

# Determinants of plant species richness and patterns of nestedness in fragmented landscapes: evidence from land-bridge islands

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**Abstract** Land-bridge islands formed by dam construction are considered to be “experimental” systems for studying the effects of habitat loss and fragmentation, offering many distinct advantages over terrestrial fragments. The Thousand Island Lake in Southeast China is one such land-bridge system with more than 1000 islands. Based on a field survey of vascular plant richness on 154 land-bridge islands during 2007–2008, we examined the effects of island and landscape attributes on plant species richness and patterns of species nestedness. We also examined the different responses of plant functional groups (classified according to growth form and shade tolerance) to fragmentation. We found that island area explained the greatest amount of variation in plant species richness. Island

area and shape index positively affected species diversity and the degree of nestedness exhibited by plant communities while the perimeter to area ratio of the islands had a negative effect. Shade-tolerant plants were the most sensitive species group to habitat fragmentation. Isolation negatively affected the degree of nestedness in herb and shade-intolerant plants including species with various dispersal abilities in the fragmented landscape. Based on these results, we concluded that the effects of habitat loss and fragmentation on overall species richness depended mostly on the degree of habitat loss, but patterns of nestedness were generated from different ecological mechanisms due to species-specific responses to different characteristics of habitat patches.

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## Introduction

Increasing human activities and land development are driving a decrease in area of natural habitats and simultaneously isolating the remaining natural habitats into discrete fragments. This process of habitat loss and fragmentation is widely considered to be one of the primary threats to global biodiversity (Wilcove et al. 1998; Fahrig 2003; Laurance 2008). Thus an important goal of landscape ecology and conservation biology is to understand the changing patterns and processes of species diversity and community structure in fragmented landscapes.

Four of the primary attributes of the remnant habitat fragments that may influence patterns of species richness and community assembly are: patch area, patch isolation, patch edge to interior ratio, and patch shape complexity (Saunders et al. 1991; Ewers and Didham 2007; Fischer and Lindenmayer 2007; Keppel et al. 2010). Area and isolation are generally considered to be the two most important factors affecting species richness and community assembly in fragmented landscapes due to their respective influences on extinction and colonization rates, as explained by the Equilibrium Theory of Island Biogeography (MacArthur and Wilson 1963; MacArthur and Wilson 1967; Lomolino 2000; Laurance 2008). Indeed, in many fragmented landscapes, the area effect is so strong that it can mask any effects of other patch or landscape attributes on species richness (Rosenberg et al. 1999; Trzcinski et al. 1999; Caley et al. 2001).

Nestedness is a useful complementary measure to species richness because it considers both the richness and identity of species in fragments, and provides important information about the pattern of community assembly (or disassembly) in response to landscape fragmentation. Nested patterns are those in which the species in the more depauperate communities are also present in species-rich communities (Atmar and Patterson 1993; Ulrich et al. 2009). The nested rank-order of sites is often related to patch area, such that more complete communities are found in larger

fragments. This may be due to passive sampling (an artifact of stochastic principles generating nestedness, which is due to rare species being less sampled in a given area than common species, Andren 1994; Higgins et al. 2006), selective extinction (Patterson 1984; Simberloff and Levin 1985; Wright et al. 1998), and/or patterns of habitat heterogeneity (Worthen 1996; Wright et al. 1998; Calme and Desrochers 1999; Honnay et al. 1999). Nested patterns may also be indirectly associated with area due to correlations between area and other factors such as fragment shape and amount of edge habitat which may modify habitat quality and/or heterogeneity (Murcia 1995; Hill and Curran 2003; Ewers et al. 2007; Laurance 2008). In addition, nested patterns may be strongly influenced by factors that are independent of area—such as patch isolation due to the selective colonization among species with different dispersal abilities (Darlington 1957).

Previous studies have documented many interesting results from the studies of habitat fragmentation (Bowman et al. 2002; Chalfoun et al. 2002; Wang et al. 2010a), but in many cases conclusions about the ecological effects of fragmentation are unclear or ambiguous. Ambiguity regarding the effects of habitat loss and fragmentation may be due to complex relationships among numerous biotic and abiotic factors; for example, the influences of the surrounding heterogenic matrices, ecological succession, and disturbances (Laurance 2008; Collins et al. 2009; Prevedello and Vieira 2010).

Land-bridge islands (islands created by rising water level with a concomitant habitat loss, Diamond 1972) and especially those formed by man-made dam construction, offer several potential advantages over terrestrial habitat patches or oceanic islands for studying the effects of habitat loss and fragmentation on biodiversity. This is because large numbers of patches are created over a relatively short time period by a single known disturbance event. In addition, land-bridge islands have well-delineated boundaries and are surrounded by an inhospitable matrix (i.e., water) that is temporally and spatially homogeneous. Also, distinct from oceanic islands which can host endemic or specialized species, the species composition of land-bridge islands are more similar to the terrestrial habitat (Terborgh et al. 1997). As a result of this combination of characteristics, land-bridge islands are sometimes considered a “model” or “experimental”

system for studying habitat fragmentation (Gotelli and Graves 1990; Diamond 2001; Terborgh et al. 2001; Wu et al. 2003; Terborgh and Feeley 2008).

Beyond patch or landscape factors, differences in the functional traits of the species themselves are likely to be important factors in determining patterns of species richness and nestedness in fragmented landscapes. In plants, different functional groups have been found to have different sensitivities to habitat loss and fragmentation and associated changes in habitat configuration or quality (Dettki et al. 1998; Henle et al. 2004; Ewers and Didham 2005; Cagnolo et al. 2009). Functional traits that are commonly hypothesized to increase species' vulnerability to fragmentation include limited dispersal, interior habitat requirements, and greater ecological specialization (Fahrig 2007; Feeley et al. 2007; Laurance 2008; Wang et al. 2009). For example, Benitez-Malvido and Martinez-Ramos (2003) found that the recruitment of trees, palms, and herbs were decreased in fragmented forests but that lianas had higher recruitment rates in fragmented forests than in continuous forests. Selective species loss depending on differences in functional traits may also be responsible for nestedness (Blake 1991; Honnay et al. 1999; Stiles and Scheiner 2008). Therefore, examining how patch attributes in a system of man-made land-bridge islands influence richness and nestedness of species within multiple functional groups may provide important insights into

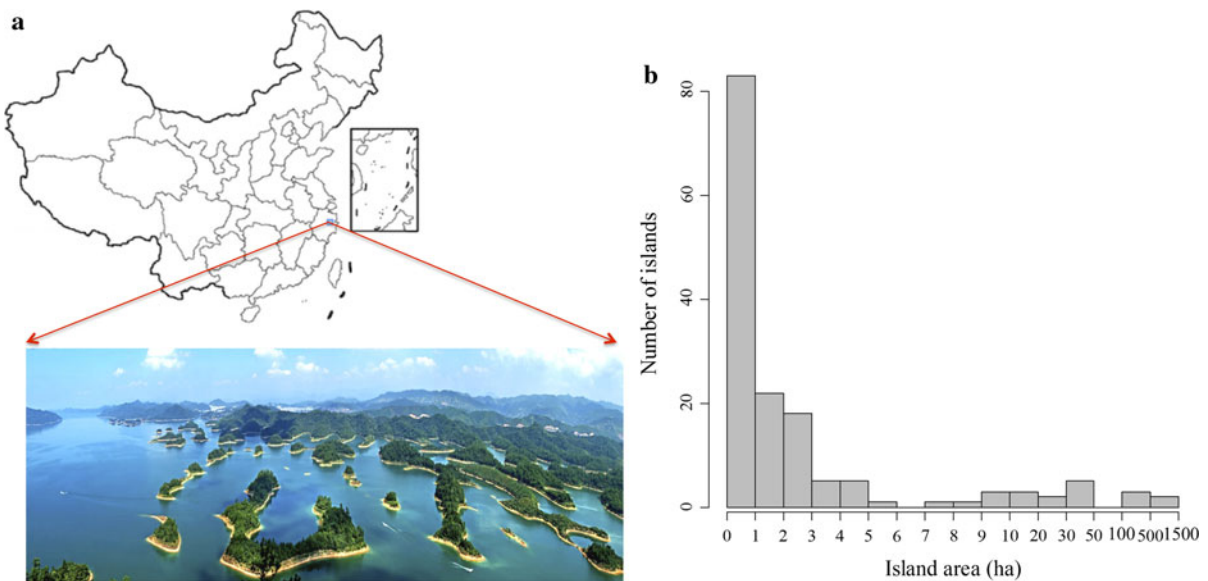
the mechanisms of how habitat loss and fragmentation affect plant communities.

In this study, we investigated species richness and nestedness of vascular plants on 154 islands in a large man-made reservoir—the Thousand Island Lake (TIL) in Southeast China. To study the contribution of the island attributes to the effects of habitat loss and fragmentation, we tested the hypothesis that area and isolation are the primary determinants of richness and nestedness of plant communities in the fragmented landscape. We also tested the hypothesis that plant groups with special habitat requirements will be more sensitive to habitat loss and fragmentation as reflected in their patterns of richness and nestedness. Specifically, we addressed three questions: (1) How do the species-area relationships and patterns of nestedness differ between plant functional groups in the TIL region? (2) What factors drive the species richness of different functional groups in the fragments? (3) What mechanisms are responsible for the observed patterns of nestedness for all plants and the different functional groups on these islands?

## Methods

### Study site

The Thousand Island Lake is a large man-made hydroelectric reservoir in western Zhejiang Province,



**Fig. 1** The **a** locations of the 154 land-bridge islands and **b** distribution of study island area in the Thousand Island Lake (TIL), China

China (located at 29°22′–29°50′N and 118°34′–119°15′E; Fig. 1a). True to its name, the inundation of a mountainous area of 573 km<sup>2</sup> following the dam construction on the Xin'an River in 1959 resulted in 1078 land-bridge islands larger than 0.25 ha when the water reached its highest level (108 m a.s.l.) (Editorial Committee of Development of Xin'an River 2009). TIL is within a middle subtropical zone with a monsoon climate (i.e., hot and wet summers and cold and dry winters). The mean annual temperature is 17.0°C, with a low of –7.6°C in January and a high of 41.8°C in July. Mean annual precipitation in the TIL region is 1,430 mm with an average of 155 days of precipitation per year with most rain falling from April to June (Wang et al. 2010b). Before dam construction and simultaneous emigration of local people, the forests on the hills were clear-cut. The lake has been protected by law and the vegetation on the islands (erstwhile hilltops) has not experienced significant human disturbance. As such, the current vegetation on islands is predominantly the result of approximately 50 years of natural succession. Currently, 88.5% of area on the islands is covered by forest and most of these forested areas (~90%) are natural secondary forests dominated by Masson pine (*Pinus massoniana*).

#### Data collection

We conducted detailed surveys of all vascular plant species on 154 islands (Fig. 1a) during the growing season (April to November) of 2007 and 2008. The study islands spanned a wide range of island areas from 0.02 to 1153.88 ha (Fig. 1b; mean ± SD: 17.74 ± 110.96 ha), but a narrow range of elevations (mean ± SD: 133.85 ± 31.21 m). During the field survey, we collected data on the occurrence of plant species (i.e., presence/absence—abundance data were not collected) through multiple visits to all focal islands. Surveys were designed to record the maximum possible number of species. On the islands <50 ha (149 islands), islands were circumnavigated and 4–16 transects were established (number and total length of transects were dependent on the shape and size of the focal island). Each transect was walked a minimum of three times by trained observers. For the other five larger islands, each >100 ha in area, surveys were conducted as above but centered on each prominent hill. Species accumulation curves indicate

that these methods were sufficient to capture all or most species present on the islands (data not shown). Most plant species were identified and recorded in the field. Specimens of species that could not be identified in the field were collected and identified in the lab with the assistance of a taxonomic expert and based on available literature (Editorial Committee of Flora of Zhejiang 1993; Zheng 2005).

For the purpose of this study, functional groups are defined as suites of species that have similar physiological and environmental requirements and similar responses to disturbance (Steneck 2001). We divided all plant species found on the study islands on the basis of two plant traits, growth form (tree, shrub, herb, or liana) and shade tolerance (shade-intolerant or shade-tolerant). Thus, there were a total of seven plant functional groups (all plants, shade-intolerant plants vs. shade-tolerant plants, and tree vs. shrub vs. herb vs. liana) included in this study. Plant trait data were based on the expert opinions and species description in the available literature (Editorial Committee of Flora of Zhejiang 1993; Zheng 2005).

#### Island (or fragment) attributes

For each of the 154 island fragments, the species richness ( $S$ ) was calculated by tallying the number of species recorded over all visits. Island area ( $A$ ) and perimeter ( $P$ ) were calculated through analysis of maps in ArcGIS 9.3 for when the water level reaches 105 m a.s.l. (generally corresponding to the edge of forest cover). These two variables were used to generate the perimeter/area ratio ( $PAR$ ), which is indicative of the relative amount of edge habitat on an island (McGarigal and Marks 1995; Wu 2004). The shape index ( $SI$ ) indicates the island shape complexity and was calculated as  $SI = P/[2 \times (\pi \times A)^{0.5}]$  (Laurance and Yensen 1991; Hoffmeister et al. 2005; Ewers and Didham 2007).  $SI$  is 1 when an island is a perfect circle and increases as the shape becomes more irregular and complex. We calculated island isolation ( $I$ ) as the shortest straight-line distance from the edge of a study island to the edge of mainland.

#### Data analysis

All statistical analyses were conducted with the software R 2.10.1 (R Development Core Team 2009)

and ArcGIS 9.3. The specific R functions used are indicated following each method described below.

For testing the multicollinearity, VIF (variance inflation factors, R function: `vif`) of all variables ( $VIF_A = 2.77$ ;  $VIF_{PAR} = 1.21$ ;  $VIF_{SI} = 3.11$ ;  $VIF_I = 1.02$ ) did not exceed 4, which is below maximum threshold of 10 suggested by Neter et al. (1996). We calculated the Pearson correlation coefficients among the island attributes (R function: `cor.test`). We also characterized the relationship between species richness within each plant group and island area using the log–log transformed power model ( $\log S = \log c + z \times \log A$ , where  $S$  is species richness on an island with area  $A$ , and  $c$  and  $z$  are constants). The value of  $z$  indicates how rapidly species richness increases with area and is commonly used as a measure of a community's sensitivity to habitat loss and fragmentation. Global Moran's I (Moran 1950) was used to test the spatial autocorrelation of island attributes (R function: `moran.test`), and Mantel test (Mantel 1967) was used to test the effect of spatial structure of islands on species richness (R function: `mantel`). We constructed a multivariate linear model, which included the area ( $A$ ), perimeter/area ratio ( $PAR$ ), shape index ( $SI$ ) and isolation ( $I$ ) of an island as follows:  $S = a + bA + cPAR + dSI + eI$ , where  $a$ ,  $b$ ,  $c$ ,  $d$ , and  $e$  are fitted parameters. Then a backward stepwise analysis was used on the basic model to find the best-fit models for all species and for each individual functional group (R function: `step`). Variable selection and model evaluation were both based on AIC. In addition, we used variation partition (Borcard et al. 1992) to estimate the relative contribution of each island attribute to species richness (R function: `varpart`).

A new nestedness metric, NODF (Nestedness based on Overlap and Decreasing Fill) was developed recently based on the difference between rows (species) and columns (sites) and the paired matching of species occurrences (Almeida-Neto et al. 2008). In comparison to the previous nestedness indices, such as matrix temperature (Atmar and Patterson 1993) or discrepancy metric (Brualdi and Sanderson 1999), NODF has better statistical properties, consistently rejects a nested pattern for different random null matrices and reduces the overestimates of the degree of nestedness. In addition, NODF can deconstruct total nestedness into the independent contributions of rows and columns which is useful in analyzing the nested patterns of species distribution and species

composition, respectively (Almeida-Neto et al. 2008). In our study, we used the maximally packed matrices of each plant group to calculate the total NODF. The NODF value was calculated using the software “NODF” (Almeida-Neto and Ulrich 2011), which yields a nestedness score ranging from 0 (non-nested) to 100 (perfectly nested). The “fixed row-fixed column” constraint model was used to randomly generate 1,000 null communities to evaluate whether the observed assemblages of plant communities are significantly more nested than expected at random. The NODF software also generates “Z-transformed scores” which are nestedness values independent of the size, shape and fill of the study matrix. Finally, Spearman rank correlations were calculated between the nested rank-order of islands and the island attributes to study the contribution of the variables to the nested patterns of the plant groups (R function: `cor.test`).

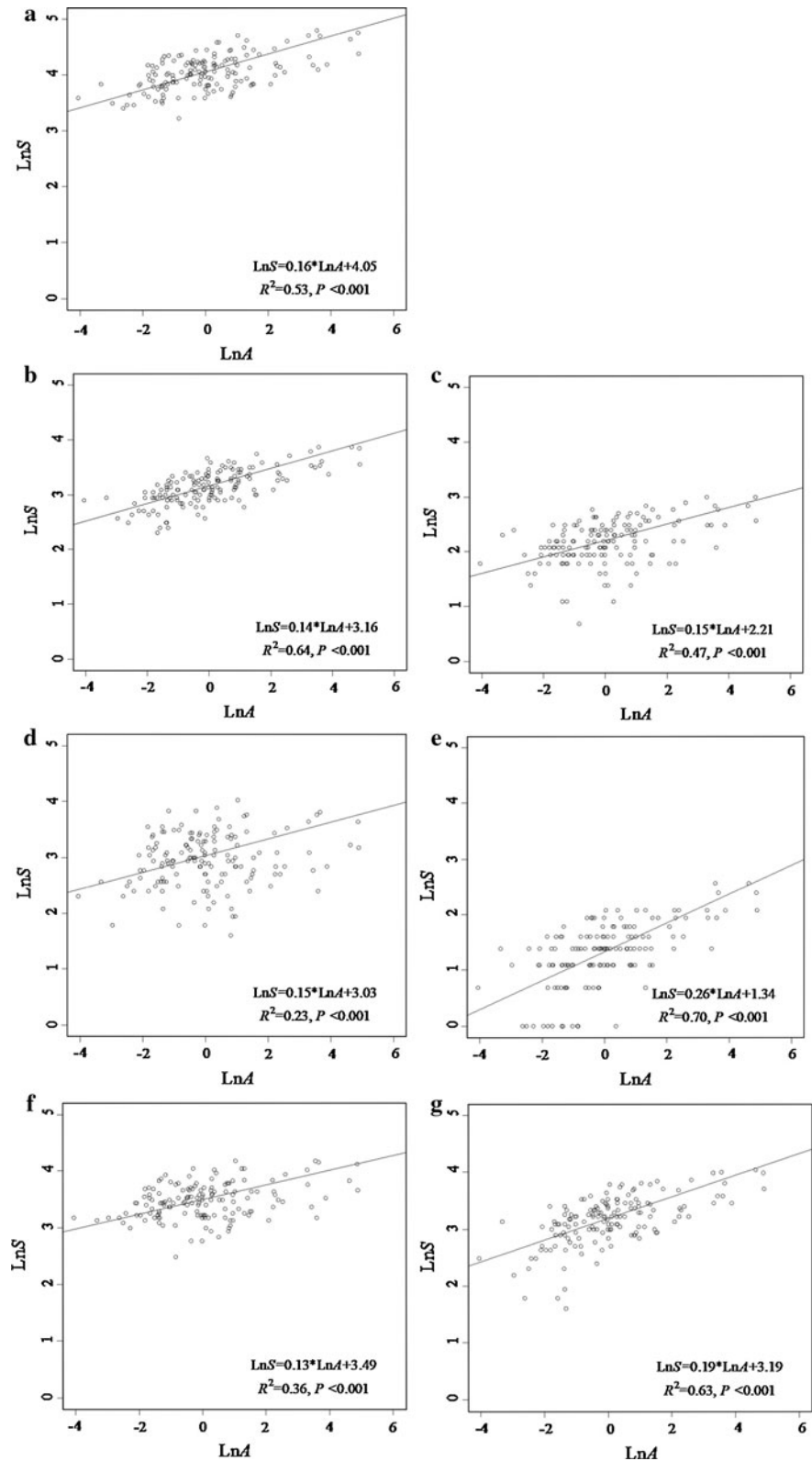
## Results

Area ( $A$ ) and  $SI$  were significantly positively correlated (correlation coefficient  $r = 0.79$ ,  $P < 0.001$ ), indicating that larger islands have more complex shapes. However,  $A$  and  $PAR$  were significantly negatively correlated ( $r = -0.21$ ,  $P < 0.01$ ), indicating that despite their more complex shape, larger islands have less edge relative to total or core area. Isolation was not significantly correlated to any of other variables (in all case,  $|r| \leq 0.06$ ,  $P > 0.05$ ). The global Moran's I showed that only  $PAR$  had significant spatial autocorrelation (Moran's I = 0.11, Z score = 3.25,  $P < 0.05$ ). However, there was no effect of spatial distance among these islands on species richness as indicated by the Mantel test ( $r = -0.004$ ,  $P = 0.414$ ).

Across the 154 study islands, we recorded a total of 456 wild vascular plant species belonging to 298 genera and 107 families. Of these species, 120 were trees, 61 shrubs, 232 herbs, and 43 lianas. We classified 229 of the species as shade-intolerant and 227 as shade-tolerant (the complete species list is given in Appendix S1 in Supplementary material).

Fits of the species-area relationships for all species groups ( $\log S = \log c + z \times \log A$ ) were highly significant, with area explaining a large

**Fig. 2** Species-area relationships of seven plant groups on 154 study islands: **a** all plants, **b** trees, **c** shrubs, **d** herbs, **e** lianas, **f** shade-intolerant plants, and **g** shade-tolerant plants. The lines are the linear regression based on the power model with the natural logarithmic transformed parameters,  $\text{Ln}S = z * \text{Ln}A + \text{Ln}c$ , where  $z$  and  $c$  are constants



proportion of variation in richness of all plants (53%), trees (64%), shrubs (47%), herbs (36%), lianas (70%), shade-intolerant plants (23%) and shade-tolerant plants (63%) (Fig. 2). The descending order of the fitted  $z$  values was lianas (0.26), shade-tolerant plants (0.19), all plants (0.16), herbs (0.15), shrubs (0.15), trees (0.14), and shade-intolerant plants (0.13).

In the backward stepwise analysis, island area, *PAR* and *SI* all had significant relationships with the species richness of all plants, trees, shrubs and shade-tolerant plants. For herbs, lianas and shade-intolerant plants, *PAR* was the only factor other than area that significantly affected species richness (i.e., *SI* was not a significant factor for these plant groups). Isolation did not significantly explain the richness of any plant group. Island area was the variable that explained the most variation in species richness of most groups in the variation partition analysis (Fig. 3). Comparing the contributions of each plant group, area effect was stronger in all plants, herb, liana and shade-intolerant plants (all pure relative explanations >0.1). In addition to area effects, *PAR* explained more variation than *SI* in most plant groups except shrubs. The richness of tree and shade-tolerant plants were more strongly affected by *PAR* (both pure relative explanations >0.1) than other groups.

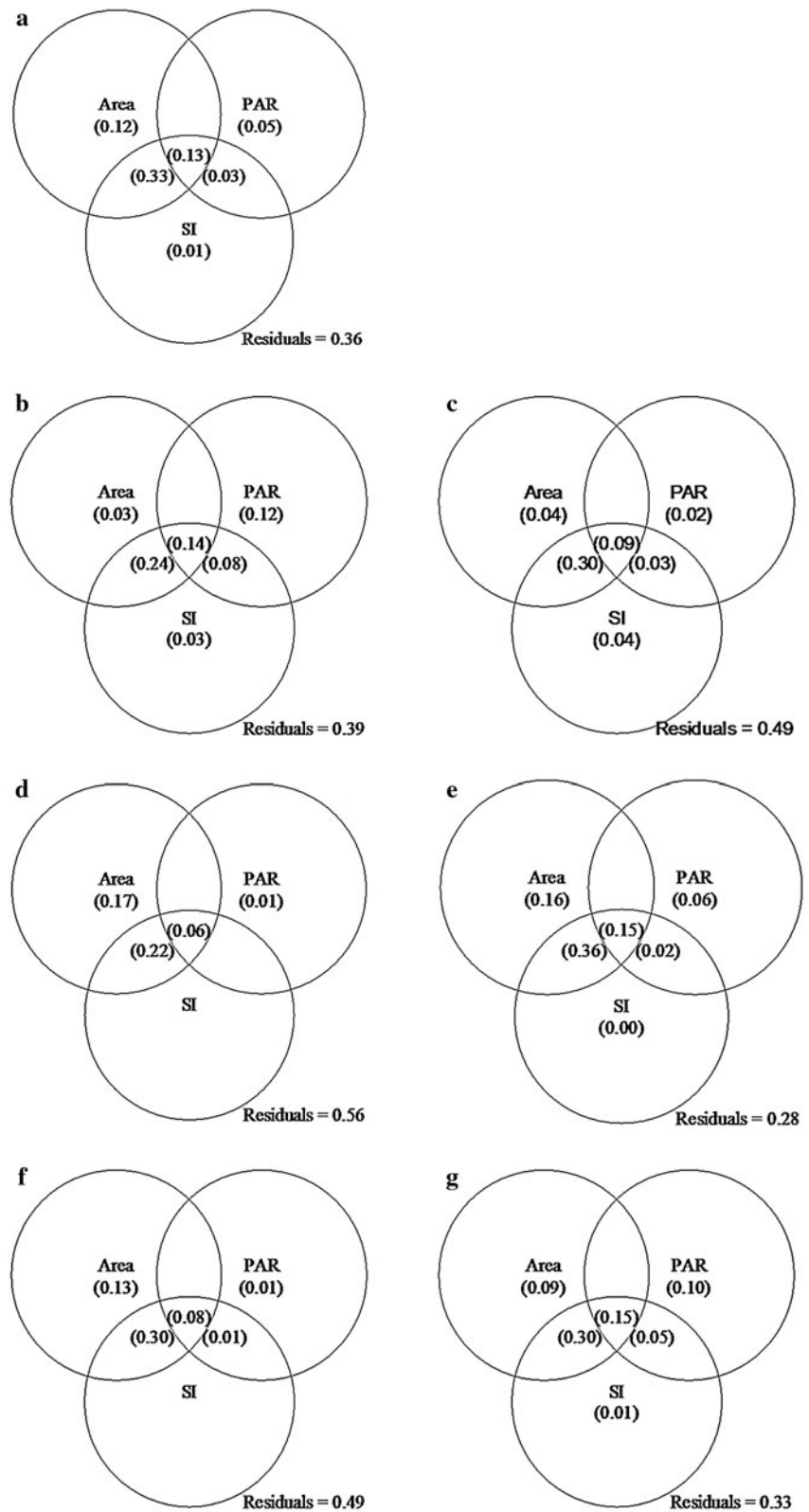
The functional groups of all plants, trees, herbs and shade-intolerant plants were all significantly nested ( $P = 0.014, 0.044, 0.004, 0.002$ , respectively) when both species and islands were sorted to maximally packed matrices. The comparison of  $Z$ -transformed scores (i.e., nestedness scores that are independent of the size, shape and fill of the study matrix) indicates that the shade-intolerant plants had the highest degree of nestedness, whereas trees had the lowest degree of nestedness (all plants = 2.07, tree = -1.67, herb = 2.63, shade-intolerant plants = 2.75). For the groups with significantly nested patterns, area and *SI* were positively related to the nested rank-order of islands in all four groups (i.e., larger islands and islands with more complex shapes tend to host richer species communities; Table 2). *PAR* was negatively related to the nested rank-order of islands for all plants, trees and shade-intolerant plants except herbs, while isolation was a significantly positive factor for the nestedness of all plants, herbs, and shade-intolerant plants except trees.

## Discussion

Compared with the large number of studies conducted with terrestrial habitat fragments (Fahrig 2003; Watson et al. 2005; Yaacobi et al. 2007), relatively few studies have taken advantage of land-bridge island systems. The majority of land-bridge systems that have been studied are from the tropics and TIL is to date the only sub-tropical land-bridge system being used to study the effects of habitat fragmentation. Terborgh et al. (1997), Feeley et al. (2007) and Feeley and Terborgh (2008) studied ecosystem decay on man-made land-bridge islands in Lago Guri, Venezuela, and showed that species loss was driven by the loss of predators and trophic cascades. Wang et al. (2010b) reported the nested patterns of birds, lizards and small mammals on the islands of the Thousand Island Lake relating to the island size and habitat heterogeneity. Although these studies of animal communities (e.g., birds, mammals, and insects) treated the vegetation as a basic attribute of habitat, in none of these studies were plants the direct focal group of interest. In contrast, our study directly examined the effects of fragmentation on patterns of plant species richness and nestedness across an unprecedented sample size of land-bridge islands (>150) at both the level of the whole plant community as well as for individual functional groups. Based on our results, it appears that island area, habitat heterogeneity and island isolation all affected the species diversity and community assembly of plant species at TIL through different ecological mechanisms.

Our results showed that island attributes such as island area (*A*), *PAR* and *SI* were strongly associated with plant species richness. Not surprisingly, area explained the most variation of species richness supporting the hypothesis that habitat area is the primary factor determining species diversity in fragmented landscapes (Morrison 2002; Fahrig 2003; Watson et al. 2005; Laurance 2008). However, as indicated by the greater explanatory power of the stepwise linear models than the SAR power functions (Table 1), it appears that other island attributes also have important effects on species richness (Fahrig 2003; Laurance et al. 2007; Laurance 2008). Contrary to our expectations, no significant relationships between island isolation and richness of any plant group were detected. This may be due to the relatively

**Fig. 3** Variation partition of effects of island attributes on the species richness of seven plant functional groups: **a** all plants, **b** trees, **c** shrubs, **d** herbs, **e** lianas, **f** shade-intolerant plants, and **g** shade-tolerant plants. The independent and combined explanatory power of each attribute are shown in parentheses (values <0 are not shown). The abbreviations are the same as in Table 1





**Table 1** Results of stepwise linear regression for each plant functional group

Plant groups	Best fitted model	$R^2$	$F$	$P$
All plants	$S = 64.06 + 0.14 * A - 176.54 * PAR + 3.51 * SI$	0.65	91.85	<0.001
Growth form				
Tree	$S = 25.58 + 0.02 * A - 91.03 * PAR + 2.61 * SI$	0.62	80.2	<0.001
Shrub	$S = 8.27 + 0.01 * A - 18.57 * PAR + 1.32 * SI$	0.52	53.45	<0.001
Herb	$S = 23.41 + 0.08 * A - 37.16 * PAR$	0.45	62.68	<0.001
Liana	$S = 5.90 + 0.02 * A - 26.87 * PAR$	0.72	197.4	<0.001
Shade tolerance				
Shade-intolerant	$S = 37.10 + 0.09 * A - 62.34 * PAR$	0.52	83.11	<0.001
Shade-tolerant	$S = 2.93 + 0.06 * A - 122.90 * PAR + 2.31 * SI$	0.68	104.7	<0.001

Only variables retained in the best-fit model are shown, with the total variance explained and the statistical significance of the respective model indicated

$S$  species richness,  $A$  island area,  $PAR$  perimeter to area ratio,  $SI$  index of shape complexity,  $I$  isolation

short distance between the study islands and mainland (mean distance was only 1,078 m and maximum distance was 4,217 m) such that isolation was not a significant barrier to dispersal. Supporting this, Wang et al. (2009, 2010b) found that isolation did not affect the species richness and community structure of birds and lizards at TIL, which are potentially important vectors for plant dispersal. The results of Moran's  $I$  and Mantel test also confirmed that the spatial location of these islands relative to other islands did not influence the species richness in TIL.

The  $z$  values of the fitted power functions of SAR have been found to generally vary between 0.2 and 0.3 across a variety of systems and species groups (Rosenzweig 1995; May and Stumpf 2000; Panitsa et al. 2006; Watling and Donnelly 2006). In our study, we found that the  $z$  values for all plants and for most of the functional groups were below 0.2 (Fig. 2). This indicates that the plant species at TIL had weaker sensitivity to area loss when compared to other insularized systems/species groups. One possible explanation is that because of the relative homogeneous vegetation dominated by Masson pine on these islands, habitat diversity is low resulting in a slow rate of species loss with decreasing area—in accordance with theories related to habitat diversity and niche availability (Rosenzweig 1995). An alternative hypothesis is that, since the islands were all formed from erstwhile hilltops (Wang et al. 2010b), they had been isolated to some degree even before inundation and thus the resident species were already “pre-adapted”

to fragmentation resulting in less subsequent relaxation and lower  $z$  values. Extinction debt (Kuussaari et al. 2009) is a possible third explanation of lower  $z$  values (i.e., some species may be committed to local extinction but have not yet gone extinct due to their long longevity and the relatively short history of fragmentation in TIL). These hypotheses may apply to all life form functional groups with the exception of lianas which differ physiologically from the other groups (van der Heijden and Phillips 2009). Although lianas are generally considered an edge-tolerant group with increasing density and diversity at tropic rain-forest edges (Laurance et al. 2000, 2001), we found liana species only on the larger islands and mostly in the interior habitats. This response of interior-prefering lianas explains their high sensitivity to fragmentation as indicated by the high  $z$  value. In the case of shade tolerant vs. shade intolerant plant species, the shade-tolerant plants had a higher  $z$  value and a greater amount of variation explained by island attributes than did the shade-intolerant plants. This indicates that plant species that “prefer” the shaded forest environment are in general more sensitive to habitat fragmentation than plant species that prefer edge habitat. This is not surprising given the decrease in shaded interior forest habitat and concurrent increase in edge habitat on smaller islands.

The index of relative amount of edge habitat,  $PAR$ , had smaller effects on overall plant richness than did area. However, the islands with more relative interior habitat (low  $PAR$ ) could support more plant species

**Table 2** Spearman rank correlations between nested rank-order of islands and island attributes

Plant groups	Nested?	<i>A</i>	<i>PAR</i>	<i>SI</i>	<i>I</i>
All plants	Yes	0.50***	−0.47***	0.40***	0.15*
Growth form					
Tree	Yes	0.67***	−0.67***	0.46***	−0.01
Shrub	No	0.45***	−0.40***	0.40***	0.03
Herb	Yes	0.17***	−0.12	0.20*	0.26**
Liana	No	0.58***	−0.58***	0.40***	0.05
Shade tolerance					
Shade-intolerant	Yes	0.30***	−0.25**	0.29***	0.19*
Shade-tolerant	No	0.63***	−0.62***	0.44***	0.08

The abbreviations are the same as in Table 1

\*  $P < 0.05$

\*\*  $P < 0.01$

\*\*\*  $P < 0.001$

once area was accounted for (Table 1). The reduction of the relative amount of interior habitat caused by fragmentation increased the risk of local extinction for shade-tolerant species and decreased species richness, especially the richness of tree species (68% of tree species lived in the interior habitat in TIL). The islands with more complex shapes (high *SI*) could support more species of all plants, woody plants (trees and shrubs) and shade-tolerant plants. The islands with high *SI* values may have elevated rates of immigration and/or high *SI* values may be indicative of greater topographic complexity and greater habitat heterogeneity allowing for the coexistence of more species.

Island attributes were also associated with nested patterns of plants across the 154 islands. Distinct from species richness, the herbs and shade-intolerant plant species exhibited stronger patterns of nestedness than the other functional groups. Island size and habitat heterogeneity both significantly influenced the nested rank-order of islands for the different functional groups, but Spearman correlation analysis indicated that island area, among all the island attributes, was most strongly correlated to the nested rank-order of the islands (Table 2). In a previous study from TIL, Wang et al. (2010b) found that patterns of nestedness in animal communities on the islands were not due to passive sampling and were instead most likely due to habitat nestedness. The relationship between area and nestedness may be due to several processes, including selective extinction of area sensitive species and/or

greater habitat heterogeneity on large islands. The fact that *PAR* and *SI* were significantly correlated to nestedness supports the idea that habitat heterogeneity played an important role in shaping nested patterns in most plant groups. An exception was the herbs which were composed almost entirely of edge species.

Isolation significantly affected the nested rank-order of islands for all plants, herbs and shade-intolerant plants, suggesting that the nested patterns exhibited by these groups are influenced by the selective colonization of islands as well as selective extinction. This may explain why these functional groups exhibited greater degrees of nestedness than other functional groups, as mentioned above. This result is contrary to that of Wang et al. (2010b) which showed little effect of isolation on patterns of nestedness in animal communities. The lack of isolation effect on bird communities was possibly due to their high vagility and frequent dispersal between islands (Yiming et al. 1998; Fleishman et al. 2002; Wang et al. 2009, 2010b). In contrast to birds, dispersal between islands was much rarer in small mammal and lizard species (which also exhibited no response to isolation) because of their poor mobility and difficulties in crossing water. Taken together, these results may indicate that selective colonization is less important in shaping patterns of nestedness in taxa with either consistently strong or poor dispersal capabilities, but instead is most important for species groups with large interspecific variations in dispersal capabilities—such

as herbs and shade-intolerant plants. Of note is that in our study, isolation did not significantly influence plant richness (Table 1). Thus, selective colonization affected nestedness through changes in species composition or similarity, not species richness.

Our findings show that the attributes of fragments differentially influence species richness and nestedness among different plant groups and help to highlight the complex nature of biodiversity conservation in fragmented landscapes. When multiple functional groups are considered, there may be no easy solutions to questions concerning the relationships between landscape patterns and biodiversity or the optimal reserve design for conservation purposes. However, understanding the mechanisms influencing patterns of species richness and nestedness, and how they differ across functional groups, in fragmented landscapes can be an important tool for developing ecological theory and assisting biodiversity conservation (Fleishman et al. 2002; Fahrig 2003; Laurance 2008; Wu 2008).

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## References

- Almeida-Neto M, Ulrich W (2011) A straightforward computational approach for measuring nestedness using quantitative matrices. *Environ Model Softw* 26:173–178
- Almeida-Neto M, Guimaraes P, Guimaraes PR, Loyola RD, Ulrich W (2008) A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* 117:1227–1239
- Andren H (1994) Can one use nested subset pattern to reject the random sample hypothesis—examples from boreal bird communities. *Oikos* 70:489–491
- Atmar W, Patterson BD (1993) The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia* 96:373–382
- Benitez-Malvido J, Martinez-Ramos M (2003) Impact of forest fragmentation on understory plant species richness in Amazonia. *Conserv Biol* 17:389–400
- Blake JG (1991) Nested subsets and the distribution of birds on isolated woodlots. *Conserv Biol* 5:58–66
- Borcard D, Legendre P, Drapeau P (1992) Partialling out the spatial component of ecological variation. *Ecology* 73:1045–1055
- Bowman J, Cappuccino N, Fahrig L (2002) Patch size and population density: the effect of immigration behavior. *Conserv Ecol* 6:1–8
- Brualdi RA, Sanderson JG (1999) Nested species subsets, gaps, and discrepancy. *Oecologia* 119:256–264
- Cagnolo L, Valladares G, Salvo A, Cabido M, Zak M (2009) Habitat fragmentation and species loss across three interacting trophic levels: effects of life-history and food-web traits. *Conserv Biol* 23:1167–1175
- Caley MJ, Buckley KA, Jones GP (2001) Separating ecological effects of habitat fragmentation, degradation, and loss on coral commensals. *Ecology* 82:3435–3448
- Calme S, Desrochers A (1999) Nested bird and micro-habitat assemblages in a peatland archipelago. *Oecologia* 118:361–370
- Chalfoun AD, Thompson FR, Ratnaswamy MJ (2002) Nest predators and fragmentation: a review and meta-analysis. *Conserv Biol* 16:306–318
- Collins CD, Holt RD, Foster BL (2009) Patch size effects on plant species decline in an experimentally fragmented landscape. *Ecology* 90:2577–2588
- Darlington PJ (1957) Zoogeography: the geographical distribution of animals. Wiley, New York
- Dettki H, Edman M, Esseen PA, Hedenas H, Jonsson BG, Kruys N, Moen J, Renhorn KE (1998) Screening for species potentially sensitive to habitat fragmentation. *Ecography* 21:649–652
- Diamond J (1972) Biogeographic kinetics—estimation of relaxation-times for avifaunas of Southwest Pacific Islands. *Proc Natl Acad Sci USA*. 69:3199–3203
- Diamond J (2001) Ecology—dammed experiments! *Science* 294:1847–1848
- Editorial Committee of Development of Xin'an River (2009) Development of Xin'an River. Zhejiang People Press, Hangzhou
- Editorial Committee of Flora of Zhejiang (1993) Flora of Zhejiang. Zhejiang Science and Technology Press, Hangzhou
- Ewers RM, Didham RK (2005) Confounding factors in the detection of species responses to habitat fragmentation. *Biol Rev* 81:117
- Ewers RM, Didham RK (2007) The effect of fragment shape and species' sensitivity to habitat edges on animal population size. *Conserv Biol* 21:926–936
- Ewers RM, Thorpe S, Didham RK (2007) Synergistic interactions between edge and area effects in a heavily fragmented landscape. *Ecology* 88:96–106
- Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Annu Rev Ecol Evol Syst* 34:487–515
- Fahrig L (2007) Landscape heterogeneity and metapopulation dynamics. In: Wu J, Hobbs RJ (eds) Key topics and perspectives in landscape ecology. Cambridge University Press, Cambridge, pp 78–89
- Feeley KJ, Terborgh JW (2008) Direct versus indirect effects of habitat reduction on the loss of avian species from tropical forest fragments. *Anim Conserv* 11:353–360

- Feeley KJ, Gillespie TW, Lebbin DJ, Walter HS (2007) Species characteristics associated with extinction vulnerability and nestedness rankings of birds in tropical forest fragments. *Anim Conserv* 10:493–501
- Fischer J, Lindenmayer DB (2007) Landscape modification and habitat fragmentation: a synthesis. *Global Ecol Biogeogr* 16:265–280
- Fleishman E, Betrus CJ, Blair RB, Mac Nally R, Murphy DD (2002) Nestedness analysis and conservation planning: the importance of place, environment, and life history across taxonomic groups. *Oecologia* 133:78–89
- Gotelli NJ, Graves GR (1990) Body size and the occurrence of avian species on land-bridge islands. *J Biogeogr* 17:315–325
- Henle K, Davies KF, Kleyer M, Margules C, Settele J (2004) Predictors of species sensitivity to fragmentation. *Biodivers Conserv* 13:207–251
- Higgins CL, Willig MR, Strauss RE (2006) The role of stochastic processes in producing nested patterns of species distributions. *Oikos* 114:159–167
- Hill JL, Curran PJ (2003) Area, shape and isolation of tropical forest fragments: effects on tree species diversity and implications for conservation. *J Biogeogr* 30:1391–1403
- Hoffmeister TS, Vet LEM, Biere A, Holsinger K, Filser J (2005) Ecological and evolutionary consequences of biological invasion and habitat fragmentation. *Ecosystems* 8:657–667
- Honnay O, Hermy M, Coppin P (1999) Nested plant communities in deciduous forest fragments: species relaxation or nested habitats? *Oikos* 84:119–129
- Keppel G, Buckley YM, Possingham HP (2010) Drivers of lowland rain forest community assembly, species diversity and forest structure on islands in the tropical South Pacific. *J Ecol* 98:87–95
- Kuussaari M, Bommarco R, Heikkinen RK, Helm A, Krauss J, Lindborg R, Ockinger E, Partel M, Pino J, Roda F, Stefanescu C, Teder T, Zobel M, Steffan-Dewenter I (2009) Extinction debt: a challenge for biodiversity conservation. *Trends Ecol Evol* 24:564–571
- Laurance WF (2008) Theory meets reality: how habitat fragmentation research has transcended island biogeographic theory. *Biol Conserv* 141:1731–1744
- Laurance WF, Yensen E (1991) Predicting the impacts of edge effects in fragmented habitats. *Biol Conserv* 55:77–92
- Laurance WF, Delamonica P, Laurance SG, Vasconcelos HL, Lovejoy TE (2000) Conservation—rainforest fragmentation kills big trees. *Nature* 404:836–837
- Laurance WF, Perez-Salicrup D, Delamonica P, Fearnside PM, D'Angelo S, Jerozolinski A, Pohl L, Lovejoy TE (2001) Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology* 82:105–116
- Laurance WF, Nascimento HEM, Laurance SG, Andrade A, Ewers RM, Harms KE, Luizao RCC, Ribeiro JE (2007) Habitat fragmentation, variable edge effects, and the landscape-divergence hypothesis. *Plos One* 2:e1017
- Lomolino MV (2000) A call for a new paradigm of island biogeography. *Global Ecol Biogeogr* 9:1–6
- MacArthur RH, Wilson EO (1963) Equilibrium-theory of insular zoogeography. *Evolution* 17:373–387
- MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton
- Mantel N (1967) The detection of disease clustering and a generalized regression approach. *Cancer Res* 27:209–220
- May RM, Stumpf MPH (2000) Ecology—species-area relations in tropical forests. *Science* 290:2084–2086
- McGarigal K, Marks BJ (1995) FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. US Forest Service General Technical Report PNV 351
- Moran PAP (1950) Notes on continuous stochastic phenomena. *Biometrika* 37:17–33
- Morrison LW (2002) Determinants of plant species richness on small Bahamian islands. *J Biogeogr* 29:931–941
- Murcia C (1995) Edge effects in fragmented forests—implications for conservation. *Trends Ecol Evol* 10:58–62
- Neter J, Kutner MH, Nachtsheim CJ, Wasserman W (1996) Applied linear statistical model: regression, analysis of variance, and experimental design. Irwin Professional Publishing, Chicago
- Panitsa M, Tzanoudakis D, Triantis KA, Sfenthourakis S (2006) Patterns of species richness on very small islands: the plants of the Aegean archipelago. *J Biogeogr* 33:1223–1234
- Patterson BD (1984) Mammalian extinction and biogeography in the Southern Rocky Mountains. In: Nitecki MH (ed) Extinctions. University of Chicago Press, Chicago, pp 247–293
- Prevedello JA, Vieira MV (2010) Does the type of matrix matter? A quantitative review of the evidence. *Biodivers Conserv* 19:1205–1223
- R Development Core Team (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rosenberg KV, Lowe JD, Dhondt AA (1999) Effects of forest fragmentation on breeding tanagers: a continental perspective. *Conserv Biol* 13:568–583
- Rosenzweig ML (1995) Species diversity in space and time. Cambridge University Press, Cambridge
- Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation—a review. *Conserv Biol* 5:18–32
- Simberloff D, Levin B (1985) Predictable sequences of species loss with decreasing island area—land birds in 2 archipelagoes. *N Z J Ecol* 8:11–20
- Steneck RS (2001) Function groups. In: Levin SA (ed) Encyclopedia of biodiversity. Academic Press, New York
- Stiles A, Scheiner SM (2008) Nestedness of remnant Sonoran Desert plant communities in metropolitan Phoenix, Arizona. *Ecology* 89:2473–2481
- Terborgh JW, Feeley KJ (2008) Ecosystem decay in closed forest fragments. In: Carson WP, Schnitzer SA (eds) Tropical forest community ecology. Blackwell Publishing, Oxford
- Terborgh J, Lopez L, Tello JS (1997) Bird communities in transition: the Lago Guri Islands. *Ecology* 78:1494–1501
- Terborgh J, Lopez L, Nunez P, Rao M, Shahabuddin G, Orihuela G, Riveros M, Ascanio R, Adler GH, Lambert TD, Balbas L (2001) Ecological meltdown in predator-free forest fragments. *Science* 294:1923–1926
- Trzcinski MK, Fahrig L, Merriam G (1999) Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. *Ecol Appl* 9:586–593

- Ulrich W, Almeida M, Gotelli NJ (2009) A consumer's guide to nestedness analysis. *Oikos* 118:3–17
- van der Heijden GMF, Phillips OL (2009) Environmental effects on Neotropical liana species richness. *J Biogeogr* 36:1561–1572
- Wang Y, Zhang J, Feeley KJ, Jiang P, Ding P (2009) Life-history traits associated with fragmentation vulnerability of lizards in the Thousand Island Lake. *China Anim Conserv* 12:329–337
- Wang J, Huang J, Wu J, Han X, Lin G (2010a) Ecological consequences of the Three Gorges Dam: insularization affects foraging behavior and dynamics of rodent populations. *Front Ecol Environ* 8:13–19
- Wang Y, Bao Y, Yu M, Xu G, Ding P (2010b) Nestedness for different reasons: the distributions of birds, lizards and small mammals on islands of an inundated lake. *Divers Distrib* 16:862–873
- Watling JI, Donnelly MA (2006) Fragments as islands: a synthesis of faunal responses to habitat patchiness. *Conserv Biol* 20:1016–1025
- Watson JEM, Whittaker RJ, Freudenberger D (2005) Bird community responses to habitat fragmentation: how consistent are they across landscapes? *J Biogeogr* 32:1353–1370
- Wilcove DS, Rothstein D, Dubow J, Phillips A, Losos E (1998) Quantifying threats to imperiled species in the United States. *Bioscience* 48:607–615
- Worthen WB (1996) Community composition and nested-subset analyses: basic descriptors for community ecology. *Oikos* 76:417–426
- Wright DH, Patterson BD, Mikkelsen GM, Cutler A, Atmar W (1998) A comparative analysis of nested subset patterns of species composition. *Oecologia* 113:1–20
- Wu J (2004) Effects of changing scale on landscape pattern analysis: scaling relations. *Landscape Ecol* 19:125–138
- Wu J (2008) Changing perspectives on biodiversity conservation: from species protection to regional sustainability. *Biodivers Sci* 16:205–213
- Wu J, Huang J, Han X, Xie Z, Gao X (2003) Three-Gorges Dam—experiment in habitat fragmentation? *Science* 300:1239–1240
- Yaacobi G, Ziv Y, Rosenzweig ML (2007) Habitat fragmentation may not matter to species diversity. *Proc R Soc B Biol Sci* 274:2409–2412
- Yiming L, Niemela J, Dianmo L (1998) Nested distribution of amphibians in the Zhoushan archipelago, China: can selective extinction cause nested subsets of species? *Oecologia* 113:557–564
- Zheng C (2005) Keys of seed plants in Zhejiang. Zhejiang Science and Technology Press, Hangzhou