Species-habitat associations change in a subtropical forest of China

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Abstract

Question: Do tree and shrub species in an evergreen broadleaf forest show similar habitat associations across different life stages?

Location: A 24-ha evergreen broadleaf forest plot in a heterogeneous landscape in Gutianshan National Nature Reserve, Zhejiang Province, Eastern China.

Methods: Species having positive associations with four habitat types (low valley, low ridge, upper valley, and upper ridge) at three life stages (sapling, juvenile, and mature stages) were compared for 60 tree and shrub species using torus-translation tests.

Results: A total of 117 significant positive associations with the four habitats were observed at the three life stages (43, 41, and 33 at the sapling, juvenile, and mature stages, respectively). For the 52 species significantly associated with habitats, only 16 were associated with the same habitat across all three stages. The majority of associated species at the juvenile stage (34 out of 40) were associated with the same habitat at their sapling stage, whereas half of species at the mature stage had consistent associations with the same habitat at their sapling stage. More species were associated with the upper ridge at the sapling and juvenile stages compared to the mature stage. Conversely, more species were associated with the low valley at the mature stage compared to the sapling and juvenile stages.

Conclusions: Our results indicate that species ecological habitat associations can differ between developmental stages beyond 1 cm DBH, as most species habitat preferences were consistent from the sapling stage to the juvenile stage but changed at the mature stage.

Keywords: Environmental heterogeneity; Evergreen broad leaf forest; Habitat preference; Life history; Species distribution; Topography.


Abbreviations: CTFS = Center for Tropical Forest Science; DBH = diameter at breast height; GNNR = Gutianshan National Nature Reserve

Introduction

Recently, many studies have demonstrated the association of species with topographic and edaphic habitat factors at local scales in large forest plots worldwide (e.g., Harms et al. 2001; Debski et al. 2002; Itoh et al. 2003; Sri-Ngernyuang et al. 2003; Valencia et al. 2004; Gunatilleke et al. 2006; Yamada et al. 2006; Queenborough et al. 2007). In these studies, many species exhibited ecological habitat preferences, despite differences in species proportions and strengths of associations at different sites. These observations highlight the importance of habitat niche partitioning versus dispersal-assembly limitation processes in the maintenance of local diversity in multi-species communities. However, most analyses of species habitat associations in these studies were based on static distributions of plant stems of $\geq 1$ cm DBH (diameter at breast height), and assumed that all individuals of a species respond similarly to habitat regardless of life stage. The validity of this assumption for plant communities is unclear because different life stages have rarely been taken into account in studies to date. According to the regeneration niche theory proposed by Grubb (1977), habitat niche partitioning of species most likely occurs during early life stages, and species may show consistent habitat preferences in subsequent life stages. However, many studies have found that species ecological preferences can shift throughout plant ontogeny, as a result of changes in physiological requirements, selective pressures, and

Recently, Webb & Peart (2000) and Comita et al. (2007) directly compared species habitat associations at two life stages for tropical trees, and their results demonstrated that most species have different responses to habitat at different life stages. However, these two studies may not confirm the validity of the above assumption. Webb & Peart (2000) only analyzed differences in habitat associations of seedling (>5 cm tall, but <1 cm DBH) and adult trees (≥10 cm DBH) of 325 species in a forest in Borneo, Indonesia, and omitted all stems between 1 and 10 cm DBH. Comita et al. (2007) compared developmental changes in positive habitat associations between small (≥20 cm tall and <1 cm DBH) and large (≥1 cm DBH) tree stages of 80 common trees and shrubs on Barro Colorado Island, Panama, and assumed that all stems ≥1 cm DBH respond similarly to habitat. In addition, assessments of species habitat associations at two life stages may be insufficient to detect developmental changes in ecological habitat preference. Hence, multi-stage analyses of common species are required to detect developmental changes of species habitat preferences at different life stages.

We examined habitat associations in a 24-ha permanent plot in a subtropical evergreen broadleaf forest in Gutianshan National Nature Reserve, eastern China (Fig. 1). The Gutianshan permanent plot is suitable for studying species habitat associations because of its heterogeneous topography. A previous study of large saplings and trees ≥1 cm DBH found that many species were significantly associated with one or more habitats (Gong et al. 2007). Here, topographic habitat associations across three different life stages are compared for 60 common species in the 24-ha permanent plot. The aim is to examine whether species show similar habitat associations across three different life stages beyond 1 cm DBH.

Methods

Study site

The study was conducted in a 24-ha permanent forest plot (29°15′6″–29°15′21″N, 118°07′1″–118°07′24″E) in Gutianshan National Nature Reserve (GNNR), Kaihua County, Zhejiang Province, eastern China (Fig. 1). GNNR covers a total area of approximately 8107 ha. The topography is characterized by steeply sloping mountains on a mainly granite substrate. The dominant soils can be classified into four types: red, red-yellow, yellow-red, and marsh soils. The mean annual temperature is 15.3°C, the hottest month is July (mean temperature of 27.9°C), and the coldest is January (mean temperature of 4.3°C). Mean annual precipitation is 1963.7 mm, with seasonal distribution: two wet seasons from March to June and in September, and two dry seasons from July to August and October to February. The number of mean frost-free days per

Fig. 1. Map of China showing the location of the 24-ha Gutianshan permanent plot.
year is 250. A total of 1991 vascular plant species, belonging to 244 families and 897 genera, have been recorded within the entire GNRR (Chen & Feng 2002; Hu et al. 2003). The dominant vegetation type is subtropical evergreen broadleaf forest dominated by Castanopsis spp., Cyclobalanopsis spp. and Schima superba (Chen & Feng 2002; Hu et al. 2003).

Data collection

In December 2004, a permanent plot covering 24-ha (400 m × 600 m, horizontal distance) was established within the evergreen broadleaf forest in GNRR as part of the Chinese Forest Biodiversity Monitoring Network. The plot was established and data were collected following the plot standards of the CTFS (Center for Tropical Forest Science) network (Condit 1998). The plot was divided into 600 20 m × 20 m quadrats using 651 posts. The relative elevation of each post was measured, and the range between the highest and lowest point in the plot was 269 m (from 446 to 715 m a.s.l.). The first tree census was conducted in 2005. All woody stems ≥ 1 cm DBH were mapped, measured, identified, and tagged. Species were grouped into three growth forms defined by the maximum height they typically attain at maturity, shrubs (<5 m), understory trees (≥ 5 and <15 m), and canopy trees (≥ 15 m).

Approximately 140 000 individuals ≥ 1 cm DBH in 49 families, with 103 genera and 159 species were encountered in the plot, with 26 shrub, 70 understory tree, and 63 canopy tree species. The most abundant species was the tall canopy tree, Castanopsis eyrei (Fagaceae), with 12 406 individuals representing 8.9% of the total number of individuals in the plot. Nearly 41% of the species (65 out of 159) recorded < 30 individuals in the entire plot.

Topographic attributes and habitat categorization

Four topographic attributes, elevation, convexity, slope, and aspect, were calculated for each 20 m × 20 m quadrat in the plot. Following Harms et al. (2001) and Valencia et al. (2004), the elevation of each quadrat was obtained from the mean elevations at the four corners of a quadrat. Following Yamakura et al. (1995), convexity of a quadrat was calculated as the elevation of the focal quadrat minus the mean elevation of the eight surrounding quadrats. For the edge quadrats, convexity was taken as the elevation of the center point minus the mean of the four corners. Each quadrat was divided into four triangular planes, each formed by joining three corners of the quadrat. The average angle of the four triangular planes that deviated from the horizontal plane and the north direction provided the slope and aspect of each quadrat, respectively. The four topographic attributes for the 600 quadrats were: elevation (252.8 m, from 457.8 to 710.6 m), convexity (35.4 m, from –16.6 to 18.6 m), slope (49.2°, from 12.8° to 62.0°), and aspect (165.3° from 93.9° to 269.2°).

A multivariate regression tree (MRT; De’ath 2002) was used to divide the 600 quadrats of the Gutianshan plot into five habitat types containing similar topographic conditions and species composition (Legendre et al. 2009). The abundance of 121 species and the value of the above four topographical attributes [aspect was represented by sin (aspect) and cos (aspect)] in the 600 quadrats were selected for habitat categorization by the MRT procedure, computed using the “mvpart” library of the R statistical language (Legendre et al. 2009). The five habitat types are presented on a map of the plot in Fig. 2. The attributes of each habitat type are summarized in Table 1.

The resulting habitat categorization formed the basis for testing species-habitat associations. However, Group 4 habitat had only eight quadrats and was spatially restricted within the study plot (Fig. 2); therefore this group was merged with Group 3, which had similar topographic characteristics (Table 1). According to topographic parameters (Table 1) and the topographic map (Fig. 2), the four habitats used for testing species-habitat associations were named: low valley (Group 1), low ridge (Group 2), upper valley (Group 3 and 4), and upper ridge (Group 5).

Analyses of species habitat associations

For the three different plant growth forms (shrub, understory tree, and canopy tree), stems of similar DBH represent different life stages. To account for this, we used standards to define the three life stages (sapling, juvenile, mature): shrub (1.0-1.5 cm DBH as sapling, 1.5-2.5 cm DBH juvenile, ≥ 2.5 cm DBH mature stages); understory tree (1.0-2.5 cm DBH as sapling, 2.5-5.0 cm DBH juvenile, ≥ 5.0 cm DBH mature stages); and canopy tree (1.0-2.5 cm DBH as sapling, 2.5-7.5 cm DBH juvenile, ≥ 7.5 cm DBH mature stages). Habitat associations were only tested for species with ≥ 24 individuals in one of the three stages in the entire 24-ha plot. Four shrub species, 30 understory tree species, and 26 canopy tree species met these requirements (Table S1; see Supporting Information for details). Associations of species with the four...
habitat types were determined using torus-translational tests, which take into account the spatial autocorrelation of plant distribution (Harms et al. 2001). Torus-translational tests compare true relative densities of focal species in a habitat with expected relative densities under a null model in which the species distribute randomly among habitats. For example, to acquire the expected values of relative densities in our study plot, the true habitat map was translated into 20-m increments along two dimensions (up, down, and left, right) to generate all possible 20-m translations of the true habitat map in the four cardinal directions. At our study plot (consisting of a grid of 600 cells), 600 unique torus-translated habitat maps were initially possible. From this, it is possible to generate three original maps to continue the two-dimensional torus translation: 180° rotation, mirror image and 180° rotation of the mirror image (Harms et al. 2001). In total, these procedures provide a total of 2399 translated maps, each of which provides a value of the expected relative density. If the true relative density of a species in the focal habitat is greater or smaller than at least 97.5% of the expected relative densities (among top or bottom 60 values), then it is determined to be statistically positively or negatively associated with that habitat (α = 0.05 level of significance for a two-tailed test). More detailed descriptions of torus-translational tests can be found in Harms et al. (2001). In this study, a revised version of the torus-translational tests, developed by Comita et al. (2007), was used in order to facilitate comparisons between habitat associations of the three different life stages. Only positive associations were tested, and the absolute stem density of each species in a habitat replaced the relative density of the focal species within that habitat. A significant positive species-habitat association was indicated if the absolute stem density of the focal species in a habitat on the true map was greater than 99% of the values (2376 out of the 2399) from translated maps (α = 0.01 level of significance for a single-tailed test).

### Table 1. The topographic parameters of habitat categories in the 24-ha Gutianshan permanent plot. †SE (%): the proportion of southeast-facing quadrats | SW(%)|: the proportion of southwest-facing quadrats.

<table>
<thead>
<tr>
<th>Habitat category</th>
<th>Habitat name</th>
<th>Number of quadrats</th>
<th>Total area (ha)</th>
<th>Elevation (m) Min</th>
<th>Max</th>
<th>Mean</th>
<th>Convexity (m) Min</th>
<th>Max</th>
<th>Mean</th>
<th>Slope (°) Min</th>
<th>Max</th>
<th>Mean</th>
<th>Aspect Min</th>
<th>Max</th>
<th>SE (%)†</th>
<th>SW (%)‡</th>
</tr>
</thead>
<tbody>
<tr>
<td>Group 1</td>
<td>Low valley</td>
<td>237</td>
<td>9.48</td>
<td>462.1</td>
<td>642.7</td>
<td>559.4</td>
<td>-16.6</td>
<td>1.8</td>
<td>-5.9</td>
<td>17.5</td>
<td>54.5</td>
<td>38.6</td>
<td>93.9</td>
<td>263.1</td>
<td>50.2</td>
<td>49.8</td>
</tr>
<tr>
<td>Group 2</td>
<td>Low ridge</td>
<td>269</td>
<td>10.76</td>
<td>457.8</td>
<td>642.8</td>
<td>570.1</td>
<td>-0.6</td>
<td>12.4</td>
<td>4.7</td>
<td>12.8</td>
<td>62.0</td>
<td>37.3</td>
<td>96.6</td>
<td>269.2</td>
<td>50.9</td>
<td>49.1</td>
</tr>
<tr>
<td>Group 3</td>
<td>Upper valley</td>
<td>42</td>
<td>1.68</td>
<td>643.2</td>
<td>682.4</td>
<td>659.6</td>
<td>-8.6</td>
<td>3.3</td>
<td>-0.9</td>
<td>17.6</td>
<td>54.7</td>
<td>35.6</td>
<td>94.2</td>
<td>263.1</td>
<td>50.0</td>
<td>50.0</td>
</tr>
<tr>
<td>Group 4</td>
<td>Upper Valley</td>
<td>8</td>
<td>0.32</td>
<td>683.2</td>
<td>710.6</td>
<td>695.5</td>
<td>-5.3</td>
<td>3.0</td>
<td>-0.6</td>
<td>15.1</td>
<td>42.9</td>
<td>35.6</td>
<td>119.2</td>
<td>254.3</td>
<td>50.0</td>
<td>50.0</td>
</tr>
<tr>
<td>Group 5</td>
<td>Upper ridge</td>
<td>44</td>
<td>1.76</td>
<td>644.0</td>
<td>703.6</td>
<td>663.3</td>
<td>3.3</td>
<td>18.6</td>
<td>8.0</td>
<td>15.8</td>
<td>49.4</td>
<td>34.9</td>
<td>95.9</td>
<td>257.3</td>
<td>45.5</td>
<td>54.5</td>
</tr>
</tbody>
</table>
Results

Based on torus-translation tests, a total of 117 significant positive associations with the four habitats were observed among 52 out of the 60 examined species at the three life stages. Fewer significant positive associations were identified at the mature stage than at the sapling and juvenile stages. Thirty-three positive associations were detected at the mature stage, compared to 43 and 41 at the sapling and juvenile stages, respectively (Table S1 and Fig. 3). In addition, species were always associated with only a single habitat at a given life stage, except for three species, *Rhododendron ovatum* at the sapling stage, *Viburnum erosum* at the juvenile stage, and *Myrica rubra* at the mature stage, which were associated with several habitats (see Table S1).

According to the methods used in examining associations, the 117 positive associations with the four habitats at the three stages had seven possible combinations of habitat and association (Fig. 3). Sixteen associations (among 16 species, see Table S1) with the same habitat were consistent across the three life stages (G pattern in Fig. 3). The majority of significant associations at the sapling stage (34 out of 43 associations, 79%) were maintained as the sapling stage matured to the juvenile stage within the same habitat (D and G patterns in Fig. 3), whereas only approximately 40% of associations (17 out of 43 associations) with that habitat were further maintained at the mature stage (F and G patterns in Fig. 3). More than one-third of significant associations at the mature stage (12 out of 33, C pattern in Fig. 3) had no corresponding associations at the sapling and juvenile stages. A lower ratio of association was identified for species-habitat combinations only at the juvenile stage or corresponding juvenile and mature stage when there was no corresponding association detected at the sapling stage (B and E patterns in Fig. 3). Only one species and habitat combination, *Adinandra millettii* with low valley habitat, exhibited a positive association at the sapling and mature stages but no positive association at the juvenile stage (F pattern in Fig. 3).

The number of associations with each habitat type differed among the three life stages (Fig. 4). In the low valley habitat, a greater number of positive associations were detected for the mature stage (22 out of 33, 67%) compared to the sapling and juvenile stages (18 and 16 positive associations, respectively). In contrast, in the other three habitats, especially upper ridge habitat, fewer positive associations were found at the mature stage than at the sapling and juvenile stages (Fig. 4). In addition, the majority of associations (104 out of 117, 88.9%) occurred in these two habitats (low valley and upper ridge). The low level of associations in the low ridge habitat, which has the largest area in the plot, suggests that a larger habitat area does not lead to a larger number of habitat associations.

Discussion

For the 52 associated species, only 16 species show consistent associations with a single habitat at all three life stages. For most species, habitat preferences were not consistent across multiple life stages beyond 1 cm DBH in this forest. The majority of habitat-associated species at the juvenile stage were associated with the same habitat at their
sapling stage, whereas half of the habitat-associated species at the mature stage lacked associations with the same habitat at their sapling stage. This suggests that for most species habitat preference remains constant for their sapling and juvenile stages but differs at their mature stage in this forest.

These results are largely consistent with previous studies comparing tropical tree species habitat associations at two stages, if the sapling stage and juvenile stage in this study correspond to the early stage and mature later stage. Webb & Peart (2000) and Comita et al. (2007) found that many tropical tree species habitat preferences differ across multiple life stages, and species that are significantly associated with a habitat in an early stage are usually not associated with that same habitat in a later stage. Nevertheless, some species were positively associated with the same habitat across all three life stages at this particular site (G pattern in Fig. 3). For example, a group of species had consistent positive associations with the low valley habitat at all three life stages; these species included *Camellia japonica*, *Castanopsis fargesii*, *C. tibetana*, *Daphniphyllum oldhamii*, *Distylium myricoides*, *Elaeocarpus japonicus*, *Ilex elmerilliana*, *Michelia thunbergii*, *Michelia skinneriana*, *Neolitsea aurata var. chekiangensis*, *Osmanthus cooperi*, and *Photinia glabra*.

A possible explanation for this pattern is based on restricted seed dispersal, which may be spatially limited and occurs primarily in close proximity to parent trees, thus maintaining the limited distribution within the same habitat (Hubbell et al. 1999; Ribbens et al. 1994; Webb & Peart 2000). Alternatively, the above species are mostly shade-tolerant and their saplings and juveniles can establish and survive in the understory. Consequently, the saplings, juveniles, and adults remain spatially associated.

For the species positively associated with a given habitat only at their sapling stage (A pattern in Fig. 3), the subsequent loss of a positive association at their juvenile and mature stages may be caused by higher mortality rates as the sapling stage matures from the juvenile stage (Comita et al. 2007). Similarly, this may explain pattern D in Fig. 3, except that the increased mortality rates occur only after the juvenile stage. There are many factors that result in reduced rates of sapling survival to the mature stage. For example, from the competitive sorting model proposed by Peet (1992), it can be deduced that in the sapling stage individuals are small and competition is low, however, competition intensifies as individual size increases and negative density dependence appears because of the high density of saplings and juveniles (Janzen 1971; Connell et al. 1984; Condit et al. 1994; Harms et al. 2000; Peters 2003). The poor competitors are forced out and a few vigorous individuals mature to become reproductive parent trees. Thus, the saplings and juveniles are strongly associated with a habitat, while mature stage trees do not maintain a positive association with the same habitat.

For species that are positively associated with a given habitat solely at the mature stage (C pattern in Fig. 4), the absence of a positive association with the same habitat at their sapling and juvenile stages may be a result of lower seedling establishment or recruitment success in that habitat (Webb & Peart 2000; Comita et al. 2007). In general, seed dispersal limitation occurs in habitats with more adult trees having a higher seed density; however, these preferred habitats of mature trees are not always suitable for subsequent seed germination and seedling establishment due to unfavorable light conditions or other biotic factors (Titus & del Moral 1998; Jones & del Moral 2005). Alternatively, higher mortality rates as the seedling matures into a sapling (≥ 1 cm DBH) may be a possible explanation for this pattern, because of the negative density dependence caused by a high density of seedlings in that habitat or ontogenetic changes in resource requirements (Comita et al. 2007). We also cannot rule out the possibility of low seed germination, low seedling establishment, or higher mortality rates from seedling to saplings ≥ 1 cm DBH. Further studies focusing on seedling establishment are required to examine these possibilities.

For the species in the other three patterns (B, E, and F patterns in Fig. 3), it is possible that, in some instances, there was a departure from standard used to define the three life stages, despite different size standards used to define the three life stages for the three growth forms. For example, *Adinandra millettii* exhibited a positive association with low valley habitat at the sapling and mature stages but no positive association at the juvenile stage, with 12.03 stem ha⁻¹ in the juvenile stage at low valley habitat (see Table S1). If only three stems were added in the juvenile stage from the sapling or mature stages at low valley habitat, the relationship of *A. millettii* with low valley habitat at the juvenile stage would be deemed a positive association by the torus-translation tests at α = 0.01 significance. Thus, *A. millettii* may actually associate with the low valley habitat across all three life stages and belong to G pattern in Fig. 3. Similarly, species observed in B or E patterns would become D and C patterns if more specific size standards for defining their three life stages were
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determined. Thus, the standards used for classifying life stages for different species should be considered in future studies. However, few such cases for the three life-stage patterns also demonstrate the validity of different standards used for the three growth forms in this study.

The association discrepancies between the mature stage and the two earlier stages may also be related to the different number of associations within each habitat type among the three life stages (Fig. 4). The notable lower number of observed associations with upper ridge habitat at the mature stage compared to sapling and juvenile stages is likely to be the result of a lack of individuals of species with a large DBH in the upper ridge (see Table S1). A fire disturbance approximately 50 years ago in the area near the upper ridge habitat may have had some impact on the community age structure and resulted in few individuals with a large DBH in that habitat. A fire disturbance likely allowed increased sunlight to penetrate during the early stages of forest recovery, which creates an environment conducive for seed germination and seedling establishment. Currently, such seedlings may have progressed into the sapling and juvenile stages, but have not yet attained the mature stage in this upper ridge habitat. This is also supported by the result that over half (16 out of 26, 62%) of the two patterns (A and D in Fig. 4) occurred in the upper ridge habitat. Conversely, two-thirds of pattern C (8 out of 12, 67%) occurred in the low valley habitat. The poor sunlight conditions resulting from a higher density of large trees and topographic factors in the low valley habitat possibly restrained seedling establishment (Denslow & Guzman 2000; McEuen & Curran 2004; Fahey & Puettermann 2007). Presumably this also resulted in more associations with the low valley at the mature stage than at the sapling and juvenile stages. Other factors may also affect habitat associations, such as local distribution of soil types and water availability. In addition, the absence of detectable associations in the low ridge and upper valley habitats across any of the three life stages is potentially due to the fact that these habitats lie in the middle section of the overarching environmental gradient in the study plot, forming an intermediate habitat (Fig. 2). Species preferring low ridge habitats may also reside in low valleys and upper valleys, and species with preferences for upper valley habitats may also commonly be found on low and upper ridges. Species such as these have a broader ecological range and less distinct habitat associations within the study plot compared to species that are concentrated in habitats that represent extremes within the local environmental gradient, i.e., low valleys and upper ridges. This was the case in the analyses of species habitat associations of the 25-ha Sinharaja permanent plot, Sri Lanka (Gunatilleke et al. 2006), which has the highest elevation range (151 m) of the CTFS plots and similar topographical conditions as the Gutianshan plot.

A possible limitation in this study is that developmental changes in species-habitat associations were determined using static distributions of all plant stems ≥ 1 cm DBH. The absence of information regarding seed dispersal and seedling distribution may have created discrepancies in the data collected. Similar studies have suggested that seed dispersal may be the driving factor in causing shifts in species habitat associations between the small and large tree stages (Webb & Peart 2000; Comita et al. 2007). For example, the pattern where these species associate with a given habitat at only the sapling stage is potentially the result of fecund adults in adjacent habitats dispersing seeds into that particular habitat. In contrast, for species associated with a given habitat at only the mature stage, the lack of association at the sapling stage likely results from seed dispersal or seedling establishment outside that habitat (Webb & Peart 2000; Comita et al. 2007). Our results also emphasize the need for further studies that include observations of seed dispersal patterns and seedling distributions in the plot in order to improve current understanding of developmental changes in species-habitat associations.

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Reference


**Supporting Information**

Additional supporting information may be found in the online version of this article:

**Table S1.** Tree and shrub habitat associations at the sapling, juvenile, and mature stages within the 24-ha Gutianshan forest permanent plot.

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