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Bird guild loss and its determinants on subtropical land-bridge islands, China

Zhifeng Ding^{1,2}, Kenneth James Feeley^{3,4}, Huijian Hu² and Ping Ding^{1*}

Abstract

Background: The guild concept is useful for understanding the community structure in a land-bridge island system, but most fragmentation studies have focused only on the importance of island area and isolation, other island attributes such as perimeter-area ratio (*PAR*) were overlooked or understudied.

Methods: We have adopted a guild approach to investigate the impacts of island attributes on bird guild richness on a set of 41 recently isolated land-bridge islands in the Thousand Island Lake (TIL), China.

Results: We found insectivores had the largest number of species (34 species), followed by understory foraging guilds (28 species), omnivores (27 species) and canopy guilds (25 species). Furthermore, our data showed that migrants and residents responded equally to island area, insectivores and understory guilds were sensitive to island area but omnivores and canopy guilds were not very sensitive. Most guild richness was determined by island area, except for omnivores and canopy guilds.

Conclusions: Although *PAR* or habitat diversity found to be important for bird species richness, our results highlight the importance of island area in maintaining bird diversity in fragmented island systems.

Keywords: Bird guilds, Island area, Land-bridge islands, *PAR*, Thousand Island Lake, *z* values

Background

Fragmentation is considered the most important cause of biodiversity loss in the world (Brooks et al. 2002; Stockwell et al. 2003; Reed 2004). Declines in species diversity due to fragmentation have been documented for birds, mammals, insects and plants from small-scale experimental studies to continental-scale analyses (reviews in Fahrig 2003; Ewers and Didham 2006). Yet, most fragmentation studies have focused only on the importance of patch area, which may not adequately explain the effects of fragmentation on habitat occupancy by birds (Helzer and Jelinski 1999). Indeed, patches of equal area may also vary significantly in the amount of their area exposed to edges, which can have significant impacts on bird communities. For example, studies by Helzer and Jelinski (1999) found that perimeter–area ratio (*PAR*) was a more effective measure of habitat patch quality than patch area. Therefore, while the maintenance of

large patches is important to the conservation of bird communities, patch characteristics such as patch shape should also be recognized and taken into account.

The guild concept (where guilds are groups of species that exploit the same class of environmental resources in a similar way, Root 1967, 2001) is very popular among ecologists (Terborgh and Robinson 1986; Hawkins and MacMahon 1989; Simberloff and Dayan 1991), and is useful for understanding community structure and the process of community organization. In addition, guilds are also often used to evaluate the collective responses of multiple species to changes in resources or ecological conditions (Block et al. 1995). For example, Canterbury et al. (2000) and O'Connell et al. (2000) used guilds to assess ecological condition. Thus, it is important to relate bird guilds to changed habitats because such relationships are useful in understanding bird community structures and species variations across different vegetation types (Wiens and Rotenberry 1981).

Previous studies have documented many general patterns from the studies of bird guilds. For example, migrants and residents seemed equally sensitive to

* Correspondence: dingping@zju.edu.cn

¹The Key Laboratory of Conservation Biology for Endangered Wildlife of the Ministry of Education, College of Life Sciences, Zhejiang University, Zijing'gang Campus, Hangzhou 310058, China

Full list of author information is available at the end of the article

fragmentation based on limited experimental studies (reviews in Lampila et al. 2004). Guilds such as insectivores appeared to be more sensitive to disturbance due to their dispersal ability or specific food requirements or specific habitat requirements (Anjos and Boçon 1999; Şekercioğlu et al. 2002; Chettri et al. 2005; Stouffer et al. 2006; Gray et al. 2007). Granivores were found to be positively affected by forest fragmentation (Marini 2001; Şekercioğlu and Sodhi 2007; Giraudo et al. 2008), and their abundance increased significantly following disturbance (Gray et al. 2007). Compared to insectivores and granivores, omnivores and carnivores were less sensitive to fragmentation (Bierregaard and Stouffer 1997; Anjos and Boçon 1999; Ribon et al. 2003).

Likewise, species that forage in certain forest strata are highly sensitive to fragmented areas. For instance, understory birds are particularly sensitive to forest fragmentation (Stouffer and Bierregaard 1995; Stratford and Stouffer 1999; Ribon et al. 2003), partly due to their low dispersal ability (Stouffer and Bierregaard 1995). Canopy birds may view a relatively fragmented landscape as one continuous cluster of forest habitat because of their large gap-crossing ability, making them relatively insensitive to remnant area (Dale et al. 1994).

However, most of these studies have been conducted in forest fragments, which are quite different from the land-bridge islands in our system. Indeed, land-bridge islands have been characterized as having several potential advantages over other study systems, such as having a common biogeographic history, well-delineated boundaries and an inhospitable matrix (Wang et al. 2010; Hu et al. 2011; Ding et al. 2013). Thus, land-bridge islands are considered as ideal systems for studying habitat fragmentation. Applying the guild approach in such systems has also been important for understanding ecological theory (MacArthur and Wilson 1967; Gilpin and Hanski 1991; Opdam 1991; Rosenzweig 1995), and for the management and conservation of biodiversity (Fahrig and Merriam 1994).

In this study, we have adopted a guild approach to investigate the impacts of island attributes on bird guilds. We first investigated the effects of fragment area on the richness of bird guilds, and had three null hypotheses. (1) Migrants and residents showed an equal response to island area; (2) insectivorous guilds were the most sensitive to island area; (3) understory guilds were the most sensitive to island area. We next considered four factors other than island area and isolation that might influence the number of coexisting bird species: *PAR*, *SI* (shape index), plant species richness, habitat diversity. Specifically, we addressed the following question: what factors drive the richness of bird guilds in island fragments?

Methods

Study sites

The study islands were located in the TIL (29°22'–29°50'N, 118°34'–119°15'E), which was formed by the Xin'anjiang dam in 1959. The TIL covers around 580 km² of water area and contains 1078 islands (0.25–1320 ha) since the water reached its final level of 108 m. The TIL is in a subtropical monsoon climate zone, with four distinct seasons, abundant rainfall and a mild climate. The mean daily temperature is 17°C, with a low of −7.6°C in January and a high of 41.8°C in July. The approximate annual rainfall is 1430 mm. The landscape is dominated by the naturally secondary forest (mainly *Pinus massoniana* Lamb.) and is mixed with lots of broad-leaved trees and shrubs.

We conducted our research on 41 islands across an area and isolation gradient. Island areas were measured using digital maps with a scale of 1:10000. We used the distance from the nearest mainland beach as a measure of isolation (Meyer and Kalko 2008; Wang et al. 2009). *PAR* was estimated as $PAR = P/A$ and *SI* was calculated as $SI = P/[2 \times (\pi \times A)^{0.5}]$ where *P* was the island perimeter (m) and *A* was the corresponding island area (ha).

Bird censuses

We conducted bird censuses following a line transect method (Bibby et al. 2000) on each of the study islands during breeding seasons (April–June) and winter seasons (November–January) from 2006 to 2009. The number of transects selected on each island was roughly proportional to the island area (Wang et al. 2010). A total of 15 censuses were taken on each island per season to increase the probability of detecting elusive or rare birds (Ralph et al. 1993). We recorded bird species richness and abundance during each census but used only species richness for our analyses (See Additional file 1: Table S1). Censuses were made between 0.5 h after dawn through to 11:00 h (local time) in the mornings and between 15:00 and 0.5 h before sunset in the afternoons, when bird activity is at its maximum, and were not made during inclement weather (rain or strong winds). To minimize potential bias, the observers alternated the order in which islands were surveyed (MacNally et al. 2002).

Guild classifications

We assigned all bird species to guilds based on their migratory status, dietary categories and foraging strata (Canterbury et al. 2000; O'Connell et al. 2000; Lampila et al. 2004; Lim and Sodhi 2004). For each ecological characteristic, the different categories were mutually exclusive and a species could only be assigned to one category (See Additional file 1: Table S2; Lim and Sodhi 2004).

We determined migratory status based on Zhuge et al. (1990) and divided species into two broad categories, migrants and residents. We classified species into one of

four mutually exclusive dietary guilds (i.e. carnivores, insectivores, omnivores and granivores) according to their predominant diet as reported by authors. Carnivores were defined as species that feed on mainly non-insect animals. Insectivores were set as birds that feed predominantly on insects and small arthropods. Omnivores eat different combinations of animal and plant materials, and granivores mainly feed on grains and seeds. Foraging strata was classified as ground, understory, mid-story, canopy and air.

Information on dietary categories and foraging strata was gathered from published species accounts and primarily from Zhuge et al. (1990). Specifically, guilds with fewer than three species were excluded from the analysis due to their lower statistical power. In other words, only guilds with more than three species in each of the 41 studied islands were used for our analysis (Weiher et al. 1998). In the present study, we used residents, migrants, insectivores, omnivores, canopy guilds and understory guilds for subsequent analyses.

Island habitat variables

We classified the habitats on the study islands into seven main types: (1) coniferous forests, (2) broadleaf forests, (3) coniferous-broad mixed forests, (4) bamboo groves, (5) shrubs, (6) grasses and (7) farmlands (Zhang et al. 2008). Habitat diversity per island was estimated by visually tallying the number of habitat types on each island (Wang et al. 2010). To determine plant species richness, we conducted detailed surveys of all vascular plant species occurring on the 41 study islands during the 2007 growing season (April to November). During the surveys, we determined the presence or absence of plant species (abundance data were not collected) through multiple visits to all islands, following traditional field methods designed to record the highest possible number of species. On all islands < 100 ha (39 islands), islands were circumnavigated and 4–16 transects were established (number and length of transects were dependent on the shape and length or width of the island). Each transect was walked a minimum of three times by trained observers. For the two islands > 100 ha in area, surveys were conducted as above but centered on each prominent hill. Most plant species were identified and recorded in the field. We collected voucher specimen for all species, which were then identified, or their identities confirmed, in the lab according to *Flora of Zhejiang* (Editorial Committee of Flora of Zhejiang 1993) and *Keys of Seed Plants in Zhejiang* (Zheng 2005).

Data analysis

Prior to the analysis, we discarded *SI* and habitat diversity because of its high Pearson's correlations (higher or equal than 0.8, Torras et al. 2008) with other variables (Table 1). For testing the multicollinearity, the VIF (variance inflation

Table 1 Correlation matrix among island area, isolation, *SI*, *PAR*, habitat diversity and plant richness

	Isolation	<i>SI</i>	<i>PAR</i>	Habitat diversity	Plant richness
Area	−0.04	0.83***	−0.56***	0.82***	0.38*
Isolation		−0.02	0.20	0.04	−0.19
<i>SI</i>			−0.51***	0.86***	0.17
<i>PAR</i>				−0.65***	−0.40*
Habitat diversity					0.21

* $p < 0.05$, *** $p < 0.001$.

factors) of all variables did not exceed 4 ($VIF_{Area} = 1.55$, $VIF_{PAR} = 1.60$, $VIF_{Plant} = 1.27$, $VIF_{Isolation} = 1.07$), which is below the maximum threshold of 10 suggested by Neter et al. (1996). Based on previous analyses (Yu et al. 2012), only isolation had significant spatial autocorrelation (Global Moran's *I*, Moran 1950) but there was no effect of spatial structure of islands on species richness (Mantel test, Mantel 1967).

We related species richness of each guild to island area using the log-log transformed power model ($\log S = \log c + z \times \log A$, where *S* is richness of bird guilds, *A* is area, and *c* and *z* represent the intercept and slope of the species-area relationship), as this model was the most common used in the literature and had higher explanatory power compared to others (Watling and Donnelly 2006). The *z* values indicated how rapidly species richness increased with island area and are considered a measure of community's vulnerability to fragmentation. Then, we used the methodology described in Zar (1996) to compare the *z* values of each regression. This method uses a *t*-test in a fashion analogous to that of testing for differences between two populations. The test statistic is calculated as $t = (b_1 - b_2) / S_{b_1, b_2}$, where the variables b_1 and b_2 are the regression coefficients and S_{b_1, b_2} is the standard error of the difference between the regression coefficients.

In addition, we used a stepwise linear regression analysis, which included four island attributes (island area, isolation, *PAR* and plant richness), to find the best fit models for richness of each guild. Goodness-of-fit was assessed using AICc values (modification of AIC for small *n*) (Burnham and Anderson 2002; Johnson and Omland 2004) for each of the candidate regression models. Variation partitioning was also used to estimate the relative contribution of each island attribute to richness of each guild.

All calculations and analyses were performed in R 2.13.1 (R Development Core Team 2011).

Results

Species-area relationships

We recorded a total of 77 bird species across the 41 study islands in TIL: 49 residents and 28 migrants. Insectivores were the best represented guild in TIL (34

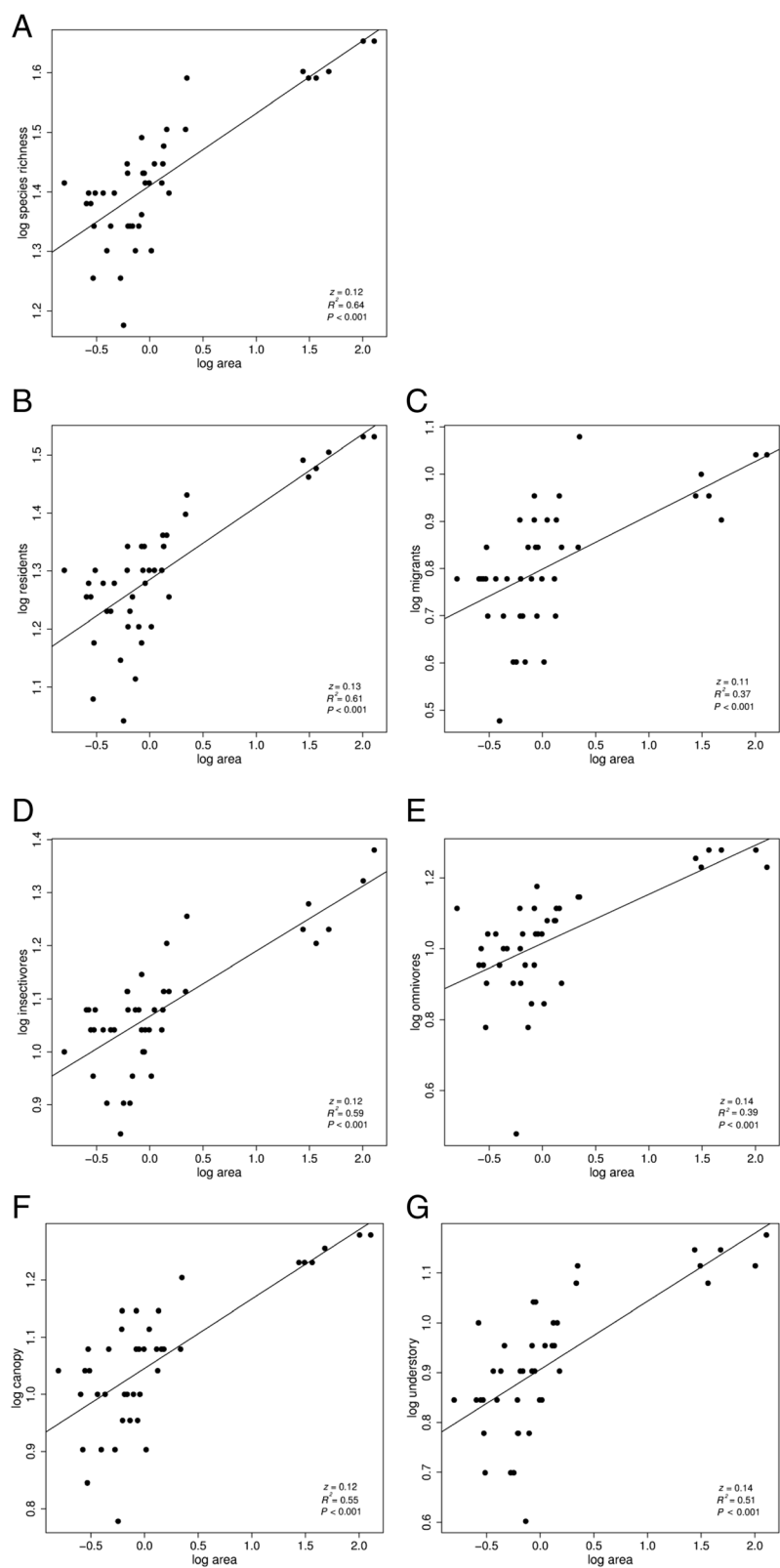


Figure 1 Response of bird guilds to island area. (A) total species richness, (B) residents, (C) migrants, (D) insectivores, (E) omnivores, (F) canopy guilds and (G) understory guilds.

species), followed by omnivores (27 species), granivores (11 species) and carnivores (5 species). Understory foraging guilds were the most common (28 species), followed by canopy (25 species), ground (13 species), midstory (8 species) and air (3 species).

The z value of total species richness and island area was 0.12. The regression coefficient for the relationship between residents and island area was 0.13, and was 0.11 for the relationship between migrants and island area (Figure 1). These slopes were not significantly different ($p > 0.05$). In dietary guilds, the fitted z values were 0.12 (insectivores) and 0.14 (omnivores), and there were no significant differences between them ($p > 0.05$). In foraging guilds, the fitted z values were 0.14 (understory) and 0.12 (canopy), and there were also no significant differences between them. Taken together, all z values were not significantly different from each other ($p > 0.05$).

Effects of island attributes on guild richness

In the backward stepwise analysis, island area and PAR all had significant relationships with the richness of all bird guilds, but only island area had a significant relationship with migrants (Table 2). Island area and PAR explained 65% of total species richness, 65% of residents, 37% of migrants, 67% of insectivores, 49% of omnivores, 62% of canopy guilds and 47% of understory guilds, while their joint effects explained nearly 30% (Figure 2). Specifically, island area had the greatest pure explanatory power for most guilds (five out of seven guilds), larger than the pure effect of PAR . For omnivorous and canopy guilds, both island area and PAR explained a similar amount of variation (Figure 2E, F).

Discussion

Species-area relationships

Previous analyses showed that the z values of birds in fragmented ecosystems were within the range 0.10–0.16 (Begon et al. 1986; Watling and Donnelly 2006). In our

case, we found that the z values for all bird guilds ranged from 0.11 to 0.14 and were similar to the average slopes reported for birds. Contrary to other predictions across a variety of systems and species groups (Preston 1962; Rosenzweig 1995; May and Stumpf 2000; Panitsa et al. 2006), the relatively low z values in the present study may suggest higher inter-island immigration rates of birds (Connor and McCoy 1979; Rosenzweig 1995; Krauss et al. 2003). This is particularly possible for birds because they are generally regarded as good dispersers (Lampila et al. 2004). In addition, low z values could also be a result of low extinction rates or a combination of high immigration and low extinction (Johnson and Simberloff 1974).

Specifically, residents and migrants showed no significant responses to island area. This was consistent with previous analyses (Brotons et al. 2003; Lampila et al. 2004), but contrary to Mönkkönen and Welsh's (1994) predictions, who indicated that forest fragmentation should affect residents more than migrants. One possible explanation is that heterospecific attraction occurs (positive interactions between migrants and residents, Mönkkönen et al. 1990), so that migrants use the presence of residents as a cue for profitable sites. In the case of dietary and foraging guilds, all of their z values were similar to each other, and there were no significant differences between them. Also, these z values were not significantly different from the z values of total species richness. This indicated that all guilds had weaker sensitivity to area loss when compared to other insularized/bird guilds, possibly due to the relatively homogeneous habitat diversity on these islands, leading to a slower rate of guild loss with decreasing island area (Hu et al. 2011; Yu et al. 2012).

Effects of island attributes on guild richness

Island area was the first variable to enter in the linear regression model, positively influencing guild richness (Table 2). It is a common trend that species richness is positively correlated to fragment area for birds on islands

Table 2 Results of stepwise linear regression for each bird guild

Guilds	Best fitted model	R^2	F	p
All guilds	$SR = 32.44 + 0.14 \times \text{Area} - 109.48 \times PAR$	0.65	38.38	<0.001
Migration strategy				
Residents	$R = 24.63 + 0.11 \times \text{Area} - (-86.53) \times PAR$	0.65	38.81	<0.001
Migrants	$M = 6.31 + 0.05 \times \text{Area}$	0.32	20.00	<0.001
Dietary guild				
Insectivores	$In = 13.85 + 0.09 \times \text{Area} - 37.71 \times PAR$	0.67	41.57	<0.001
Omnivores	$Om = 14.28 + 0.05 \times \text{Area} - 58.43 \times PAR$	0.49	19.87	<0.001
Foraging guild				
Canopy	$Ca = 14.51 + 0.05 \times \text{Area} - 54.09 \times PAR$	0.62	33.63	<0.001
Understory	$Un = 10.44 + 0.05 \times \text{Area} - 36.33 \times PAR$	0.47	18.93	<0.001

SR means richness of all birds, R residents, M migrants, In insectivores, Om omnivores, Ca canopy, and Un understory.

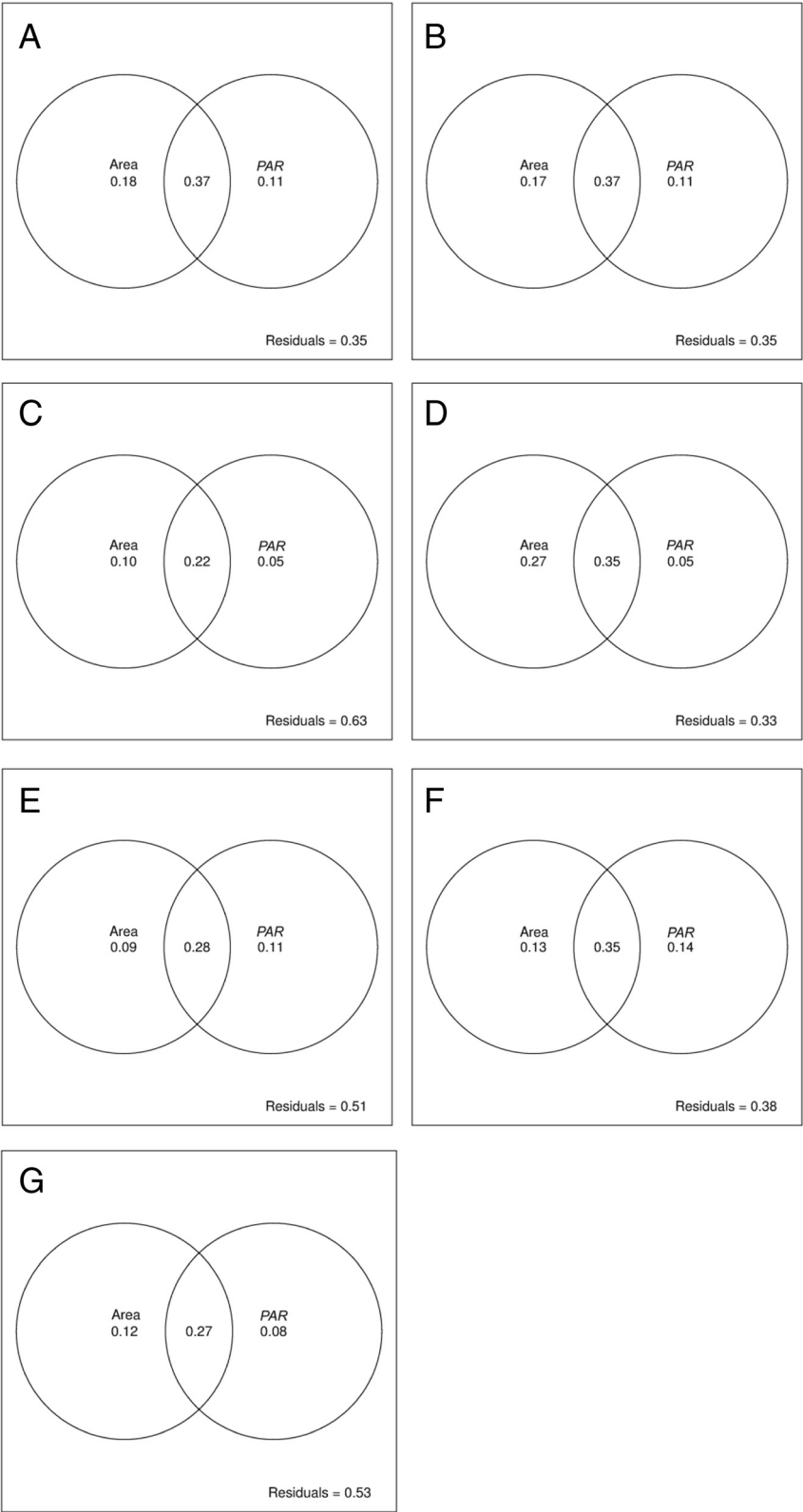


Figure 2 Venn diagram showing the effects of island attributes on guild richness. **(A)** total species richness, **(B)** residents, **(C)** migrants, **(D)** insectivores, **(E)** omnivores, **(F)** canopy guilds and **(G)** understory guilds.

or fragments (reviews in Ricklefs and Lovette 1999; Watling and Donnelly 2006; Benassi et al. 2007), and also for other animals (reviews in Watling and Donnelly 2006) or plants (Hu et al. 2011). Additionally, *PAR* had significantly negative effects on guild richness, possibly because the islands with less relative interior habitat (high *PAR*) increased the risk of local extinction and thereby decreased guild richness. Indeed, Helzer and Jelinski (1999) also found that bird species richness decreased with increased *PAR* in wet meadow grasslands. Contrary to general expectations, isolation had little effect on the richness of all guilds. The lack of an isolation effect might be due to the high mobility of birds and/or the narrow range of isolation values included in this study (Watling and Donnelly 2006). Likewise, plant richness was also not correlated with guild richness. This might indicate that some plant species retain higher bird species richness than other plant species did. For example, MacGregor-Fors (2008) found that bird species richness was not related to tree species richness, but was instead related to specific tree taxa.

The results of variation partitioning indicated that island area was of prime importance for the distribution of total species richness, residents, migrants, insectivores and understory guilds. This is not surprising because large areas may have more habitats (higher habitat diversity, and hence more species, Williams 1964) and/or lower extinction rates than small areas (MacArthur and Wilson 1967). In the case of omnivores and canopy guilds, both island area and *PAR* contributed equally in explaining guild richness (Figure 2E, F). This indicated that omnivores and canopy guilds were not very sensitive to fragments, as also indicated by previous analyses (Dale et al. 1994; Bierregaard and Stouffer 1997; Anjos and Boçon 1999; Ribon et al. 2003).

Conclusions

Our findings showed insectivores had the largest number of species (34 species), followed by understory foraging guilds (28 species), omnivores (27 species) and canopy guilds (25 species). The low richness of other guilds might be due to the characteristics of the study site and/or food resources (Gray et al. 2007; Ding et al. 2013). That is, the relatively homogeneous habitat diversity and/or the lack of specific food resources at TIL might account for the low richness of such guilds. Furthermore, our data showed that migrants and residents responded equally to island area, insectivores and understory guilds were sensitive to island area but omnivores and canopy guilds were not very sensitive. Most guild richness was determined by island area, except for omnivores and canopy guilds. Although *PAR* or habitat diversity (plant species richness) or isolation has been found to be important for bird species richness (Helzer and Jelinski 1999; Ricklefs and Lovette 1999; Watling and

Donnelly 2006), our results highlight the importance of island area in maintaining bird diversity in fragmented island systems.

Additional file

Additional file 1: Table S1. Island × species abundance matrix for birds on 41 islands in the Thousand Island Lake, China. **Table S2.** Species × trait data matrix for birds on 41 islands in the Thousand Island Lake, China.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

ZD, KJF and PD conceived and designed the experiments, and ZD and PD performed the experiments. All the authors participated in the data analysis and paper writing. All the authors read and approved the final version of the manuscript.

Acknowledgements

We thank Prof. Mingjian Yu for helpful suggestions on field surveys of island habitat variables, Guang Hu and Xingfeng Si for constructive suggestions on data analyses and helpful suggestions on R programming. We also thank Lauren Barry for providing extensive comments on the draft manuscript. We are grateful to numerous graduates in our group for helping with species investigation, and to the Chun'an Forestry Bureau and the Thousand Island Lake National Forest Park for the permits necessary to conduct the research in the TIL. We also thank the anonymous reviewers for their numerous helpful comments and suggestions. This study was supported by the National Natural Science Foundation of China (No. 31170397), and the Fundamental Research Funds for the Central Universities.

Author details

¹The Key Laboratory of Conservation Biology for Endangered Wildlife of the Ministry of Education, College of Life Sciences, Zhejiang University, Zijing'gang Campus, Hangzhou 310058, China. ²Guangdong Entomological Institute & South China Institute of Endangered Animals, Guangzhou 510260, China.

³Department of Biological Sciences, Florida International University, Miami, FL 33199, USA. ⁴Center for Tropical Plant Conservation, Fairchild Tropical Botanic Garden, Coral Gables, FL 33156, USA.

Received: 28 July 2014 Accepted: 26 March 2015

Published online: 15 June 2015

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