# BETA DIVERSITY PATTERN AND ITS DRIVING FORCES OF FENGSHUI WOODS IN SOUTH CHINA

## WW Song, GJ Lin[1], HL Cao[2] and L Ma[3]*

*State Environment Protection Key Laboratory of Urban Environment & Ecology, South China Institute of Environmental Science, Ministry of Environmental Protection, P. R. China*

*Key words:* Fragmented forest, Nestedness, Spatial turnover, Stochastic processes, Variation partitioning

## Abstract

Based on the inventory of 67 fengshui woods, we first decomposed the beta diversity of these communities into nestedness and spatial turnover; then we quantified the relative contribution of abiotic factors to the variation of species composition using variation partitioning method at the meta-community scale. We found that the species composition was heterogeneous with high beta diversity and characterized by obvious spatial turnover pattern. Abiotic variables explained only a little variation of species composition; instead, undefined environmental variables and stochastic processes were the main factors driving species assemblage of fengshui woods in this study. For the sustainability of fengshui woods, management and conservation efforts should be devoted to a large range of fengshui communities instead of only focusing on several ones. Furthermore, linking the conservation of traditional culture and nature is likely to be more effective in managing and conserving fengshui woods than ignoring traditional beliefs, values and institutions.

## Introduction

Study on variation in species composition among fragmented communities (beta diversity) is a fundamental step for the conservation of biodiversity and for ecosystem management (Legendre *et al.* 2009, Carvalho *et al.* 2011). Beta diversity reflects two different phenomena: spatial turnover and nestedness (Baselga *et al.* 2007). Spatial turnover occurs when species in one site is substituted by different species in other sites. Contrary to spatial turnover, nestedness of species assemblages means the species of sites with smaller numbers of species are subsets of the species at richer sites (Almeida-Neto *et al.* 2011). The intrinsic value of separating the contribution of nestedness and spatial turnover patterns is for a deep understanding of the composition of beta diversity and for management and conservation issues (Baselga 2010). Spatial turnover pattern implies that a large number of different sites should be devoted management and conservation efforts, whereas nestedness pattern requires that sites with the richest species should have management and conservation priority.

A variety of deterministic and stochastic mechanisms can lead to the nestedness or spatial turnover pattern of beta diversity. Ulrich *et al.* (2009) reviewed that passive sampling, neutrality, selective environmental tolerances and habitat quality had been proposed for explaining nestedness. Similarly, spatial turnover pattern was considered as a consequence of environmental sorting or spatial and historical constraints (Baselga 2010). Furthermore, perfectly nestedness or spatial turnover is rare in nature; most communities are combinations of nestedness and spatial turnover patterns (Carvalho *et al.* 2011). Therefore, understanding processes behind beta diversity pattern, analyses of nestedness and spatial turnover patterns should be accompanied by appropriate environmental gradient and spatial analyses.

*Author for correspondence. <qdmalei@sina.com>. [1]Changjiang Water Resources Protection Institute, Qintai Road 515, Wuhan, 430051, P.R. China. [2]South China Botanical Garden, Chinese Academy of Sciences, Xingke Road 723, Guangzhou, 510650, P.R. China. [3]Key Laboratory of Geospatial Technology for the Middle and Lower Yellow River Regions, College of Environment and Planning, Henan University, Jingming Road, Kaifeng, 475001, P. R. China.

Environmental gradient and spatial distance are perhaps the two predictors that are most widely invoked to explain the beta diversity pattern (Laliberté *et al.* 2009, Jamoneau *et al.* 2012). According to the niche theory, species distribution is determined by habitat heterogeneity because species differ in their response to resources (Freestone and Inouye 2006). As dispersal process is strongly spatial independent, beta diversity is predicted to increase along spatial gradients (Cottenie 2005). Beyond dispersal limitation, other stochastic processes may influence the beta diversity pattern (Smith and Lundholm 2010). Although early studies investigated the effects of stochastic processes on extinction and beta diversity pattern (Chase and Myers 2011), stochastic processes is often ignored by field ecologists because of its impenetrability and difficulties in its application (Gravel *et al.* 2011). To increase the identification of drivers of beta diversity pattern and for the sustainability of forest communities, it is important to clearly disentangle the contribution of habitat heterogeneity, dispersal limitation and other stochastic processes on beta diversity pattern, especially for fragmented forests. These types of knowledge will add to our understanding of fengshui communities to achieve sustainability, but are still poorly studied. In this study, we examined the beta diversity pattern and its determinants based on sampled data from fengshui woods in South China. This study will deepen our understanding of beta diversity in these forests.

**Materials and Methods**

The study was carried out in Guangzhou city (E 112°57'~114°3', N 22°26'~23°56'), China (Fig. 1). The prevailing climate is subtropical monsoon climate. Rainfall mainly occurs between April and September with a mean annual precipitation of 1600 mm. The annual average temperature is 22.8°C. The native forests are mainly composed by universal tropical- and temperate-originated species. Fengshui woods, as one kind of fragmented natural heritage forests, distributed widely in the South China. Fengshui woods have been protected by generations of villagers. They have retained features of original vegetation, and have been influenced by human beings because it is so close to villages (Ma *et al.* 2015).
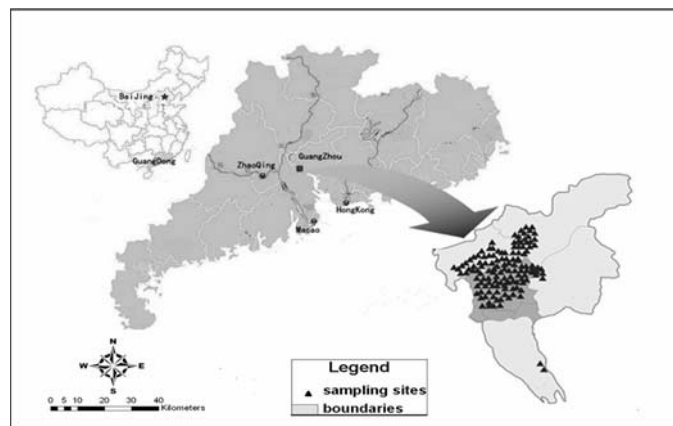


Fig. 1. Sixty seven fengshui wood patches were selected randomly in Guangzhou city.

In 2010, 67 fengshui wood patches were selected randomly in Guangzhou city (Fig. 1). Among these 67 patches, the smallest one was 1.10 ha, the largest was 41.10 ha, and the average patch size was 11.33 ha. We established 20 m × 20 m plots (Echeverría *et al.* 2007) in the centre of

each fengshui wood patch. Species were identified within each plot. Elevation, slope and aspect of each plot were recorded.

In this study, we used the method developed by Carvalho *et al.* (2011):

Total beta diversity $\beta_{cc} = (b + c)/(a + b + c)$        (1)

Replacement (turnover) $\beta_{-3} = 2 \times \min (b,c)/(a + b + c)$     (2)

Richness differences (nestedness) $\beta_{rich} = |b - c|/(a + b + c)$    (3)

$\beta_{cc} = \beta_{-3} + \beta_{rich}$                                (4)

where a is the number of species common to both sites, b is the number of species present in the first site but not in the second site and c is the number of species that occur in the second but not in the first.

We wanted to quantify the relative contributions of environmental factors, spatial distance and stochastic events to the dissimilarity of fengshui communities using the variation partitioning method. The species abundance data table of our 67 fengshui plots was considered as response matrix, and spatial and topographic variables were considered as explaining matrices. The spatial matrix was structured using the Principal Coordinates of Neighbor Matrices (PCNM) method (Dray *et al.* 2006, Jones *et al.* 2008).

All of our analyses were completed using R language (version 2.13.0) (R development core team 2010). Fig. 1 was plotted with "mapdata" and "googleVis" packages (Brownrigg *et al.* 2011, Gesmann and Castillo 2011).

## Results and Discussion

In each plot, each stem with diameter at breast height (DBH) no less than 1 cm was identified to species. As a result, 184 species belonging to 119 genera and 53 families were recorded. *Saurauia tristyla, Caryota maxima, Castanopsis fissa, Litsea rotundifolia, Ligustrum quihoui, Acronychia pedunculata,* and *Ficus microcarpa* were the seven most abundant species with more than 200 individuals recorded.

Total beta diversity ($\beta_{cc}$), turnover ($\beta_{-3}$) and nestedness ($\beta_{rich}$) do not appear to correlate with spatial distance (Fig. 2), and turnover between pairwise plots is significantly greater than nestedness (p value was less than 2.20e-16). The average $\beta_{cc}$, $\beta_{-3}$ and $\beta_{rich}$ of all possible pairwise plots are 0.81, 0.61 and 0.20, respectively.

Spatial distance between our sampling plots ranges from 0.3 km to 61.7 km and the average distance is 26.3 km. Five PCNM variables were selected from the total 35 PCNM variables to represent spatial effect. The result of variation partitioning shows that topography and spatial distance contribute little (0.9 and 5.8%, respectively) for the dissimilarity of fengshui wood communities (Fig. 3). Most of the variations have not been explained.

Due to environmental variation or dispersal limitation, heterogeneous species composition may be common in fragmented forest (Jamoneau *et al.* 2012). However, our result (Figure 3) showed that topographic variables and dispersal limitation was not good predictors for the variation of species composition of fengshui communities. Significant spatial effect does not equal to significant dispersal limitation effect, because potential spatially-structured environmental variables that we did not investigate may result in an overestimation of dispersal limitation effect (Jones *et al.* 2008). Conversely, any dissimilarity independent of spatial distance could refute the impact of dispersal limitation (Chase and Myers 2011). In our analysis (Fig. 3), pure spatial variables only contributed less than 6% variation of species composition among different fengshui communities. This provided strong evidence to ignore the effect of dispersal limitation on the structuring of beta diversity pattern of fengshui communities. Meanwhile, although the adjusted

r-square of topographic variables was very low (Fig. 3), we cannot neglect the contribution of habitat heterogeneity to the beta diversity pattern of fengshui communities, because there are many environmental factors were not included in our analysis (e.g., soil properties) that may be important for fengshui community assemblage; instead, based on our results, we can only infer that topographic factors have little influence on the beta diversity pattern of fengshui communities.
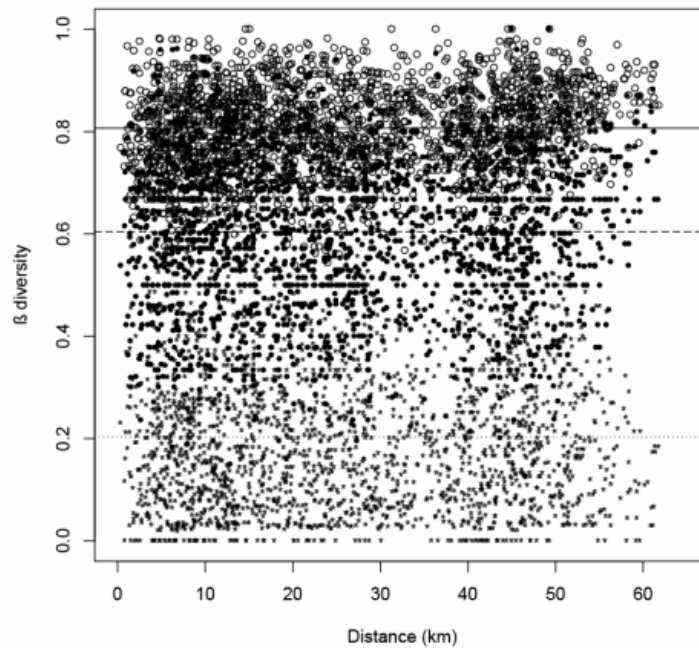


Fig. 2. Beta diversity decomposition. The hollow circle, solid circle and asterisk are pairwise total beta ($\beta_{cc}$), turnover ($\beta_{-3}$) and nestedness ($\beta_{rich}$), respectively. The soild, long-dash and dotted lines are the mean value of $\beta_{cc}$, $\beta_{-3}$ and $\beta_{rich}$, respectively.
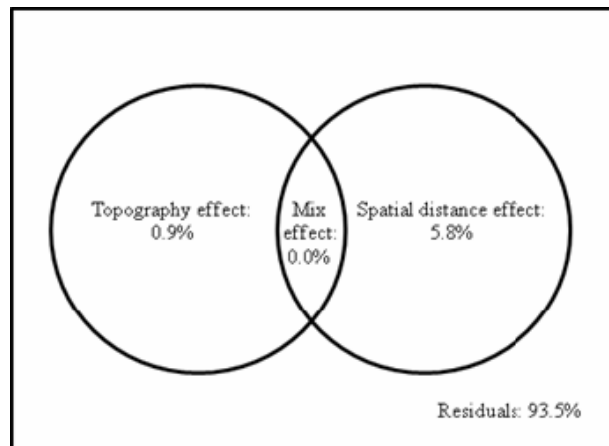


Fig. 3. Fractions issued from variation partitioning using the dissimilarity of fengshui wood communities versus topographic and spatial explanatory tables. The value in the circle represents the explanatory power (adjusted r-square) of each fraction.

Chiarucci *et al.* (2008) reported that complex geological, topographical and land use patterns lead to high beta diversity. Kreft *et al.* (2008) presented a meta-analysis of 488 island and 970 mainland floras showing that environment was a strong factor explaining composition variation. Undefined habitat heterogeneity (e.g., differentiation of soil properties) may contribute highly to the community heterogeneity of fengshui woods.

Unexplained fraction of variation of species composition masks two components of uncertainty: inadequate characterization of the exact environment and stochastic processes (Legendre *et al.* 2009); whatever, the reality that most variation of species composition of fengshui wood communities had not been explained by topography and dispersal limitation implied the prominent effect of stochastic events on species assemblage. This is not strange because forest management-associated disturbances can produce heterogeneity and make species assemblages more random than expected (Jamoneau *et al.* 2012). For hundreds of years, fengshui woods have constantly been directly or indirectly influenced by villagers to varying degrees. Through the years, some species may have disappeared from one fengshui wood patch because of natural and/or human disturbance, while other species may have appeared through accidental importing. Some studies (Laurance 2008, Riitters *et al.* 2012) reported that fragmentation would drive the homogenization of the remaining forest, as tree species composition was expected to shift towards edge-adapted species. Furthermore, this edge effect is supposed to increase with neighbored agriculture intensity (Cardelus *et al.* 2012). Fengshui woods are usually surrounded by cultivated fields and human villages; however, it is obvious that the species composition of fengshui woods has not been homogenized. Contemporary and historical random processes have overcome the homogenization effect and driven the species turn over pattern of fengshui woods.

Heterogeneous communities, characterized by obvious spatial turnover pattern require great management and conservation efforts to sustain the fengshui woods. On the one hand, heterogenization of species composition increases the maintaining value of forest communities because of its increased biodiversity and other ecological service functions. The high beta diversity (Fig. 2) suggests that fengshui woods deserve to make great effort for managing and conservation. On the other hand, high proportion of turnover in total beta diversity means that protecting one or several fengshui communities will provide limited benefit for regional species diversity conservation. In order to conserve a large range of species, it is necessary to protect all of the fengshui wood communities. Linking the conservation of traditional culture and nature is likely to be more effective in conserving fengshui woods than ignoring traditional belief, values and institutions.

**References**

Almeida-Neto M, Frensel DMB and Ulrich W 2011. Rethinking the relationship between nestedness and beta diversity: a comment on Baselga. Global Ecol. Biogeogra. **21**(7): 772-777.

Baselga A 2010. Partitioning the turnover and nestedness components of beta diversity. Global Ecol. Biogeogra. **19**: 134-143.

Baselga A, Jimenez-Valverde A and Niccolini G 2007. A multiple-site similarity measure independent of richness. Biol. Letters. **3**: 642-645.

Brownrigg R, Becker RA and Wilks AR 2011. Extra map databases. R package (version 2.1-4).

Cardelus CL, Lowman MD and Eshete AW 2012. Uniting church and science for conservation. Science. **335**: 915-916.

Carvalho JC, Cardoso P and Gomes P 2011. Determining the relative roles of species replacement and species richness differences in generating beta-diversity patterns. Global Ecol Biogeogra. **21**(7): 760-771.

Chase JM and Myers JA 2011. Disentangling the importance of ecological niches from stochastic processes across scales. Roy. Soc. Philos .T. Biol. Sci. **366**: 2351-2363.

Chiarucci A, Bacaro G and Rocchini D 2008. Quantifying plant species diversity in a Natura 2000 network: Old ideas and new proposals. Biol. Conserv. **141**: 2608-2618.

Cottenie K 2005. Integrating environmental and spatial processes in ecological community dynamics. Ecol. Lett. **8**: 1175-1182.

Dray S, Legendre P and Peres-Neto PR 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecol. Model. **196**: 483-493.

Echeverría C, Newton AC, Lara A, Benayas JMR and Coomes DA 2007. Impacts of forest fragmentation on species composition and forest structure in the temperate landscape of southern Chile. Global Ecol Biogeogra. **16**: 426-439.

Freestone AL and Inouye BD 2006. Dispersal limitation and environmental heterogeneity shape scale-dependent diversity patterns in plant communities. Ecology **87**: 2425-2432.

Gesmann M and Castillo DD 2011. googleVis: Interface between R and the Google Visualisation API. R package (version 0.2.11).

Gravel D, Guichard F and Hochberg ME 2011. Species coexistence in a variable world. Ecol. Lett. **14**: 828-839.

Jamoneau A, Chabrerie O, Closset-Kopp D and Decocq G 2012. Fragmentation alters beta-diversity patterns of habitat specialists within forest metacommunities. Ecography **35**: 124-133.

Jones MM, Tuomisto H, Borcard D, Legendre P, Clark DB and Olivas PC 2008. Explaining variation in tropical plant community composition: influence of environmental and spatial data quality. Oecologia. **155**: 593-604.

Kreft H, Jetz W, Mutke J, Kier G and Barthlott W 2008. Global diversity of island floras from a macroecological perspective. Ecol. Lett. **11**: 116-127.

Laliberté E, Paquette A, Legendre P and Bouchard A 2009. Assessing the scale-specific importance of niches and other spatial processes on beta diversity: a case study from a temperate forest. Oecologia. **159**: 377-388.

Laurance WF 2008. Theory meets reality: How habitat fragmentation research has transcended island biogeographic theory. Biol. Conserv. **141**: 1731-1744.

Legendre P, Mi X, Ren H, Ma K, Yu M, Sun I-F and He F. 2009. Partitioning beta diversity in a subtropical broad-leaved forest of China. Ecology **90**: 663-674.

Ma L, Huang M, Shen Y, Cao H, Wu L, Ye H, Lin G and Wang Z 2015. Species diversity and community structure in forest fragments of Guangzhou, South China. J. Trop. For. Sci. **27**: 148-157.

R development core team. 2010. R: a language and environment for statistical computing. Available online at: http://www.r-project.org/; last accessed July 22, 2013.

Riitters KH, Coulston JW and Wickham JD 2012. Fragmentation of forest communities in the eastern United States. For Ecol Manage **263**: 85-93.

Smith TW and Lundholm JT 2010. Variation partitioning as a tool to distinguish between niche and neutral processes. Ecography. **33**: 648-655.

Ulrich W, Almeida-Neto MR and Gotelli NJ 2009. A consumer's guide to nestedness analysis. Oikos. **118**: 3-17.

*(Manuscript received on 20 May, 2016; revised on 6 October, 2016)*