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Patterns of bird functional diversity on land-bridge island fragments

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Summary

1. The loss of species diversity due to habitat fragmentation has been extensively studied. In contrast, the impacts of habitat fragmentation on functional diversity remains relatively poorly understood. We conducted bird functional diversity studies on a set of 41 recently isolated land-bridge islands in the Thousand Island Lake, China.

2. We analysed differences in bird species richness and a recently developed suite of complementary functional diversity indices (FRic, volume of functional space occupied; FEve, evenness of abundance distribution in the functional trait space; FDiv, divergence in the distribution of abundance in the trait volume) across different gradients (island area and isolation).

3. We found no correlations between FRic and FEve or FEve and FDiv, but negative correlations between FRic and FDiv. As predicted, island area accounted for most of the variation in bird species richness, whereas isolation explained most of the variation in species evenness (decreasing species evenness with increasing isolation). Functional diversity appears to be more strongly influenced by habitat filtering as opposed to limiting similarity. More specifically, across all islands, both FRic and FEve were significantly lower than expected for randomly assembled communities, but FDiv showed no clear patterns. FRic increased with island area, FEve decreased with island area and FDiv showed no clear patterns.

4. Our finding that FEve decreases with island area at TIL may indicate low functional stability on such islands, and as such large islands and habitat patches may deserve extra attention and/or protection. These results help to demonstrate the importance of considering the effects of fragmentation on functional diversity in habitat management and reserve design plans.

Key-words: bird community, functional divergence, functional evenness, functional richness, habitat filtering, land-bridge islands, Thousand Island Lake

Introduction

Habitat fragmentation is widely recognized as one of the greatest threats to global biodiversity (Laurance & Bierregaard 1997; Peres & Michalski 2006) as reduced habitat area and increased isolation almost invariably lead to rapid decline in local species richness and/or to increased extinction risk of remnant populations (MacArthur & Wilson 1967; Hanski 1999; Fahrig 2003). Given the increasing prevalence of habitat fragmentation due to human activities (Groom & Schumaker 1993; Davies & Margules 1998), ecologists have dedicated intensive efforts to understanding and mitigating the negative impacts of habitat fragmentation on biodiversity (Fahrig 2003). Indeed, habitat fragmentation has become a central issue in conservation biology (Harrison & Bruna 1999), attracting much interest in recent decades (Fahrig 2003).

MacArthur & Wilson's (1967) equilibrium theory of island biogeography is often used as the basic conceptual model for understanding the effects of habitat fragmentation (Laurance 2008). This theory asserted that number of species on islands (including habitat patches or fragments) results from a dynamic equilibrium between area-dependent extinction and isolation-dependent colonization, and as such smaller and more isolated islands will contain fewer species than there larger and/or better connected counterparts (MacArthur & Wilson 1967). Yet,

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despite its widespread application to conservation biology and nature reserve design, a growing consensus of ecologists recognizes the limitations of island biogeography theory (Lomolino 2000). For example, the theory could not address patterns in species composition due to the implicit assumption that all species are equivalent. In this case, the theory just concerns how many species inhabit the islands, not which species inhabit the islands. This has led to calls to broaden the theory to consider additional parameters such as compositional differences and ecological differences among species (Lomolino 2000). For example, by taking into account trophic interactions, Gravel *et al.* (2011) found a strong support for their trophic extension of the Theory of Island Biogeography. Likewise, by framing research of fragmentation within the context of the island biogeography theory, questions have generally focused either on species number or on the presence or absence of individual species in fragments, while other important components of biodiversity have frequently been overlooked (Díaz & Cabido 2001). For example, relatively few studies have investigated the effects of fragmentation on other components of biodiversity such as functional diversity (Laurance 2008).

'Functional diversity' measures the range and values of species traits present in a community accounting for the composition of organisms (Tilman 2001). In this respect, functional diversity metrics have potential advantages for expanding the existing island biogeography theory. Since 1999, many different metrics of functional diversity have been developed (reviewed in Petchey & Gaston 2006; Mouchet *et al.* 2010; Schleuter *et al.* 2010). These metrics can be broadly classified as either discontinuous or continuous (reviewed in Petchey & Gaston 2006). Discontinuous measures of functional diversity classify species into distinct functional groups often on the basis of arbitrary criteria and differences between species within groups are ignored. Continuous measures of functional diversity, in which species are not arbitrarily classified into groups, are generally considered superior to discontinuous measures and have consequently increased in prominence (reviewed in Petchey & Gaston 2006). However, most published metrics are highly correlated and quantify only the richness of functional diversity (Mouchet *et al.* 2010). It is now generally accepted that measures of functional diversity should ideally be continuous and take into account functional traits, species abundances and measure multiple facets of functional diversity (Mason *et al.* 2005; Villéger, Mason & Mouillot 2008; Mouchet *et al.* 2010). Moreover, metrics of functional diversity should not be trivially related to species richness, and should rely, if possible, on original data rather than data transformed through classification or ordination processes (Villéger, Mason & Mouillot 2008). A new suite of complementary indices, Functional Richness (FRic), Functional Evenness (FEve) and Functional Divergence (FDiv), meet all these criteria and in comparisons with other candidate diversity indices (Villéger, Mason & Mouillot 2008; Mouchet *et al.* 2010), each performed best in measuring richness, evenness and divergence of functional diversity respectively.

Analyses with simulated data have shown that FRic and species richness are highly associated ($r = 0{\cdot}872$, $P < 0{\cdot}001$), while FDiv and FEve exhibit weak relationships with species richness ($r = 0{\cdot}011$, $P > 0{\cdot}05$; $r = -0{\cdot}065$, $P > 0{\cdot}05$ respectively) (Villéger, Mason & Mouillot 2008). Thus, these metrics can be used to compare communities with different species richness without bias (Villéger, Mason & Mouillot 2008). Moreover, the three functional diversity indices are independent of each other, which allow us to test differences in functional divergence or evenness with different functional richness values (Villéger, Mason & Mouillot 2008). Finally, the three indices were all much more sensitive to community assembly rules (limiting similarity and habitat filtering) than species richness, as limiting similarity yields higher functional diversity values and habitat filtering yields lower functional diversity than does neutral community assembly (random assembly). Therefore, these three indices were able to efficiently differentiate assembly rules independent of species richness (Mouchet *et al.* 2010).

Field assessments of functional diversity have revealed several emerging patterns. For example, Pakeman (2011) found that the three functional indices were orthogonal to each other and that only FRic was highly correlated with species richness. Furthermore, analyses of field data have indicated a general prevalence of habitat filtering in ecosystems. For example, using FRic as their measure of functional diversity, Cornwell, Schwilk & Ackerly (2006) showed that the observed FRic was significantly lower than would be expected by chance for a California woody-plant community, a result consistent with habitat filtering. Likewise, in a study of Scottish plant communities, Pakeman (2011) also found that most of his study plots (23 of 30) had significantly lower FRic values than expected for random assemblages potentially due to habitat filtering.

In this study, we examine patterns of taxonomic and functional diversity for communities of birds inhabiting a set of 41 recently isolated land-bridge islands in a large man-made lake in Eastern China. Land-bridge island systems such as this have been considered ideal systems for studying habitat fragmentation (Diamond 2001; Terborgh *et al.* 2001; Wu *et al.* 2003; Terborgh & Feeley 2008). Our study had three specific objectives. First, we tested the independence of the three metrics of functional diversity (as indicated by previous tests with simulated data) and the relationships between taxonomic diversity (species richness and evenness) and the three functional diversity indices. Secondly, we compared the observed patterns of functional diversity as measured by each of the three indices with expectations for random assemblages to elucidate the underlying ecological assemblage processes. Finally, we examined the effects of island area and isolation on taxonomic diversity and measures of functional diversity.

Materials and methods

STUDY SYSTEM

The Thousand Island Lake (TIL) is a hydroelectric reservoir created in 1959 by the damming of the Xin'anjiang River. TIL is located in the western part of Zhejiang province, China, (29°22′ ~29°50′N, 118°34′~119°15′E) and has *ca*. 580 km^2 of water surface area and 1078 land-bridge islands (created by the isolation of erstwhile hilltops) greater than 0·25 ha in area. The elevations of the islands range from 120 to 600 m.a.s.l. (water level is 108 m.a.s.l.). The natural vegetation of this area is a mix of subtropical deciduous and coniferous forest. The primary habitat on the islands is forest (mean forest coverage per island = 82·6%) and the dominant plant species are *Pinus massoniana* Lamb., *Smilax davidiana* A. DC., *Grewia biloba* G. Don., *Rhamnus utilis* Decne., *Vaccinium henryi* Hemsl., *Eurya muricata* Dunn., *Lespedeza virgata* (Thunb.) DC. and *Loropetalum chinense* (R. Br.) Oliv. (Sun *et al*. 2008). The climate is typical of the subtropical monsoon zone and is characterized by four distinct seasons with hot summers and cold winters. The mean daily temperature is approximately 17 °C and average total annual precipitation is 1430 mm (Wang *et al*. 2010).

BIRD SURVEYS

We censused the presence and abundance of bird species on each of 41 study islands using standard line transect methods (Bibby *et al*. 2000). Birds were censused during the breeding seasons (April-June) and winter seasons (November-January) each year from 2006 to 2009. Each of the study islands was censused 15 times per season to increase the probability of detecting elusive or rare species (Ralph *et al*. 1993). The total length of transects on each island was roughly proportional to island area (Table S1) as proportional sampling has been previously shown to be effective in characterizing species–area relationships (Schoereder *et al*. 2004). During each survey, a trained observer recorded all birds seen or heard while traversing each section of a transect. Surveys were conducted between 30 min after dawn to 11:00 h (local time) and in the afternoons between 15:00 h and 30 min before sunset (Wang *et al*. 2010). We did not conduct surveys at mid-day due to low bird activity. Censuses were not conducted during inclement weather (rain or strong winds). To minimize potential bias, the observers randomly varied the order in which islands were surveyed. In studying the nestedness patterns in the Thousand Island Lake, Wang *et al*. (2010) found that there were low turnover rates between sampling years for birds and that our sampling design and intensity is adequate to detect the island's avian residents.

SPECIES TRAIT DATA

Our selection of functional traits was constrained to those traits that are commonly measured and commonly used in functional diversity research (Petchey *et al*. 2007; Flynn *et al*. 2009). Specifically, we used one continuous species trait and three categorical traits, two with four binary attributes and one with five (Table 1), all of which are related to resource use (Petchey *et al*. 2007; Flynn *et al*. 2009). The one continuous trait was body mass. Body mass is often considered to be the single most informative trait of animal species (Brown 1995) because it is related to the resource and/or energy requirements of individuals as well as the impacts of the species on other trophic levels. The three categorical traits characterize feeding guild, behaviour and location (Table 1). Trait data were extracted from published species accounts – primarily from Zhuge, Gu & Cai (1990), based on measurements of birds collected in a similar environment (in Zhejiang province).

DIVERSITY INDICES

Five metrics of diversity were computed for each of the island bird communities. These included two measures of taxonomic diversity (species richness and Pielou's evenness index) and three functional diversity metrics: FRic, FEve and FDiv. FRic measures the volume of the functional space occupied by the community (Cornwell, Schwilk & Ackerly 2006; Villéger, Mason & Mouillot 2008); FEve describes the evenness of abundance distribution in the functional trait space and FDiv represents the divergence in the distribution of abundance in the trait volume (Mason *et al*. 2005; Villéger, Mason & Mouillot 2008).

As we included mixed categorical/binary and continuous trait variables, we performed the following steps to obtain a subset of the PCoA (Principal co-ordinates analysis) axes as the new 'traits' for use in computing the functional diversity indices (Laliberté & Legendre 2010). First, we computed the functional distance between all the bird species pairs according to their trait values using the Gower's distance (Gower 1966). Secondly, we performed a PCoA on this functional distance matrix to obtain a subset of the PCoA axes (Table S2). Functional diversity indices were estimated using the new 'trait' data and the relative abundance data (Tables S3, S4). The functional diversity metrics were calculated using the FD package in R 2.13.1 (R Development Core Team 2011) using the function dbFD (Laliberté & Legendre 2010; Laliberté & Shipley 2011).

NULL MODEL

Although the use of null models has had a long and controversial history, they continue to be useful in detecting patterns in ecological and biogeographic data, particularly when conventional statistical analyses fall short (Gotelli 2001; de Bello 2012). We used a matrix swap randomization (Manly 1995) iterated 999 times to test whether the observed functional diversity indices recorded on each island were significantly higher or lower than 999 simulated assemblages ($\alpha = 0{\cdot}05$). The simulated assemblages were constructed using all the species recorded across all the islands while maintaining the observed patterns of abundance and the species richness on each island and thereby avoiding the Jack Horner

Table 1. Traits used to measure bird functional diversity indices

Trait type	Trait	Range or categories
Resource quantity	Body mass (ln, g)	Continuous, 1·74–7·31
Feeding guild	Carnivore, granivore, insectivore, omnivore	Binary
Foraging behaviour	Glean, probe, leap, sally	Binary
Foraging location	Ground, understorey, midstorey, canopy, air	Binary

effect (incorrectly rejecting a true null hypothesis, Wilson 1995). To obtain a significance test, we calculated a standardized effect size (SES) for each islands. The SES measures the number of standard deviations between the observed and expected value. It takes the form: $\mathrm{SES} = (\mathrm{Obs}-\mathrm{Exp})/\mathrm{SD}_{\mathrm{exp}}$, where Obs is the functional diversity values obtained from the observed data, Exp is the mean of the 999 randomizations and $\mathrm{SD}_{\mathrm{exp}}$ is the standard deviation of the 999 indices from the simulated communities. Assuming a normal distribution of deviations, approximately 95% of the SES values should fall between −1·96 and +1·96 (Gotelli & Rohde 2002; Wittman *et al.* 2010). SES values outside this confidence interval were considered to be statistically significant at $P < 0{\cdot}05$. In addition, we also tested our observed functional diversity values against the expected values (the expected values were calculated as the mean of the values produced by the random communities in accordance with convention, Mason *et al.* 2007) using paired two-tailed Wilcoxon signed-rank tests (Sokal & Rohlf 1995).

DATA ANALYSIS

We used correlation analysis (Pearson) to test if the functional diversity indices (FRic, FEve and FDiv), SES values and the taxonomic diversity indices (species richness and Pielou's evenness) were statistically independent of each other. Following previous studies (Mason *et al.* 2008; Pakeman 2011), we used linear and quadratic regression to relate diversity indices and island characteristics, as a quadratic relationship has been shown to exist between species diversity and disturbance (Grime 1973; Connell 1978). Goodness-of-fits were assessed using AICc values (modification of AIC for small *n*) (Burnham & Anderson 2002; Johnson & Omland 2004) for each of the candidate regression models (Murtaugh 2009). Delta AICc (ΔAICc) was calculated as the difference between a given model and the best fitted model. Moreover, an Akaike weight (ωi) was also calculated for each model following the method described by Johnson & Omland (2004). If an Akaike weight is greater than 0·5 in the case where there are two candidate models, we could conclude that such a model provide the better fit to the data (Plank & Codling 2009; Hurlbert & Jetz 2010), and so on. Linear or quadratic relationships are only reported for the models with highest adjusted r^2 and higher Akaike weights (Murtaugh 2009) (Table 2). All calculations and analyses were performed in R 2.13.1 (R Development Core Team 2011).

Results

The 41 study islands in TIL ranged in area from less than 0·5 ha to greater than 140 ha (Table S1). Isolation of the study islands, measured as the straight-line distance from the island to the nearest mainland beach, ranged from less than 25 m to over 2·25 km (Table S1) (Isolation measured as the distance to the nearest neighbouring island or to the nearest 'large' island produced the same patterns, data not shown). Island area and isolation are not significantly correlated ($r = -0{\cdot}09$, $P > 0{\cdot}05$).

RELATIONSHIPS BETWEEN FUNCTIONAL DIVERSITY INDICES AND SPECIES RICHNESS

As expected, there was a strong positive correlation between species richness and FRic (Table 3). In addition, species richness was weakly negatively correlated with FEve, and strongly negatively correlated with the SES of FRic. There was a negative correlation between FRic and FDiv. In general, the correlations between all pairs of variables were not very strong ($r < 0{\cdot}50$, Cohen 1988) with the exceptions being between species richness and FRic, and between species richness and the SES of FRic.

DIFFERENCES FROM EXPECTED FUNCTIONAL DIVERSITY INDICES

The expected FRic values (mean FRic of 999 randomizations) increased quadratically with species richness across the 41 study islands ($P < 0{\cdot}001$, $r^2 > 0{\cdot}99$, regression coefficient was −0·0061 for the square term and 0·94 for the first-order term; Fig. 1a), whereas the expected FEve values (mean FEve of 999 randomizations) decreased

Table 2. The best fitted models based on adjusted r^2 and Akaike weights

The best fitted models	AICc values	ωi	*F* statistics	*P* values	The adjusted R^2
SR = 24·09 + 9·83*log(*A*)	105·63	0·76	135·50	$P < 0{\cdot}001$	0·77
log(*P*) = −0·11–0·000028**I*	−254·67	0·56	12·96	$P < 0{\cdot}001$	0·23
FRic = 6·54 + 2·53*log(*A*)	85·59	0·68	14·66	$P < 0{\cdot}001$	0·25
log(FEve) = −0·49–0·058*log(*A*)	−219·84	0·58	13·23	$P < 0{\cdot}001$	0·23
FEve = 0·33–0·000044**I* + 0·000000017* I^2	−245·96	NC	4·01	$P < 0{\cdot}05$	0·13
Log(FDiv) = −0·053 −0·000038* +0·000000011* I^2	−311·59	NC	4·19	$P < 0{\cdot}05$	0·14
EFRic = −8·11 + 0·94*SR 0·0061* SR^2	−157·27	1·00	17712·11	$P < 0{\cdot}001$	>0·99
EFEve = 0·43 + 0·000049*SR 0·000080* SR^2	−320·91	0·53	71·34	$P < 0{\cdot}001$	0·78
EFDiv = 0·81 + 0·00058*SR	−495·36	0·76	134·68	$P < 0{\cdot}001$	0·77
SFRic = −0·88–0·53*log(*A*)	−54·50	0·45	19·37	$P < 0{\cdot}001$	0·31

A, Island area; I, isolation; SR, species richness; P, Pielou's evenness; FRic, functional richness; FEve, functional evenness; FDiv, functional divergence; EFRic, expected FRic; EFEve, expected FEve; EFDiv, expected FDiv; SFRic, SES of FRic; NC, not calculated (Akaike weights for FEve-isolation model and FDiv-isolation model were not calculated because of their low explanatory power).

Table 3. Correlation matrix between species richness per island, species evenness (Pielou) and functional indices: FRic, functional richness; FEve, functional evenness; FDiv, functional divergence; SES, standard effect size.

	Species evenness	FRic	FEve	FDiv	SES FRic	SES FEve	SES FDiv
Species richness	−0·13	0·66***	−0·48**	−0·20	−0·61***	0·18	−0·27
Species evenness		−0·34*	−0·08	0·27	−0·18	−0·44**	0·31*
FRic			−0·15	−0·38*			
FEve				0·14			
SES FRic						0·17	−0·11
SES FEve							−0·17

$^{*}P < 0·05$, $^{**}P < 0·01$, $^{***}P < 0·001$.

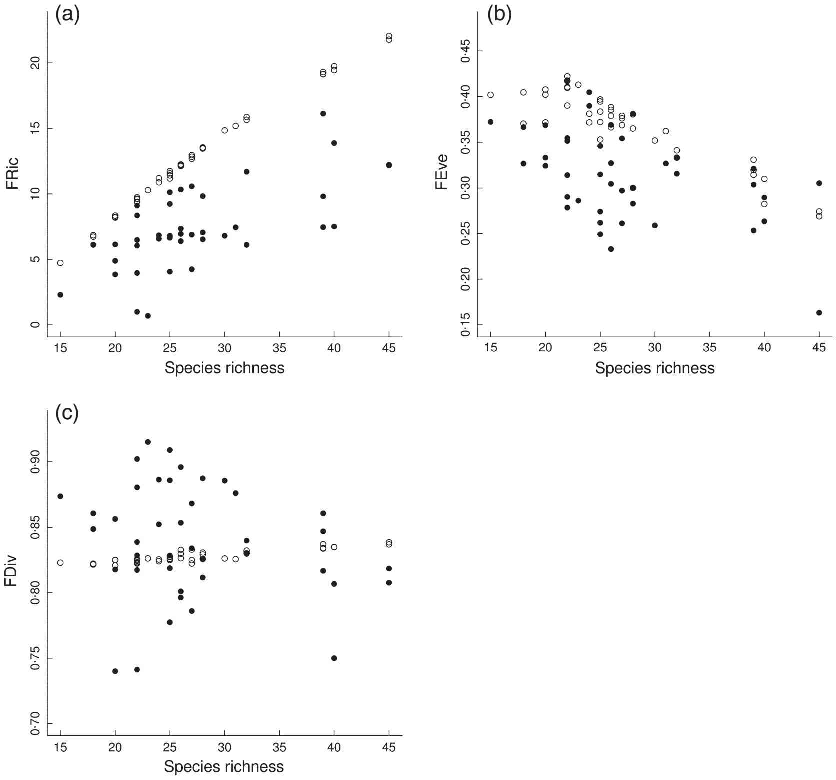

Fig. 1. Observed (solid circles) and simulated (open circles) diversity indices vs. species richness for the three metrics of functional diversity.

quadratically with species richness ($P < 0·001$, $r^2 = 0·78$, regression coefficient was −0·000080 for the square term and 0·000049 for the first-order term). The expected FDiv values (mean FDiv of 999 randomizations) increased linearly with species richness ($P < 0·001$, $r^2 = 0·77$, regression coefficient was 0·00058).

For four of the 41 study islands, FRic was significantly less than values calculated for the corresponding simulated communities (four islands had SES of FRic values which were located outside the lower confidence bounds). For all study islands, the observed FRic values were less than the median/mean of the simulated communities ($P < 0·001$, two-tailed Wilcoxon signed-rank test; Fig. 2a).

Five of the 41 study islands had FEve values which were significantly lower than values calculated for the corresponding simulated communities. Across all 41 islands, FEve values were also significantly lower than expected ($P < 0·001$, two-tailed Wilcoxon signed-rank test; Fig. 2b). For FDiv, none of the islands were significantly different from than null distributions, and there was also no significant difference between the observed FDiv values and the expected values across the 41 islands ($P > 0·05$, two-tailed Wilcoxon signed-rank test; Fig. 2c).

DIVERSITY INDICES AND ISLAND CHARACTERISTICS

Variation in bird species richness was best explained by island area (ΔAICc = 0, ωi = 0·76, $r^2 = 0·77$, $F = 135·50$, $P < 0·001$, linear coefficient = 9·83 ± 0·84; Fig. 3a). There was no significant relationship between species richness and

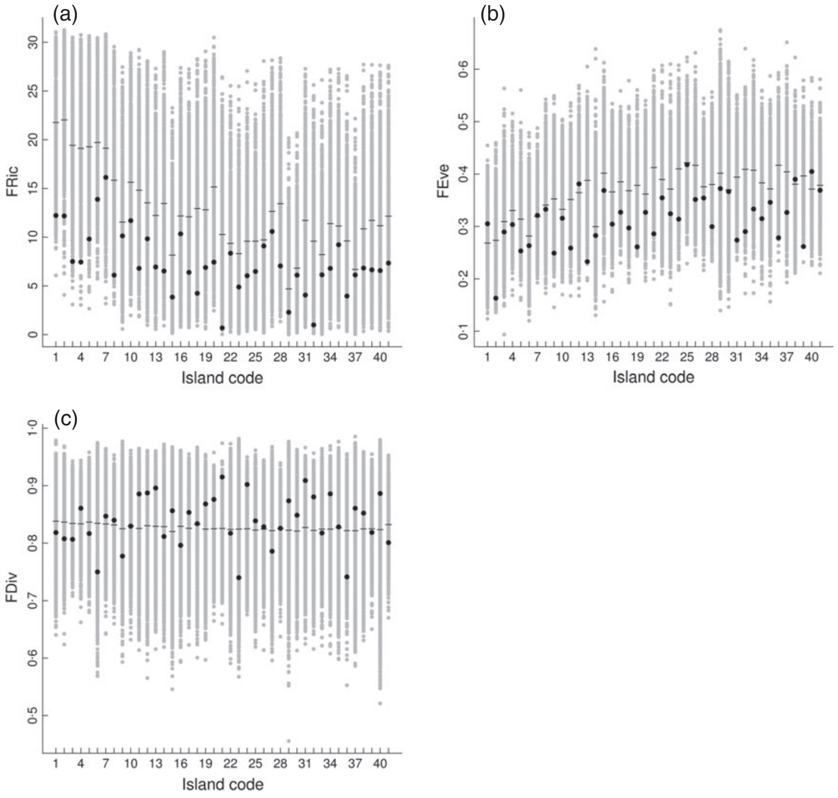

Fig. 2. Histograms showing the position of observed functional diversity values in 999 null distributions, solid circles are observed values, grey circles are 999 randomized values and short dashes are the mean of the 999 randomizations.

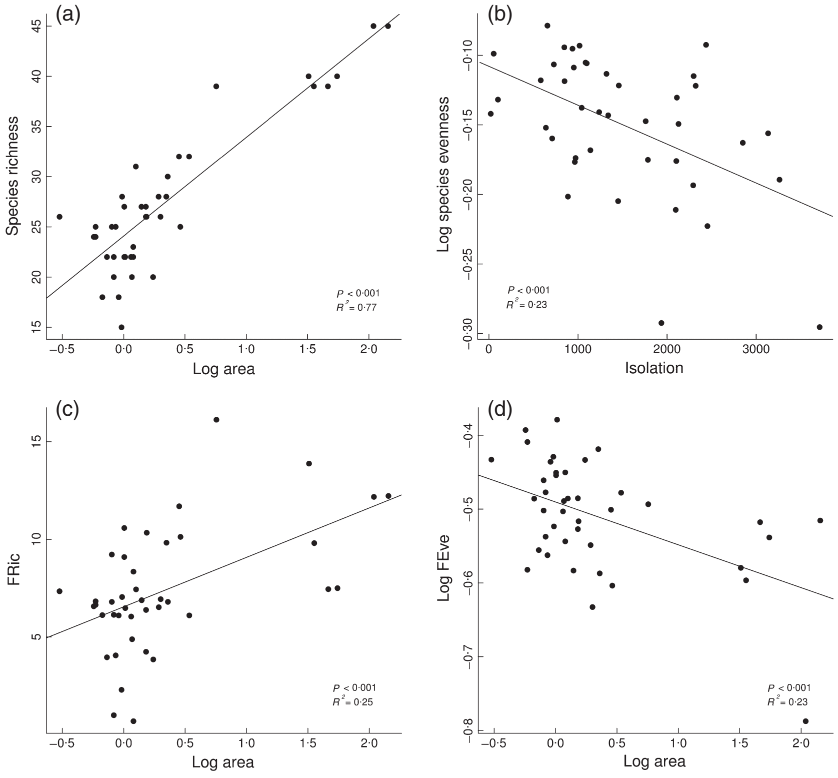

Fig. 3. Response of species richness, evenness and the metrics of functional diversity to island characteristics.

isolation ($P > 0{\cdot}05$). In contrast, most of the variation in bird species evenness was explained by a negative relationship with island isolation (ΔAICc = 0, ωi = 0·56, $r^2 = 0{\cdot}23$, $F = 12{\cdot}96$, $P < 0{\cdot}001$, linear coefficient = −0·000028 ± 0·0000078; Fig. 3b).

Patterns in the functional diversity indices varied substantially. FRic increased linearly with increased area (ΔAICc = 0, ωi = 0·68, $r^2 = 0{\cdot}25$, $F = 14{\cdot}66$, $P > 0{\cdot}001$, linear coefficient = 2·53 ± 0·66; Fig. 3c), whereas FEve decreased linearly with area (ΔAICc = 0, ωi = 0·58, $r^2 = 0{\cdot}23$, $F = 13{\cdot}23$, $P < 0{\cdot}001$, linear coefficient = −0·058 ± 0·016; Fig. 3d). FDiv increased with the quadratic model with increased isolation, but the explanatory power was very low ($r^2 = 0{\cdot}14$). SES of FRic decreased linearly with area (ΔAICc = 0, ωi = 0·45, $r^2 = 0{\cdot}31$, $F = 19{\cdot}37$, $P < 0{\cdot}001$, linear coefficient = −0·53 ± 0·12), while other fitted model of SES values and island characteristics had a very low explanatory power.

Discussion

RELATIONSHIPS BETWEEN FUNCTIONAL DIVERSITY INDICES AND SPECIES RICHNESS

Our results showed that at TIL, FRic and species richness were strongly correlated - this is not surprising as it is expected that more species will fill a larger volume of trait space (sampling effect, Cornwell, Schwilk & Ackerly 2006; Villéger, Mason & Mouillot 2008). Also, we found a negative correlation between FRic and FDiv. This was contrary to the results from previous studies using simulated data sets (Villéger, Mason & Mouillot 2008; Mouchet *et al.* 2010), as well as the results of Pakeman (2011). One possible reason for such findings is that at TIL, a few species are very abundant, and this skewed abundance pattern could lead to a negative correlation between FRic and FDiv. For example, the three most abundant species, *Aegithalos concinnus* Gould, *Hemixos castanonotus* Swinhoe and *Parus major* Linnaeus, account for 22%, 17% and 8% of the individuals respectively.

DIFFERENCES FROM EXPECTED FUNCTIONAL DIVERSITY INDICES

The expected FRic values increased quadratically with species richness (Fig. 1a) and the expected FEve values decreased in relation to species richness in a quadratic fashion (Fig. 1b). As indicated by Mouchet *et al.* (2010), the expected FRic values would monotonically increase with species richness whatever the underlying assembly rules. In this respect, this pattern was not caused by assembly rules, but rather by an increase in convex hull volume. Specifically, a large and diverse species pool will lead FRic to saturate at higher species richness (Pakeman 2011) and relative small species pool will lead FRic to increase quickly, just as FRic increased with species richness in our analyses. Moreover, previous studies using simulated data sets (Villéger, Mason & Mouillot 2008; Mouchet *et al.* 2010) found that expected FEve declined non-significantly with species richness, and FEve will decrease either when abundance is less evenly distributed among species or when functional distances among species are less regular (Villéger, Mason & Mouillot 2008). Thus, our results, expected FEve declined in a quadratic fashion, may arise from the uneven abundance patterns. Expected FDiv increased linearly with species richness in this study (very slowly), whereas the simulated values in Villéger, Mason & Mouillot (2008) and Mouchet *et al.* (2010) were unrelated to species richness. Our results might be due to the specific trait combinations of species which means that this index cannot display the theoretical absence of a relationship with species richness.

Only four of the 41 islands at TIL had FRic values lower than expected based on random community assembly, but it is important to note that all islands had lower FRic values than median/mean of the randomizations at each island ($P < 0{\cdot}001$). The specific mechanisms for these patterns remain unclear (Petchey *et al.* 2007) as the assemblage of communities depends on various complex factors (Mouchet *et al.* 2010) such as environmental filtering, limiting similarity and neutral processes, which may co-occur simultaneously and obscure the observed patterns (Helmus *et al.* 2007). One possible explanation for the observed patterns at TIL is that environmental filtering has a stronger influence on the communities than does limiting similarity, thus causing decreased functional diversity values relative to random communities. Indeed, the habitats on the TIL study islands are relatively homogeneous and the forests on all islands are dominated by *Pinus massoniana* Lamb.. Thus, it may be expected that relatively few additional niches become available as island area increases (Hu *et al.* 2011; Yu *et al.* 2012). In this scenario, environmental factors limit the presence of certain functional traits and thus the occurrence of species with these traits on islands (Mouillot, Dumay & Tomasini 2007). For example, we found that insectivores and understorey birds were very sensitive to island area. Although we cannot identify specific explanations for their absence on small islands, existing evidence has shown that trophic constraints may contribute to diversity on islands (Gravel *et al.* 2011), in other words, the lack of specific food (i.e. insect) (Zanette, Doyle & Trémont 2000; Ford *et al.* 2001) or the lack of specific habitat (Pearman 2002) in small fragments may explain their absence respectively.

In addition, we found that five of 41 islands had lower FEve values than expected for randomly assembled communities, and the observed FEve were also lower than the means of the randomizations across 41 islands ($P < 0{\cdot}001$). Low FEve values may indicate the prevalence of habitat filtering (Mouchet *et al.* 2010), and thus our results further support the importance of habitat filtering in structuring the bird communities at TIL. In contrast, the FDiv values were no different from random expectations ($P > 0{\cdot}05$).

This is because the most abundant species do not have either extreme trait values nor do they cluster around the average trait values.

DIVERSITY INDICES RESPONDED TO ISLAND CHARACTERISTICS

Anthropogenic changes to biodiversity are evident across the planet, and we may turn to islands for several important lessons (Diamond 2005). The results of this study of land-bridge islands in TIL were partially consistent with island biogeography theory (MacArthur & Wilson 1967). Specifically, we found island area accounted for most of the variation in bird species richness as compared with isolation ($r^2 = 0{\cdot}77$). This is consistent with general predictions by MacArthur & Wilson (1967), who predicted that number of species will increase with increasing island area. However, in contrast with the predictions of the island biogeography theory, isolation had little effects on bird species richness. The lack of an isolation effect on species richness may be due to the high mobility of birds and/or the narrow range of isolation values included in this study (Watling & Donnelly 2006). Furthermore, we found that isolation had negative effects on species evenness. Taken together, these findings demonstrate that isolation may be important in determining the species abundance distributions, and that such an effect can be found even in the absence of a corresponding effect on species richness.

Island biogeography theory has served as a useful conceptual model for understanding the effects of habitat fragmentation, but it fails to consider the ecosystem consequences of biodiversity loss (Laurance 2008), which is clearly important for understanding long-term sustainability and stability under changing environmental conditions (Dı́az & Cabido 2001). Thus, based on patterns of functional diversity at TIL, we have several new insights beyond the classic theory of island biogeography.

First, our findings indicate that habitat filtering is the dominant mechanism structuring the bird communities at TIL. Previous studies have found habitat filtering to be a fundamental process of community assembly (Lebrija-Trejos *et al.* 2010) and that habitat filtering is of increased prevalence in disturbed systems (e.g. Flynn *et al.* 2009; Lebrija-Trejos *et al.* 2010; Thompson *et al.* 2010; Pakeman 2011) and that the relative influences of assembly rules may depend on the scale of observation, as the limiting similarity process has been found to be important at smaller spatial scales while habitat filtering dominates at larger scales (Mouchet *et al.* 2010). In accord with this pattern, our study indicates that habitat filtering had a stronger influence on the assembly of avian communities at TIL than either limiting similarity or neutral processes. In our analyses, both FRic and FEve showed lower values than expected based on random community assembly, a result consistent with habitat filtering. SES of FRic decreased linearly with area, also suggesting that there is stronger filtering in progress on the larger islands. Furthermore, FEve showed a negative relationship with island area (Fig. 3d). This may indicate that both species presences and abundances are distributed less evenly in functional space on large islands than on small ones (Villéger, Mason & Mouillot 2008; Mouchet *et al.* 2010). Such patterns can also be taken to suggest that the habitat filtering is a stronger influence within communities because of the significant negative relationship between species richness and FEve, and the relative low FEve values on large islands.

Secondly, we found that FRic increased with island area, which was similar to species richness pattern on islands (MacArthur & Wilson 1967). Such a pattern could be the result of the sampling effect, which occurs when large convex hull volume are more likely to contain more species (Cornwell, Schwilk & Ackerly 2006). Also, FEve decreased with island area, indicating that abundance is less evenly distributed on large islands, which was not predicted by island biogeography theory, but may be more important for ecosystem stability (Wittebolle *et al.* 2009). Our finding that functional evenness was promoted by an increased degree of fragmentation (decreased island area in this study, Trzcinski, Fahrig & Merriam 1999), is similar to the finding of Pakeman (2011), who found that functional evenness was promoted by increased levels of disturbance and an earlier timing of disturbance. This pattern might result from a positive relationship between disturbances and evenness (Cardinale, Nelson & Palmer 2000). Furthermore, existing evidence shows that when a community is highly uneven, or when there is extreme dominance by one or few species, ecosystem functioning is less resistant to environmental fluctuations (Balvanera, Kremen & Martinez-Ramos 2005; Wittebolle *et al.* 2009). Thus, in our analyses, large islands had low species and functional evenness indicating that these islands had relatively low functional stability and resilience.

Furthermore, FDiv showed no clear patterns across all islands at TIL. Specifically, we found no significant difference between observed FDiv and expected FDiv, and no significant associations between FDiv and island area or isolation. These findings are consistent with patterns found in plant communities (Pakeman 2011). Since there was no strong evidence of general patterns in this data, more studies are needed to test the performance and behaviour of FDiv in other real world systems with different taxa.

Conclusions

Given the attention paid to habitat fragmentation and its effects (Groom & Schumaker 1993; Davies & Margules 1998), it is surprising that impacts of habitat fragmentation on bird functional diversity have not been explored in more depth. Traditionally, effects of habitat fragmentation on species richness have usually been studied using the theory of island biogeography (MacArthur & Wilson

1967; Brown 1971; Diamond & May 1981; Harris 1984); however, the simplest explanation for the decline in species richness with decreasing island size is generally not sufficient to guide conservation management (Lomolino 2000). Thus, the effects of fragmentation on functional diversity should be more explicitly considered in reserve design. In our analyses, we found habitat filtering was a dominant process structuring bird communities. This pattern is consistent with bird communities in other disturbed systems, e.g. agricultural or urbanization system (Petchey *et al.* 2007; Flynn *et al.* 2009). Taken together, we believe that habitat filtering may be dominant in bird communities in fragmented systems even there was little empirical evidence relevant to this topic (bird functional diversity in fragmented systems). Furthermore, large island communities which exhibit relatively low FEve values may have low functional stability and therefore may deserve extra attention and/or protection.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1 Characteristics of the study islands in the Thousand Island Lake, China.

Table S2 Explanation percentage of the PCoA axes.

Table S3 Island × species abundance matrix for birds on 41 islands in the Thousand Island Lake, China.

Table S4 Species × trait data matrix for birds on 41 islands in the Thousand Island Lake, China.