distributions of tree species. *Ecology*, 94(11): 2436-2443.
- Silvertown, J. 2004. Plant coexistence and the niche. *Trends Ecological Evolution*, 19: 605-611.
- Svenning, J. 1999. Microhabitat specialization in a species rich palm community in Amazonian Ecuador. *Journal Ecology*, 87: 55-65.
- Tilman, D. and Pacala, S. 1993. The maintenance of species richness in plant communities. *Species Diversity in Ecological Communities* (eds R.E. Ricklefs & D. Schluter), University of Chicago Press, Chicago, Illinois, USA. pp. 13-25.
- Tilman, D. 1982. *Resource Competition and Community Structure*. Princeton University Press Princeton, USA.
- Webb, C. and Peart, D. 2000. Habitat associations of trees and seedlings in a Bornean rain forest. *Journal Ecology*, 88: 464-478.
- Wiegand, T., Gunatilleke, C., Gunatilleke, I. and Huth, A. 2007. How individual species structure diversity in tropical forests. *Proceedings of the National Academy of Sciences*, 104(48): 19029-19033.
- Yamada, T., Zuidema, P., Itoh, A., Yamakura, T., Ohkubo, T., Kanzaki, M., Tang, S. and Ashton, P. 2007. Strong habitat preference of a tropical rain forest tree does not imply large differences in population dynamics across habitats. *Journal Ecology*, 95(2): 332-342.