

Fude LIU, Wenjin WANG, Ming ZHANG, Jianwei ZHENG, Zhongsheng WANG,
Shiting ZHANG, Wenjie YANG, Shuqing AN

Species association in tropical montane rain forest at two successional stages in Diaoluo Mountain, Hainan

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Abstract Species association is one of the basic concepts in community succession. There are different viewpoints on how species interaction changes with the progress of succession. In order to assess these relationships, we examined species associations in the tropical montane rain forest at early and late successional stages in Diaoluo Mountain, Hainan Island. Based on data from a 2×2 contingency table of species presence or absence, statistical methods including analysis of species association and χ^2 tests were applied. The results show that: 1) an overall positive association was present among tree species in the communities during the two successional stages and were statistically significant at the late stage. The number of species pairs with positive and negative associations decreased throughout the process of succession, while the number with null associations was greatly increased. The same trend existed among the dominant and companion species. The results indicate that the communities are developing towards a stable stage where the woody species coexist in harmony. 2) In the early-established and later invading species, all positive associations were not significant. Compared with positive and null associations, fewer negative associations were found. This implies that these species are inclined to coexist independently through partitioning of resources. 3) Among the later invading species, positive associations were significant and no negative associations were found which suggest that these species

have similar adaptive ability in the habitat and occupied overlapping niches in the community.

Keywords interspecies association, community succession, dominant species, niche, tropical montane rain forest

1 Introduction

Vegetation communities are composed of coexisting species that are correlated temporally and spatially. Interspecies associations determine the structure and dynamics of the community. There are complex connections between different species in the community. Therefore, studies on these relationships will benefit dealing with differences in the stability and evolution of the community. The interspecies association represents the spatial relationship among different species, which is usually caused by differences in community habitat affecting species distribution (Greig-Smith, 1983; Wang et al., 1995). As a form of community correlation, interspecies association is an important characteristic as well as the basis of community form, maintenance and succession. Measuring the extent of spatial association is important in studying the formation of structures at the community level, population evolution and the dynamics of community succession. Association analysis as a diagnostic method illustrating the mechanism of species interaction is favored by ecologists, especially by ecologists in community research (Schluter, 1984; Wang and Peng, 1985; Myster and Pickett, 1992; Peng, 1996). However, disputes about the relationships between interaction of species and dynamics of community succession also exist (Thompson, 1982). Interspecies association is one of focus problems for community successional theory (Pickett and McDonnell, 1989).

Previous studies for species interspecies association were usually based on an investigation of one successional stage or on an analysis of dominant species and key

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Fude LIU, Jianwei ZHENG, Zhongsheng WANG, Shiting ZHANG, Wenjie YANG, Shuqing AN (✉)
Laboratory of Forest Ecology and Global Changes, School of Life Science, Nanjing University, Nanjing 210093, China
E-mail: anshq@nju.edu.cn

Wenjin WANG
Shanghai Garden Administration Bureau, Shanghai 200023, China

Ming ZHANG
Nanjing Institute of Environmental Sciences, State Environmental Protection Administration of China, Nanjing 210042, China

species association. However, these studies largely focused on vegetation located at temperate, subtropical and south subtropical zones (Myster and Pickett, 1992; Du et al., 1995; Peng, 1996; Zhou et al., 2000; Zhang and Tao, 2003). In this study, we selected a tropical montane rain forest with high species diversity as our study area where plots were set up in early successional and late successional stages. Interspecies associations were measured and dynamic changes during the course of succession were probed. As a consequence of our study, we uncovered the interaction of interspecies association and community succession.

2 Study site

Our study was conducted in the tropical montane rain-forest at Diaoluo Mountain in southeastern Hainan. Diaoluo Mountain (18°42'–18°52'N, 108°49'–108°53'E) is the main part of the mountains of southern Hainan. The foot of the mountain is 50 m above sea level and the highest peak is 1520 m. According to the records of weather stations, the mean annual temperature of the tropical rain forest at 600 m elevation is 20.8°C. The mean maximum temperature is 23.9°C. The mean minimum temperature is 16.3°C and the accumulated temperature above 10°C up to 7989°C for the whole year. The period from November to January is the dry season and from April to October, the wet season. Annual rainfall is about 2566 mm with precipitation predominantly occurring during the wet season. From the lowest point to the highest peak of the mountain, the soil changes from a huangshan latersol (< 300 m elevation), to mountain yellow soil (300–1200 m high), to mountain-shrub-meadow soil (> 1200 m) (Wang et al., 1999).

Our plots were located at the Xinan Forest Farm of Diaoluo Mountain, with elevations ranging from 920 to 980 m. The vegetation type is a tropical montane rainforest. At an early successional stage, the structure of the community is simple, the vegetation, mainly tree seedlings and saplings or shrub, with most diameters at breast height (DBH) at less than 5 cm and height ranging from 3 to 5 m. The canopy density of this community is 0.86 with high species diversity in the understory, such as *Blechnum orientale*, *Polystichum tialooshanense*, *Dryopteris acutidens* etc.

At the late successional stage, the community structure is complex with big trees. The canopy is divided into three layers, the top layer ranging from 24 to 28 m, the DBH ranges from 40 to 60 cm, the maximum 100 cm. The height of the second layer ranges from 15 to 23 m and DBH from 15 to 30 cm. The height of the third layer ranges from 8 to 14 m and DBH from 5 to 10 cm. The canopy density of this community is 0.97 with a large number of species. On the basis of the number of trees

by family, species of the Lauraceae family are the most frequently occurring trees, accounting for 10.5% of all species. The proportion of Fagaceae was 10.0%, that of Myrtaceae 5.6% and Theaceae 4.9%. Among the 120 species, the dominant species were *Altingia obovata*, *Cyclobalanopsis augustinii* and *Schefflera octophylla*. In the plots surveyed, broom of bamboo and aerophytes were abundant, but buttress roots and interlayer plants were few. There was an occasional strangler phenomenon. Fallen trees and standing dead trees existed in the plots. There was little vegetation under the canopy and the litter layer was thick (Wang et al., 1999).

3 Methods

3.1 Field survey

Four permanent quadrats were surveyed. Two of them belong to early successional stages (plots 1 and 2) and the other two quadrats belong to later successional stages (plots 3 and 4). The area of each quadrat was 100 m × 50 m and then was subdivided into 50 small plots (10 m × 10 m). On each subplot all stems DBH ≥ 1 cm were counted and identified by species. We also recorded the relative coordinate of each plant (DBH ≥ 1 cm) within each plot. Nomenclature of family, genus, species and growth forms followed the *Flora hainanica* (Chun, 1964, 1965; Guangdong Institute of Botany, 1974, 1977).

3.2 Methods

3.2.1 Overall species association test

According to a theory by Schluter (1984), we can test overall species association (VR) based on the presence or absence of a species, formulated as follows:

$$VR = \frac{S_T^2}{\delta_T^2} \quad (1)$$

where $S_T^2 = \frac{1}{N \sum_{j=1}^N (T_j - t)^2}$, S_T the number of species, N the number of plots, T_j the number of species in plot j , t the average number of species per plot, $t = (T_1 + T_2 + \dots + T_N)/N$; $\delta_T^2 = \sum_{i=1}^m \frac{n_i}{N} (1 - \frac{n_i}{N})$, and n_i the number of plots with species i .

Given the null hypothesis of independence, $VR = 1$, if $VR > 1$, it indicates a positive association among species; if $VR < 1$, the association among species is negative; positive and negative associations can counteract each other. The statistic W ($W = N \cdot VR$) is used to test VR specifically,

if $\chi^2_{0.95,N} < W < \chi^2_{0.05,N}$, the association is insignificant; otherwise, it is significant.

3.2.2 Calculation of interspecific association coefficient

The association coefficient (*AC*) is used to indicate the degree of species association. It is an effective and simple method to test the association of species. Interspecies associations are calculated from a 2×2 contingency table and χ^2 is used to test the degree of interspecies correlation. Because the sites, which were selected randomly, were not continuous, we used the correction for continuity by Yates to calculate χ^2 (Greig-Smith, 1983; Wang and Peng, 1985; Müller-Dombois and Ellenberg, 1986). The formula is as follows:

$$\chi^2 = \frac{N(|ad - bc| - N/2)^2}{(a+b)(c+d)(a+c)(b+d)} \quad (2)$$

where *a* is the number of plot with two species occurred simultaneously, *b* and *c* the number of plots with one species occurred only, *d* the number of plot with two species absent simultaneously. If $\chi^2 < \chi^2_{0.01,1} = 2.706$, there is no correlation. If $\chi^2_{0.01,1} \leq \chi^2 < \chi^2_{0.05,1} = 3.841$, there are significant correlations between species. If $ad > bc$, the correlations are positive, otherwise, the correlations are negative (Zhang and Zheng, 2002).

3.2.3 Dominant species identification

Dominant species of the community were identified by a method based on their degree of dominance (Ohsawa, 1984). In this method, the relative basal area (*RBA*, %) of each species is calculated and taken as the degree of dominance. Given their values, species are ranked from high to low. Equation (3) is used to identify the dominant species of a community:

$$d = \frac{1}{S_T} \left[\sum_{i \in Q} (x_i - x)^2 + \sum_{j \in U} x_j^2 \right] \quad (3)$$

where *d* is the index of dominant species, x_i the *RBA* of the dominant species, *Q* the number of dominant species, *x* is the ideal percentage share of dominant species, x_j the *RBA* of the remaining species, *U* the number of remaining species. If only one species is dominant in the community, its ideal percentage share is 100%. If there were two

dominant species in the community, the ideal percentage share of each of the two species would be 50%. In the case of three dominant species in the community, the ideal percentage share of each of the three species is 33.3%. The ideal percentage shares of larger numbers of species may be deduced by analogy. The basal area is the cross sectional area at breast height.

4 Results

4.1 Community association variation

The results show $VR > 1$ in the two plots of the early successional stages, indicating a positive species association. But the association is not significant ($\chi^2_{0.95,50} = 34.764 < W < \chi^2_{0.05,50} = 67.505$). At the late successional stages, *VR* values in the two plots were 2.009 and 2.238, respectively, and the *W* values are larger than $\chi^2_{0.05,50}$ (67.505). The overall species association shows a significant positive correlation. Accordingly, we inferred that the positive correlation of the overall species was strengthened through the process of succession (Table 1).

4.2 Changes of the association proportion among overall species in the community

The proportion of positive and negative association of species-pairs shows a declining trend, while the proportion of null association species-pairs clearly increased. At the two late successional stages, the proportions were 76.34% and 81.20% respectively (Fig. 1).

The statistical result indicated that in the two plots, the positive association pairs accounted for 4.3% and 3.1% of the total positive pairs at the early successional stage, while the proportion dropped to 1.3% and 0.8% at the late successional stage. In the four plots, the proportion of negative association species-pairs accounted for of the total negative species-pairs were 4.6%, 3.7% and 3.9% and 4.3% respectively.

4.3 Association of dominant and companion species, the early-established species and later invading species at different successional stages

According to the method of degree of dominance, there were 14 dominant species at the early successional stages,

Table 1 Dynamics of associations among tree species in the tropical montane rain forest cover in Diaoluo Mountain, Hainan

successional stage	plot	<i>VR</i>	<i>W</i>	$(\chi^2_{0.95,50}, \chi^2_{0.05,50})$	test results
early stage	plot 1	1.018	50.9	(34.764, 67.505)	positive correlation
	plot 2	1.232	61.6	(34.764, 67.505)	positive correlation
late stage	plot 3	2.009	100.5	(34.764, 67.505)	significant positive correlation
	plot 4	2.238	111.9	(34.764, 67.505)	significant positive correlation

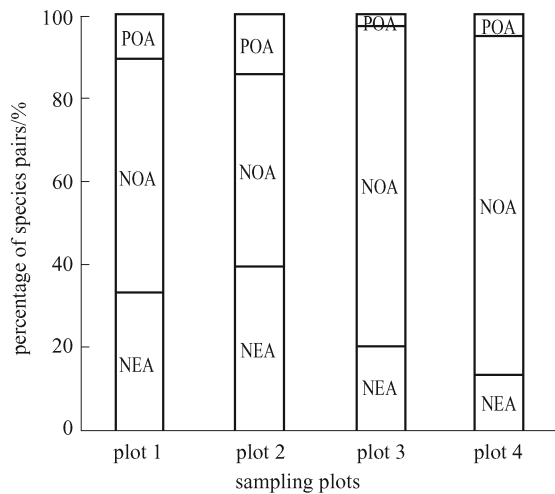


Fig. 1 Proportions of tree species-pairs with positive association (POA), negative association (NEA) and null association (NOA) at two successional stages in the tropical montane rain forest of Diaoluo Mountain, Hainan. Plots 1 and 2 are plots at an early stage and plots 3 and 4 are plots at a late stage.

such as *Symplocos poilanei*, *Lithocarpus caudatilimbus* and *Daphniphyllum paxianum* and 20 dominant species at the late successional stages, including *Altingia obovata*, *Cyclobalanopsis augustinii* and *Xanthophyllum hainanense*. Four species *Lithocarpus caudatilimbus*, *Polyspora balansae*, *Schefflera octophylla* and *Pentaphyllax euryoides* occurred at both early and late successional stages (Table 2). From the early stage to the late stage, the proportion of negative associations among the dominant and companion species dropped from 49.2% to 5.9% and that of positive association also declined, from 40.9% to

Table 2 Dominant species in tropical montane rain forest at early and late successional stages in Diaoluo Mountain, Hainan (Dominant species are ranked by degree of dominance)

dominant species at early successional stage	dominant species at late successional stage
<i>Symplocos poilanei</i>	<i>Altingia obovata</i>
<i>Lithocarpus caudatilimbus</i>	<i>Cyclobalanopsis augustinii</i>
<i>Daphniphyllum paxianum</i>	<i>Xanthophyllum hainanense</i>
<i>Eurya cuneata</i>	<i>Cyclobalanopsis championii</i>
<i>Polyspora balansae</i>	<i>Lithocarpus caudatilimbus</i>
<i>Schima superba</i>	<i>Lithocarpus handelianus</i>
<i>Alniphyllum fortunei</i>	<i>Eriobotrya deflexa</i>
<i>Symplocos pseudobarberina</i>	<i>Podocarpus imbricatus</i>
<i>Schefflera octophylla</i>	<i>Schefflera octophylla</i>
<i>Pentaphyllax euryoides</i>	<i>Syzygium araiocladum</i>
<i>Lindera kwangtungensis</i>	<i>Dacrydium pierrei</i>
<i>Podocarpus elliotii</i>	<i>Polyspora balansae</i>
<i>Decaspermum gracilentum</i>	<i>Ilex goshiensis</i>
<i>Rhamnus longipes</i>	<i>Cinnamomum rigidissimum</i>
	<i>Pentaphyllax euryoides</i>
	<i>Diospyros hainanensis</i>
	<i>Michelia shiluensis</i>
	<i>Antidesma maclurei</i>
	<i>Engelhardia unijuga</i>
	<i>Castanopsis carlesii</i>

30.9%. In contrast, the proportion of null association rose from 9.9% to 63.2% (Table 3). This result was similar to the changes in all the species associations with the process of community succession, i.e., the proportion of positive and negative association decreased and that of null association increased markedly. The proportion of positive associations among the dominant and companion species was more than that of negative associations at the late successional stage.

If we take the early dominant species as the early established species and the more recent species as the later invading species, we found six new invading species at the late stage, being *Cyclobalanopsis augustinii*, *Cyclobalanopsis championii*, *Ilex goshiensis*, *Cinnamomum rigidissimum*, *Diospyros hainanensis* and *Castanopsis carlesii*. The studies on the association among 14 early-constructive species and six later invading species indicated that of the 111 species-pairs, only 23 pairs (accounting for 20.7%) had negative association, while of the 21 later invading species pairs, there were seven pairs (33.3%) showing positive association and 14 pairs showing null association (accounting for 66.7%). What is more, among the early established species and later invading species pairs, there were 42 pairs (37.8%) with positive association and 46 pairs (41.5%) with null association. While there was no negative association among the later invading species pairs, the positive species association pairs (accounting for 33.3%), which is statistically significant.

In the top five species pairs ranked by positive association of the early successional stage, four species pairs were dominant species pairs and one was a dominant-companion species pair. The top five species pairs ranked by negative association all were dominant-companion species. In the top five species pairs ranked by positive association of the late successional stage, three species pairs were both dominant species pairs and two species pairs were dominant-companion species pairs, while the top five species pairs ranked by negative association all were dominant-dominant species pairs (Table 4). The variation in the *AC* values indicated that the highest positive association of the early successional stage was higher than that of late successional stage, while the highest negative association shows a reverse trend, indicating that the absolute value of the maximum interspecific association coefficient declined with the process of community succession.

5 Discussion

Interspecies association is usually the result of one of the following conditions: 1) species have similar (positive association) and different (negative association) environmental requirements; 2) one species created adaptive

Table 3 Number of species-pairs and proportion showing positive, negative and null associations for the dominant and companion species, the early established species and later invading species in the rainforest of Diaoluo Mountain, Hainan

association type	I	II	III	IV	V
positive	194 (40.9%)	256 (30.9%)	60 (65.6%)	7 (33.3%)	42 (37.8%)
negative	233 (49.2%)	522 (63.2%)	28 (30.8%)	0 (0)	23 (20.7%)
null	47 (9.9%)	49 (5.9%)	3 (3.3%)	14 (66.7%)	46 (41.5%)

Notes: Values outside the brackets is the number of species-pairs, the inside the proportion; I: between early dominant and companion species, II: between late dominant and companion species, III: between early established species, IV: between later invading species, V: between early established and later invading species.

Table 4 Top five species-pairs ranked by positive (POA) and negative association (NEA) at early and late successional stages, in tropical montane rain forests of Diaoluo Mountain, Hainan

	species pairs	association coefficient
top five species-pairs ranked by positive association at the early stage	<i>Rhamnus longipes</i> – <i>Decaspermum gracilentum</i>	0.7475
	<i>Rhamnus longipes</i> – <i>Daphniphyllum paxianum</i>	0.7405
	<i>Eurya cuneata</i> – <i>Daphniphyllum paxianum</i>	0.7321
	<i>Rhamnus longipes</i> – <i>Symplocos angustifolia</i>	0.6970
	<i>Daphniphyllum paxianum</i> – <i>Symplocos poilanei</i>	0.6429
top five species-pairs ranked by negative association at the early stage	<i>Decaspermum gracilentum</i> – <i>Symplocos angustifolia</i>	–0.8861
	<i>Syzygium chunianum</i> – <i>Eurya cuneata</i>	–0.8810
	<i>Daphniphyllum paxianum</i> – <i>Syzygium championii</i>	–0.8663
	<i>Eurya cuneata</i> – <i>Symplocos angustifolia</i>	–0.8095
	<i>Symplocos poilanei</i> – <i>Illicium ternstroemioides</i>	–0.7959
top five species-pairs ranked by positive association at the late stage	<i>Schefflera octophylla</i> – <i>Polyalthia rumphii</i>	0.5308
	<i>Schefflera octophylla</i> – <i>Goniothalamus gardneri</i>	0.5308
	<i>Engelhardia unijuga</i> – <i>Dacrydium pierrei</i>	0.3061
	<i>Altingia obovata</i> – <i>Syzygium araiocladum</i>	0.2888
	<i>Xanthophyllum hainanense</i> – <i>Antidesma maclurei</i>	0.2599
top five species-pairs ranked by negative association at the late stage	<i>Schefflera octophylla</i> – <i>Polyspora balansae</i>	–0.7024
	<i>Castanopsis carlesii</i> – <i>Antidesma maclurei</i>	–0.5370
	<i>Michelia shiluensis</i> – <i>Cyclobalanopsis championii</i>	–0.5238
	<i>Diospyros hainanensis</i> – <i>Cyclobalanopsis championii</i>	–0.4898
	<i>Altingia obovata</i> – <i>Diospyros hainanensis</i>	–0.4361

habitat conditions for another species, forming a positive association; 3) negative association is formed by two species in conflict with each other in resource competition; 4) the indirect effect of physical or chemical factors may cause positive or negative association (Greig-Smith, 1983; Kershaw and Looney, 1985). At the early community successional stages of the tropical montane rain forest in Diaoluo Mountain, some positive pioneer trees such as *Symplocos poilanei*, *Lithocarpus caudatilimbus*, *Daphniphyllum paxianum* and *Eurya cuneata* first occupy bare land or grass fields. They have similar environmental requirements. However, they have competitive utilization of environmental resources, especially for light, resulting in the high positive and negative association proportions among the overall species in the community (Fig. 1 and Table 3) and positive but insignificant associations of overall species in the community. At the late successional stage, as the pioneer species die, neutral and shade tolerant species appear and the early community, predominated by saplings and herbage, gradually changed to a late community with three canopy layers and a complex structure. At the same time, the average species density and proportion of null associations increased noticeably and the

proportion of negative association decreased dramatically (Fig. 1 and Table 3), while the overall species association shows a significant positive correlation. With the process of succession, the structure and category of community also presented a positive correlation in order to attain a stable stage where species coexist in harmony (Du et al., 1995; Liu et al., 1996). The overall species association reflects the stability of the community in each successional stage, especially that exhibited by significant positive correlations in the late stage (Zhang and Tao, 2003). Thus, the changes of species relationships confirm this viewpoint and indicate that the community was inclined to stability and maturity at the late stage.

With the process of community succession, the constituent species shows dynamic changes and therefore, the function and relationships in different communities also changed. During the successional course, the proportion of interspecies association (i.e., the ratio of positive or negative association pairs in the total species pairs) and association intensity (the statistical degree of significance) also increased over time (O'Connor and Aarssen, 1987). The basis for this deduction is that the number and intensity of interactive species in the community increased with

the process of succession (Pickett and Bazzaz, 1978; Bazzaz, 1979; Parrish and Bazzaz, 1982).

Whereas, during the community successional course of the tropical montane rain forest in Diaoluo Mountain, the proportion and intensity of interspecies associations among dominant and companion species indicated that null associations clearly increased (Fig. 1 and Table 3) and the competition among species gradually decreased, the number of dominant species increased and the layered community structure, as well as phenomenon of niches division, became more complex. As a result, the dependence among species largely decreased and species inclined to an independent distribution. The change in proportion of interspecies association and density was inconsistent with the deduction reached above. The reason for this disagreement might be that previous studies largely took seedlings as study objects in early succession while our study focused on saplings in early succession. The community succession of tropical montane rain forests is a long term and complex process. Myster and Pickett (1992) studied the dynamic succession of different aged communities from 1 to 31 years after farming stopped in Somerset and Buell, New Jersey, USA. The results indicated that 7 to 12 years after farming ended, the proportion of positive association species pairs in the community shows at first an increasing trend and then gradually decreased after 12 years. The proportion of null association pairs decreased and then, increased, while negative association pairs show a decline from year 7 to year 31, after farming stopped. These results do not agree with the deduction that the species interaction increases over time of succession.

During the course of community succession, the niches division became complex with increasing species diversity (Bazzaz, 1975; Carson and Pickett, 1990). The later invading species and early-established species may have shown negative associations, while the later invading interspecies generally show positive associations (Myster and Pickett, 1992). In the tropical montane rain forest in Diaoluo Mountain, the association between early-established species and later invading species consisted of almost positive and null associations. This is not at all similar to the studies reported by Myster and Pickett (1992) where possibly the annual and biennial plants were taken as early-established species and the woody species appeared later as invading species. In our study, the dominant species of the early successional stage were seen as the early-established species and the dominant species in late successional stage as later invading species. The effect of herbage was not considered and the process of succession in our study was much longer. However, our studies on the interspecies association for later invading species were similar to the prediction by Myster and Pickett (1992), where positive associations accounted for 1/3, which are statistically significantly, while the other 2/3 were null associations and no negative associations appeared, indicating that these invading species

had similar adaptive ability to the habitat and usually were mutually depended to make the best of resources available, but they largely existed independently.

6 Conclusions

From our studies we can conclude that an overall positive association was present among tree species of the communities during the two successional stages, which became statistically significant at the late stage. These results indicate that the communities are developing towards a stable state where the tree species coexist in harmony. The proportion of negative interspecies associations among dominant and companion species decreased while the development of succession increased. The proportion of null interspecies associations increased dramatically, species inclines towards independence. There was no negative associations among later invading species, but positive associations were significant. The associations between early-established species and later invading species were close to positive and null associations. They coexisted independently through changes in the community structure and partitioning of resources.

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