Global patterns and predictors of bird species responses to forest fragmentation: Implications for ecosystem function and conservation

Tom P. Bregman [a,*], Cagan H. Sekercioglu [b], Joseph A. Tobias [a]

[a] Edward Grey Institute, Department of Zoology, University of Oxford, Oxford OX1 3PS, UK
[b] Department of Biology, University of Utah, 257 South 1400 East, Salt Lake City, UT 84112–0840, USA

ABSTRACT

The fragmentation of forests is a dominant human impact worldwide with major implications for the conservation and management of ecosystems. Although many studies have assessed the effects of fragmentation on biodiversity at local scales, our understanding of the ecological implications for different functional groups of organisms remains limited, particularly at global scales. Here, we use linear mixed models to explore patterns of occurrence and ecological function of 2844 bird species at 293 localities spanning five continents. We show that sensitivity to fragmentation varies according to functional group and body mass, with the prevalence of insectivores and large frugivores declining in relation to fragment size, particularly under 100 ha. However, the most severe effects were restricted to the tropics, whereas fragmentation had no significant impact on the basic ecological structure of temperate bird communities. We conclude that land-use change in tropical systems is likely to disrupt biotic processes, including seed dispersal and the control of insect herbivores. Our findings highlight the importance of latitude in mediating the impacts of habitat loss, and offer general guidelines for the minimum size of fragments required to prevent the collapse of key ecosystem processes in sensitive regions.

© 2013 Elsevier Ltd. All rights reserved.

1. Introduction

Widespread declines in terrestrial biodiversity have largely been driven by the loss and fragmentation of natural habitats, particularly in forested regions (Turner, 1996; Fahrig, 2003). According to a range of forecasts, these processes are likely to accelerate as the growing demand for food and energy places increasing pressure on land over the next century (Sala et al., 2000; Godfray et al., 2010; McLaughlin, 2011). Faced with the challenge of preventing biodiversity loss and maintaining ecosystem function in increasingly fragmented landscapes, it is therefore vital to understand how the effects of fragmentation vary across groups of organisms with different ecological roles (Lewis et al., 2013).

Most studies of fragmentation have focused on the extent to which the loss of species richness in forest isolates can be explained by factors such as species-area relationships (Lees and Peres, 2006; Banks-Leite et al., 2012), edge effects (Murcia, 1995), isolation (Beier et al., 2002), habitat complexity (Norton et al., 2000), and characteristics of the habitat matrix (Gascon et al., 1999; Martensen et al., 2012). However, extinction of species from forest fragments is potentially non-random in relation to

functional traits, and thus patterns of species richness tell us little about the structure and function of assemblages surviving in human-modified landscapes (Robinson et al., 1992). In particular, several studies have highlighted the importance of dietary niche (Sekercioglu et al., 2002; Yong et al., 2011) and trophic level (Van Nouhuys, 2005; Murphy and Romanuk, 2012) as factors influencing sensitivity to fragmentation, suggesting that this form of land-use change may have predictable effects on trophic processes integral to ecosystem function.

Although the importance of understanding anthropogenic effects on the function of forest ecosystems has been highlighted by numerous studies (e.g. Van Nouhuys, 2005; Sekercioglu, 2012; Newbold et al., 2013), few generalities have emerged about the impacts of fragmentation on different functional groups of organisms (Watson et al., 2005). For example, a decline in insectivores is thought to increase insect herbivory in degraded or fragmented forests (Skoczylas et al., 2007; Van Bael et al., 2008), whereas the opposite pattern of increased insectivory and reduced herbivory has been reported in others (Gonzalez-Gomez et al., 2006; De la Vega et al., 2012). Similarly, seed dispersal appears to decline in some fragments (Watson et al., 2003) yet increase in others (Donoso et al., 2004). One possible explanation for these inconsistent results is that spatial variation in life history traits such as dispersal (Salisbury et al., 2012) or the strength of biotic interactions (Schemske et al., 2009) drive

* Corresponding author. Tel.: +44 1865 271 173.
E-mail address: tom.bregman@zoo.ox.ac.uk (T.P. Bregman).

latitudinal gradients in the impacts of forest fragmentation (Stratford and Robinson, 2005). However, most studies have focused at the local level (e.g. Sisk et al., 1997; Norton et al., 2000; Lens et al., 2002; Lindenmayer et al., 2002), whereas analyses at regional scales have been restricted to the temperate zone or the tropics (e.g. Gray et al., 2007; Newbold et al., 2013). Thus, it is difficult to determine how much information local results provide about general patterns, and we still lack a global synthesis of functional responses to fragmentation, particularly in vertebrates (Vandewalle et al., 2010).

Here, we address this issue using a linear mixed modelling approach to test the impact of forest fragmentation on bird communities in 293 human-created forest fragments worldwide. For each of these fragments, we recorded its size and latitude. We then compiled functional trait data (see Appendix A: Supplementary methods and results) for all 2844 species reported as present in at least one study site. We focused on habitat preferences, feeding guild, dispersal and body mass as these traits are known to predict sensitivity to land-use change, and are also relevant to the functioning of ecosystems (Sekercioglu, 2006b; Newbold et al., 2013).

Birds offer a useful system for understanding broad-scale fragmentation processes for three reasons. First, they are popular study species and readily surveyed, and thus detailed species lists have been compiled for numerous forest fragments using standard techniques. Second, they are the best-known class of organisms and provide the most comprehensive dataset of inter-specific variation in functional traits (Vandewalle et al., 2010). Third, they perform critical roles in forest systems, partly through top-down processes, such as predation on insect herbivores (Van Bael et al., 2003), and also through the ubiquitous plant–animal mutualisms underpinning pollination and seed dispersal (Sethi and Howe, 2009; Anderson et al., 2011). Because of their key role in forest dynamics linked to plant dispersal and recruitment, birds are sometimes described as 'mobile-links', connecting various parts of the landscape and mediating the resilience of forests to anthropogenic change (Lundberg and Moberg, 2003; Sekercioglu, 2006b).

Previous studies have shown that avian species richness declines with forest fragment size, approximately in accordance with classic species-area relationships (e.g. Lees and Peres, 2006; Banks-Leite et al., 2012). Much less is known about how these relationships vary across latitude, and between functional groups. For example, dispersal limitation in tropical forest birds (Moore et al., 2008) is thought to be a major factor explaining their sensitivity to rainforest fragmentation (Lens et al., 2002; Barlow et al., 2006; Tobias et al., 2013), whereas many temperate zone species with similar functional roles are migratory or highly dispersive (Salisbury et al., 2012) and thus potentially better able to withstand habitat fragmentation (Stratford and Robinson, 2005).

Our goal in this study is to assess the effects of fragment size on different functional components of the bird community, particularly in relation to insect predation and seed dispersal. The methods are designed to shed light on broad-scale patterns relevant to the structure and functioning of human-modified ecosystems, rather than species conservation. Thus, we focus not only on species richness but the relative prevalence of different foraging guilds in the community. In addition, we use body mass to assess within-guild patterns of resilience as the impacts of anthropogenic change may vary across different size classes of organisms, even within functional groups (Crooks, 2002). Our approach allows us to test (1) whether sensitivity to fragmentation varies between the tropics versus the temperate zone and (2) whether there are differences in the size of fragment required to maintain key ecosystem processes in both regions.

2. Materials and methods

2.1. Literature review

Using Web of Science and Google Scholar, we compiled all relevant research articles published between 1962 and June 2012 that contained the following key words: (bird* OR avian) AND (habitat fragmentation* OR forest fragmentation* OR habitat degradation* OR land-use change* OR habitat loss) AND (community structure* OR species list* OR community assembly* OR community list* OR community). We also conducted an extensive search of grey literature available in the Alexander Library, Department of Zoology, University of Oxford, one of the world's premier collections of ornithological literature. Citations in all articles and reports were examined for relevant information.

Articles were checked for comprehensive species inventories from fragmented or continuous forests worldwide. We restricted our search by applying the following criteria. (1) Broad-leaved or coniferous forest: we excluded very dry woodlands as these tended to involve scrub or stunted thorn forest, supporting communities with a different balance of ecological functions, and therefore likely to obscure general patterns relevant to forests. (2) Mature closed-canopy forest: we excluded fragments dominated by secondary forest, or forest that had recently been logged or burnt, so that the effects of fragmentation were not confounded with other processes. (3) Natural fragments: we excluded data from any natural forest fragments such as forest patches in natural grasslands or montane 'sky-islands'. (4) Consistent isolation: given the importance of habitat isolation to metacommunity dynamics under fragmentation, we removed all non-isolated fragments from analyses, e.g. fragments connected to other blocks of forest by corridors or recent secondary regrowth (Ferraz et al., 2007). (5) Total community: we excluded all studies focusing on a subset of the avian community, e.g. only passerines or forest-dependent species. This is because we were interested in quantifying impacts of fragmentation on forest-dependent species relative to the entire community, and these impacts cannot be explored with incomplete datasets.

For each community, we compiled data on total species composition, habitat patch size and latitude, excluding sites for which any of these three details were unavailable. The final dataset (Supplementary data 1) contained a total of 293 avian communities from 56 study regions (Fig. 1). Sites were classified as either 'tropical' (<23.6° N/S; $N = 115$) or 'temperate' (>23.6° N/S; $N = 178$).

2.2. Dealing with extinction filters and extinction debt

Examining responses to fragmentation at global scales is challenging because of the contrasting histories of land-use across latitudes, with the time elapsed since deforestation events being generally long in the temperate zone, and more recent in the tropics. These differences are potentially important as, in theory, fragmented bird communities only fully collapse after an extended time delay (Brooks et al., 1999; Ferraz et al., 2003), such that young fragments may still have to pay an 'extinction debt' (Tilman et al., 1994). Moreover, unlike recently cleared regions (e.g. much of the tropics), fragments in historically cleared regions (e.g. Europe, North America) may have already passed through an 'extinction filter' during which sensitive species were removed (Balmford, 1996). To address these problems, we sampled continuous forest habitat, defined as habitat patches >100,000 ha in extent, in both the tropical ($N = 20$) and temperate zones ($N = 9$). Although extensive primeval forest in the Nearctic region has lost at least two bird species through habitat loss and hunting (Fuller, 2002), these extinctions affect different functional groups and are too rare to explain general patterns. Similarly, few recorded extinctions have
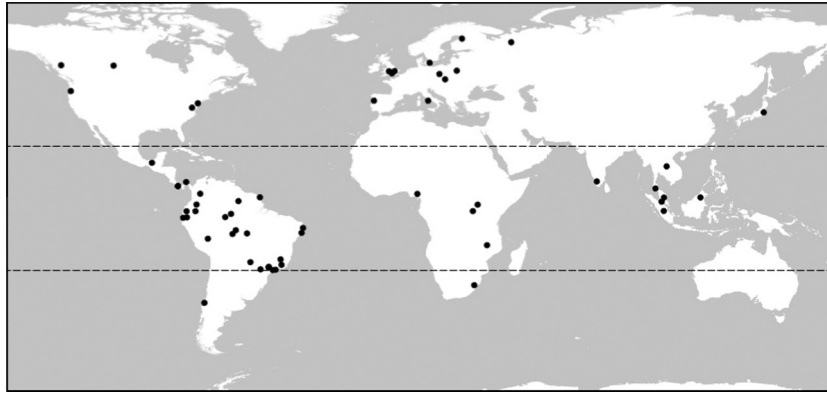
Fig. 1. Distribution of 56 regions generating data for the 293 fragments included in this study. Dashed lines indicate the tropics of Capricorn and Cancer. Details of locations and data sources are provided in Supplementary data 1.

occurred in extensive lowland tropical forests, where the component of extinct species is likely to be negligible in relation to overall species richness. Thus, we assumed that the avifauna of continuous forest in all regions was intact, providing a baseline against which fragment communities can be compared.

2.3. Functional traits

We classified species according to four key ecological or life-history traits: habitat preference, migratory behaviour, feeding guild and body mass (Appendix A: Supplementary methods and results; Supplementary data 2). Species were assigned to one of two habitat categories according to whether they are primarily detected in (i) forest or (ii) non-forested habitats. We defined forest as any type of evergreen or deciduous woodland lacking gaps between tree canopies. Bird species associated with these habitat types are henceforth termed 'forest dependent'. To focus on functional groups typically associated with ecosystem dynamics in forest patches, rather than those restricted to the non-forest matrix, we used forest-dependent species as the focal group in analyses.

Species were assigned to one of two categories of migratory behaviour according to whether they were (i) long-distance migrants or (ii) either sedentary or short-distance migrants. The latter category includes elevational migrants and species undertaking regional movements, seasonally or otherwise. Species were then allocated to one of eight categories of feeding guild—insectivores, frugivores, granivores, nectarivores, carnivores, herbivores, scavengers and omnivores—based on datasets of Sekercioglu et al. (2004), with updates from Belmaker et al. (2011). Dietary categories represent the primary diet, with species categorised as omnivores if no primary diet was apparent. Finally, data on body mass were collated for each species, primarily from Dunning (2008). For a complete list of species with functional trait definitions, data and sources, see Supplementary data 2.

We focused on breeding species as these form the predominant functional component of avian communities, either present year-round, or at least during the leaf-growing, flowering and fruiting season of plants. In contrast, non-breeding migrants often appear briefly or sporadically. In excluding non-breeding species from communities, long-distance migrants were thus retained in temperate communities (where they breed) but removed from tropical communities (where they occur as non-breeding visitors). To test whether our results held when focusing exclusively on resident species, we re-ran analyses with all migrants removed from both temperate and tropical zones (Appendix A: Supplementary methods and results).

Although the contribution of biodiversity to ecosystem functioning depends on a range of complex factors including network structure and trophic complementarity among species (Poisot et al., 2013), the efficiency and stability of ecosystem function is expected to increase with species richness, partly as a natural consequence of limiting similarity among species (Naeem and Li, 1997; Naeem et al., 2012). We thus used raw species richness as a basic measure of the contribution of each guild to ecosystem function. However, this measure may give a misleading impression of fragmentation effects across latitudes because overall species richness varies so dramatically with distance from the equator, in line with the latitudinal diversity gradient. Thus, we also calculated the proportional contribution of each guild to the total species richness within each community and used it as a response variable in our models.

2.4. Analytical approach

We used Generalised Linear Mixed Models (GLMM) to test for differences in sensitivity using the MCMCglmm package (Hadfield, 2010) in R (R Development Core Team, 2013). The advantage of a mixed modelling framework is that it allows us to consider the effects of multiple factors, including latitude, fragment size and dietary guild, as well as their interactions. In addition, we were able to explore non-linearity in effects by including fragment size as a quadratic term in models of both species richness and proportion; this tests for changes in the rates at which species were lost, or at which communities shifted in structure, across the fragmentation gradient. Finally, as some studies reported data for multiple communities clustered geographically, we accounted for potential spatial autocorrelation and pseudoreplication by including 'study' (i.e. publication) as a random effect in all models. Fragment size was log-transformed before analysis to ensure model residuals were normally distributed. We ran six sets of analyses.

Analysis 1. To test the effect of fragment size on raw species richness in key functional groups, we focused on three major guilds (frugivores, granivores and insectivores) of forest-dependent species. The response variable was the richness of species in each of these guilds, with fragment size as the explanatory variable. We ran models for temperate and tropical communities separately as sample sizes for some guilds were too low in the temperate zone.

Analysis 2. To examine the effect of fragment size on the prevalence of forest-dependent species within communities, we ran a multi-predictor model with species grouped by habitat preference (forest and non-forest). The response variable was the proportion of forest-dependent species in the community, with fragment size and latitudinal zone included as covariates.

Analysis 3. To explore latitudinal variation in the functional composition of fragment communities, we subdivided each community into eight feeding guilds. We then calculated the

proportion of each guild in each community, based on species richness, and then averaged across communities for four different datasets: (i) all species in all communities; (ii) forest-dependent species in all communities; (iii) all species in intact communities; and (iv) forest-dependent species in intact communities. To compare the proportions of key guilds between latitudinal zones in datasets (i–ii), we used arcsine transformation to normalise data then conducted t-tests. Sample sizes in datasets (iii–iv) were too small for this approach, so we used Mann–Whitney U-tests.

Analysis 4. To test the effect of fragment size on different functional groups, we subdivided forest-dependent species into categories of feeding guild and then calculated the proportion of each guild present in each community. We then re-ran the model described in analysis 2. Rather than including latitudinal zone as a covariate, models for temperate and tropical communities were run separately to improve model convergence and facilitate interpretation.

Analysis 5. To test for variation in the effects of fragmentation across scales, we classified sites into three broad size categories: 0–100 ha, 100–1000 ha and >1000 ha. We then compared the proportion of each feeding guild occurring in each category of fragment size (see analysis 3). This approach is complementary to our analyses treating fragment size as a continuous variable, allowing us to compare fragments against extensive continuous forests where size has not been estimated.

Analysis 6. As proportional data calculated from patterns of species richness may conceal other more subtle impacts of fragmentation on functional traits, we modelled the effect of fragment size on body mass, to test the prediction that fragmentation has a disproportionate effect on large species. We used the same analytical framework as analysis 3 to test whether the average body mass of each guild of forest-dependent species differed among categories of fragment size.

Because of latitudinal gradients in the history of fragmentation, communities were not evenly sampled across spatial scales (Supplementary data 1). Specifically, in the temperate zone all forests classified as >1000 ha were essentially continuous (>100,000 ha), whereas the same category in the tropical zone contained a mixture of very large fragments (1000–100,000 ha; N = 8) and continuous forests (>100,000 ha; N = 20). However, there was no significant difference in the proportion and average body mass of guilds in these two samples of tropical forests (Appendix A: Supplementary methods and results), suggesting that they are similar from a functional perspective. Thus, we pooled large fragments and continuous forests in analyses 4 and 5. Model results are presented using P and DIC (Deviance Information Criterion) statistics. Minimum adequate models can increase the rate at which Type I errors occur so we report the full model DIC and examine the relative importance of predictors by calculating the change in the DIC when each predictor is removed (for further details on these statistics see the extended methods section in the appendices) (Hadfield, 2010).

3. Results

3.1. Broad-scale patterns

Species richness was far higher in tropical than temperate fragments (Table 1), in line with the latitudinal diversity gradient, and the effects of fragmentation also differed across latitudinal zones. In the tropics, species richness declined with fragment size in all three major guilds (Analysis 1; Fig. 2; Table A1). The decline was steepest in insectivores, both in relation to frugivores and granivores, and also in comparison with temperate zone fragments (Fig. 2). Moreover, in both tropical and temperate fragments, we found that the rate of insectivore loss was non-linear across the

gradient of fragment size, with rates increasing in small fragments (Fig. 1 and Table A1). In contrast, the rate of decline in richness for frugivores and granivores was similar across the entire gradient of fragment size in the tropical zone, and this linearity also appeared to hold true outside the tropics, with the caveat that frugivores and granivores are relatively rare and therefore poorly sampled in the temperate zone.

These three guilds—insectivores, frugivores and granivores—together make up approximately 90% of species richness within fragment communities in both tropical and temperate zones (Fig. 3b). Insectivores predominate throughout, but the relative contributions of the major guilds differ significantly across latitudes. Specifically, the frugivore component was significantly larger in the tropics whereas the granivore component was much larger in the temperate zone (Analysis 3). There were also dramatic latitudinal differences among minor guilds, with some being dominant in the tropics (e.g. nectarivores) and others dominant in the temperate zone (e.g. herbivores). Although these general patterns take no account of fragment size, they were similar in intact forests (Fig. 3c). Thus, they are likely to reflect underlying gradients in guild structure caused by latitudinal differences in climate and resource availability (e.g. year-round availability of fruits and flowers in the tropics) (Belmaker et al., 2011; Kissling et al., 2012; Tobias et al., 2013). Modelling habitat preferences (Analysis 2) revealed that the proportion of forest-dependent species occurring in fragment communities was strongly predicted by habitat patch size, with smaller fragments containing a relatively low proportion of forest-dependent species (P = 0.002; Fig. 3a; Table A2). However, we detected no effect of latitudinal zone or the interaction between latitudinal zone and fragment size (Table A2), suggesting that the effect of fragment size on the proportion of forest-dependent species is similar in the temperate zone and the tropics.

3.2. Structure and function of fragmented bird communities

Given that latitude drives variation in the guild structure of communities, particularly in relation to smaller guilds, it is difficult to compare the effects of fragmentation across both latitudinal zones simultaneously. To overcome this problem, we ran models separately for each latitudinal zone, and for each of the three major feeding guilds (Analysis 4). The results revealed distinct latitudinal patterns of sensitivity to fragmentation in forest-dependent birds mediated by feeding guild (Fig. 3 and Table A3). In the tropics, decreasing fragment size was associated with a decrease in the insectivore component of avian communities, an increase in the granivore component, and no change in the frugivore component. As predicted by the increasing rates of insectivore loss in small fragments (Analysis 1), the decline in the proportion of insectivores was also non-linear, with an accelerating collapse of the insectivore component in small tropical fragments. In contrast, in the temperate zone, fragment size had no effect on the proportion of any of the three key functional groups, or changes in their proportions across the fragment size gradient.

To provide further insight into latitudinal effects, we compared guild-specific responses to fragmentation among small (<100 ha), mid-size (100–1000 ha) and large fragments (>1000 ha). We found no change in the proportion of any guild when comparing between small and mid-size fragments, or between mid-size and large fragments, in either the tropics or the temperate zone. The only exception was that small fragments in the tropics contained a lower proportion of forest-dependent insectivores than did mid-size fragments (Table A4). Differences increased when comparing across widely contrasting fragment sizes in the tropics, with small fragments containing a lower proportion of insectivores and frugivores, and a higher proportion of granivores, than large fragments (Fig. 4 and Table A5). In contrast, we detected no difference in the

Table 1
Community sampling and structure. Data shown are means ± SE (proportion ± SE) of forest-dependent species belonging to different focal groups.

Latitudinal zone	Sample	Species richness	Forest species	Insectivores	Frugivores	Granivores	Migrants
Tropical	20/95	93.43 ± 6.67	62.67 ± 4.99 (0.64 ± 0.01)	54.26 ± 3.92 (0.57 ± 0.01)	17.53 ± 1.33 (0.19 ± 0.01)	5.29 ± 0.44 (0.06 ± 0.004)	8.29 ± 1.36 (0.05 ± 0.01)
Temperate	9/169	22.40 ± 1.14	13.24 ± 0.52 (0.62 ± 0.01)	13.88 ± 0.66 (0.63 ± 0.01)	0.70 ± 0.09 (0.03 ± 0.003)	3.84 ± 0.16 (0.19 ± 0.01)	9.30 ± 0.01 (0.38 ± 0.01)

Sample = number of continuous forests/number of fragments; species richness = overall mean richness of fragments included in the analyses ± SE (proportional data cannot be calculated for overall species richness).
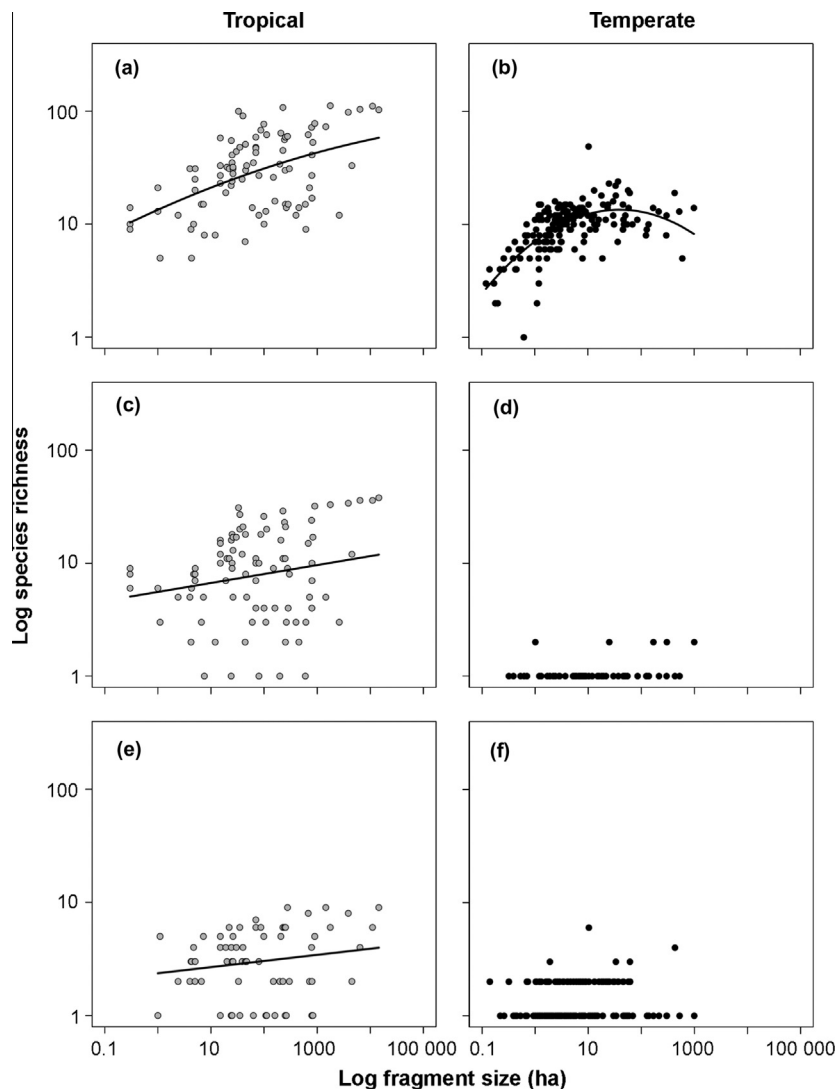

Fig. 2. The effect of fragment size on species richness of forest-dependent insectivores (a and b), frugivores (c and d) and granivores (e and f) in avian communities occurring in tropical ($N = 95$) and temperate ($N = 169$) forest fragments. Species richness data are shown on a logarithmic scale; trend lines are plotted for significant relationships calculated using regression analysis in a mixed effects framework.

proportion of insectivores, frugivores and granivores in small and large fragments in the temperate zone.

When we ran similar tests of latitudinal differences in fragmentation effects mediated by body mass (Analysis 6), we found similar results. There was no change in the average mass of species when comparing between small and mid-size fragments, or between mid-size and large fragments, in either the tropics or the temperate zone (Table A6). Mass differences between the smallest (<100 ha) and largest habitat patch categories were more pronounced, and again highly variable among feeding guilds (Fig. 5

and Table A7). The average mass of tropical frugivores and temperate insectivores was significantly lower in small forest patches (Table A7). However, the average mass of granivore, temperate frugivore and tropical insectivore communities did not change significantly in the smallest forest fragments (Fig. 6).

3.3. Sensitivity analysis

To test whether the difference in sensitivity between tropical and temperate guilds is driven by the removal of non-breeding
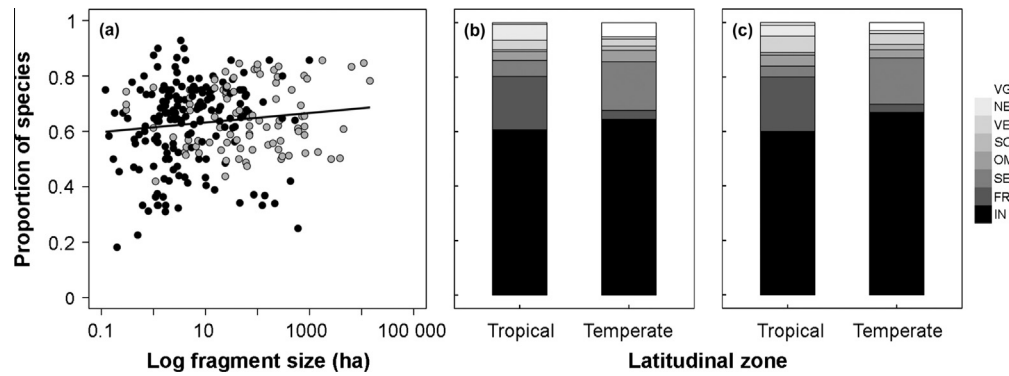
Fig. 3. The effect of forest patch size and latitude on the structure and function of fragmented bird communities. (a) shows how the proportion of forest species occurring in each community varies with patch size in tropical (N = 95) and temperate (N = 169) fragments; the regression line is given for the pooled dataset. (b and c) show the ecological structure of tropical and temperate communities; (b) shows the proportion of forest-dependent species belonging to each guild in forest fragments. (c) Shows the proportion of all species (both forest dependent and independent) belonging to each of the guilds in continuous forests. Foraging guilds: insectivores (IN), frugivores (FR), granivores (GR), omnivores (OM), scavengers (SC), carnivores (CA), nectarivores (NE), herbivores (VG). We focused on insectivores, frugivores and granivores in our analyses because of their global dominance.
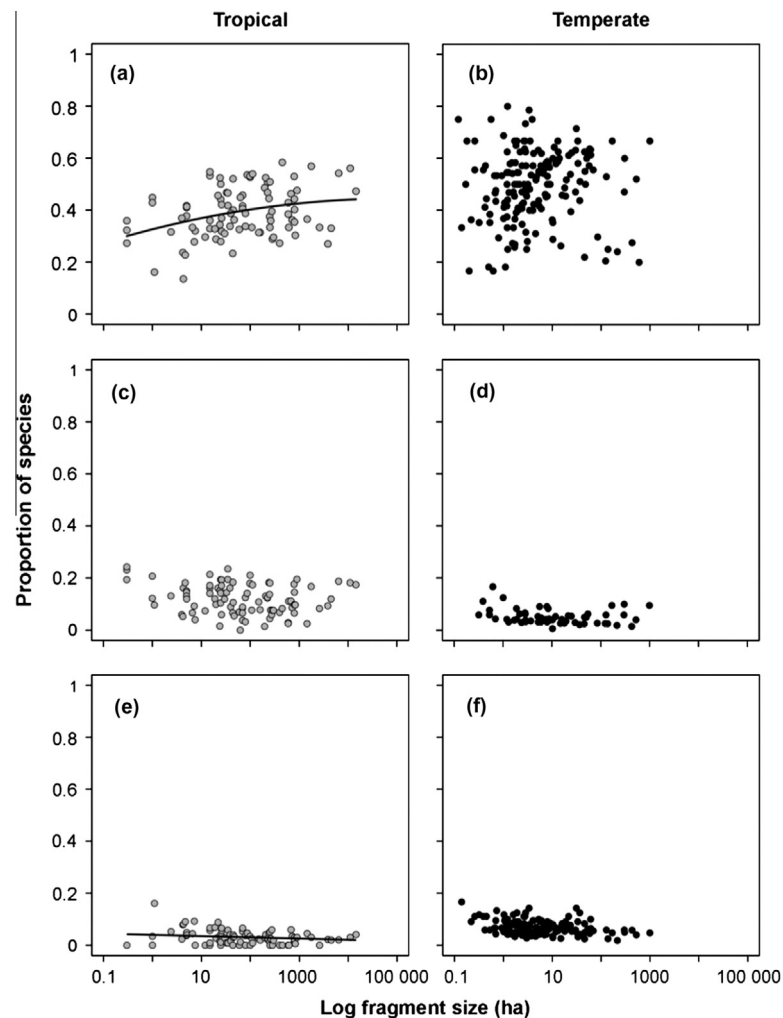

Fig. 4. The effect of fragment size on the prevalence of forest-dependent insectivores (a and b), frugivores (c and d) and granivores (e and f) in avian communities occurring in tropical (N = 95) and temperate (N = 169) forest fragments. Data shown are the proportion of the total community of each fragment made up of each functional group. Trend lines are plotted for significant relationships calculated using regression analysis in a mixed effects framework.

migrants in tropical communities we re-ran analyses for temperate guilds after removing migratory species (Tables A10–A13). Fragment size remained a significant predictor of the proportion

of forest-dependent species and the trend still did not vary between communities in the tropical and temperate zones (Table A10). None of the guilds changed in their relative proportion
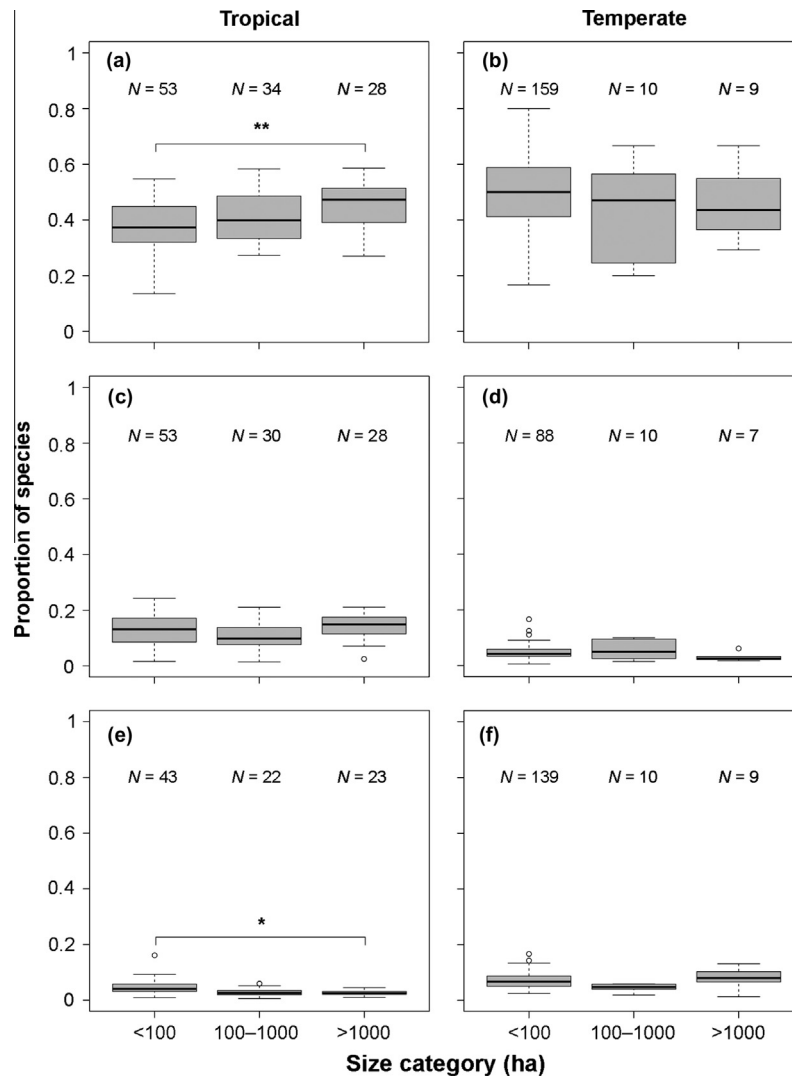
Fig. 5. The effect of habitat patch size on the prevalence of different feeding guilds in avian communities inhabiting tropical ($N = 115$) and temperate ($N = 178$) sites, calculated for forest-dependent insectivores (a and b), frugivores (c and d) and granivores (e and f). Data are calculated as a proportion of total species richness in the community. Whiskers shown on Tukey boxplots include points within $1.5\times$ interquartile range. Sample sizes vary as foraging guilds were absent from some communities. The largest category (>1000 ha) contained some ($N = 28$) large fragments in the tropical zone, but in the temperate zone it only contained continuous forest (>100,000 ha; $N = 9$). Statistics are from ANOVA in a mixed effects framework (analysis 5); $^{*}P < 0.05$, $^{**}P < 0.01$.

4. Discussion

We have shown that raw species richness and the proportion of forest species declines with fragment size, in accordance with numerous previous studies (e.g. Kattan et al., 1994; Beier et al., 2002; Fahrig, 2003; Lees and Peres, 2006). However, the effects of fragmentation varied both within and between feeding guilds, with implications for the functioning of fragmented ecosystems. Specifically, the proportion of insectivorous birds within communities declined in relation to fragment size, whereas the proportion of frugivores and granivores did not. Similarly, the loss of insectivores (species richness and proportion) accelerated when fragments became very small, in line with classical theory on

as fragment size declined (Table A11 and A12). Furthermore, when we assessed how these effects are mediated by body size, we found that large insectivores were still sensitive to a decline in fragment size with the greatest change in small relative to large fragments (Table A13).

species-area relationships (Rosenzweig, 1995), but rates of species loss in frugivores and granivores remained constant across the gradient of fragment size. In parallel, fragmentation was associated with reduced body mass in frugivorous birds, but not in insectivores or granivores. The sensitivity of insectivores and large frugivores to forest fragmentation and disturbance has been reported from studies focused at the local scale (Sekercioglu et al., 2002; Barlow et al., 2006; Terborgh et al., 2008; Yong et al., 2011). Our results confirm that these impacts hold in forest fragments across the tropics, and yet are far less severe in the temperate zone. We conclude that the effect of fragmentation on the structure of forest bird communities is strongly mediated by latitude, and that general rules about ecosystem responses to land-use change can only be developed in the context of understanding this spatial variation.

Fragmentation has a clear impact on the species richness of temperate forest birds. This is in part because fragmentation reduces the breeding success of migrant species (Robinson et al., 1995), some of which appear unable to survive in smaller fragments (Wilcove et al., 1986). However, our results suggest that local extinctions from land-use change in temperate systems are
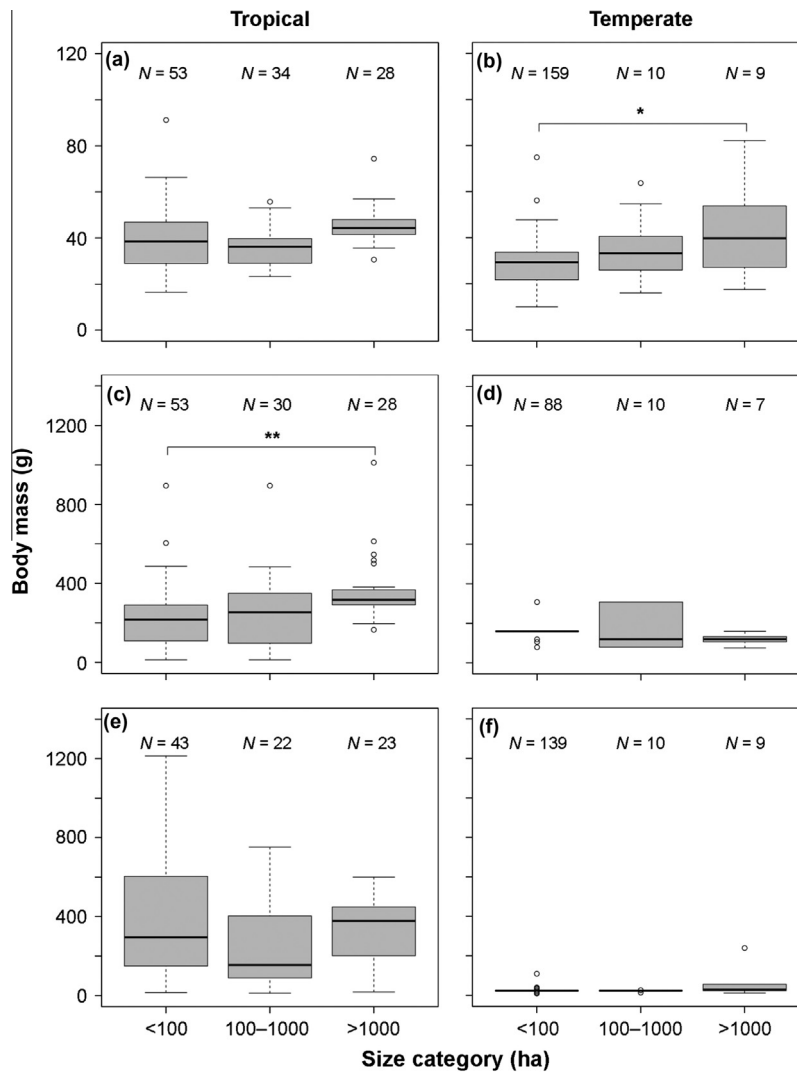
Fig. 6. The effect of habitat patch size on the body mass of forest bird species in temperate (*N* = 178) and tropical (*N* = 115) communities, calculated for forest-dependent insectivores (a and b), frugivores (c and d) and granivores (e and f). Whiskers shown on Tukey boxplots include points within 1.5× interquartile range. Sample sizes vary as foraging guilds were absent from some communities. The largest category (>1000 ha) contained some (*N* = 28) large fragments in the tropical zone, but in the temperate zone it only contained continuous forest (>100,000 ha; *N* = 9). Statistics are from ANOVA in a mixed effects framework (analysis 6); *$P < 0.05$, **$P < 0.01$.

a product of random species loss rather than guild-specific sensitivity to fragmentation. This makes sense for two reasons. First, the difference between forest and non-forest vegetation, and between the avian communities occupying these habitats, is often less dramatic in the temperate zone than the tropics (Salisbury et al., 2012). Thus, forest specialists may be replaced by non-forest species with similar ecological roles in smaller fragments. Second, the seasonally fluctuating climate of the temperate zone, as well as the climatic upheaval associated with recent ice ages, have selected for traits associated with broad climatic tolerance and dispersal (Dynesius and Jansson, 2000). These traits increase the likelihood that temperate forest birds can accommodate higher levels of land-use change, and disperse across non-forest habitats. Our results support the view that temperate birds are therefore better equipped to survive in fragmented landscapes, and to recolonize fragments after local extinction (Stratford and Robinson, 2005; Tobias et al., 2013).

In contrast, tropical birds may be more sensitive than temperate birds to habitat fragmentation for several reasons. First, the patchy distribution of many tropical species (Meyer et al., 2008) means they are more likely to be absent from a particular fragment

because they did not originally occur within its boundaries (Ferraz et al., 2007; Laurance et al., 2011). Second, factors such as low population density, large home ranges and slow reproductive output are also more prevalent in tropical species, increasing the likelihood of population extinction in small habitat patches, over a range of timeframes (Tobias et al., 2013). Third, adaptation to relatively stable climates and microhabitats may lead to narrower physiological tolerance in tropical birds (Janzen, 1967). This is important because tropical forest fragments are often warmer, brighter and less humid than intact forests (Laurance et al., 2011), and thus potentially unsuitable for forest specialists (Stratford and Robinson, 2005).

One of the most commonly cited predictors of sensitivity to fragmentation is dispersal limitation, as this reduces the potential for gap-crossing and re-colonisation after extinction events (Fahrig and Merriam, 1994; Thomas, 2000; Lees and Peres, 2009), thus disrupting key metacommunity processes (Hanski, 1999). A growing number of empirical and comparative studies suggest that dispersal limitation is more extreme in tropical forest species (Moore et al., 2008; Salisbury et al., 2012). One obvious reason is that they tend to be highly sedentary due to climatic stability; another is

that they are relatively specialised in terms of dietary (Belmaker et al., 2011) or microhabitat niches (Salisbury et al., 2012). Many tropical birds are therefore poorly adapted for sustained flight, and unlikely to disperse across a non-forest matrix where suitable resources may be absent. Thus, our finding that sensitivity to fragmentation peaks in the tropics may be explained by an array of mechanisms ranging from the purely spatial to intrinsic processes mediated by demography or ecological adaptation.

Similar mechanisms may also explain why sensitivity to fragmentation varies across functional groups. The least dispersive rainforest bird species are typically insectivores, many of which are year-round territorial (Tobias et al., 2011), and struggle to cross even narrow gaps such as roads (Laurance et al., 2004) or small stretches of water (Moore et al., 2008). This problem is compounded in some insectivores which also require large home ranges because of behavioural specialisation, e.g. army ant followers (Willis and Oniki, 1978). In contrast, forest frugivores are generally non-territorial and highly dispersive because they are adapted to tracking temporally and spatially patchy food resources across the landscape (see Salisbury et al., 2012; Tobias et al., 2013). Meanwhile, granivores do not tend to hold year-round territories, prefer more open habitats, and are relatively insensitive to fragmentation, often thriving in small habitat patches, agricultural areas, and the intervening landscape between forest fragments (Donoso et al., 2004; Lees and Peres, 2008; Sekercioglu, 2012). Thus, it makes sense that the proportion of insectivores declines in smaller tropical fragments, while the proportion of frugivores remains constant and granivores increase. This pattern is also consistent with recent analyses identifying fragmentation as a key threat to insectivorous birds (Sekercioglu et al., 2002; Barlow et al., 2006; Yong et al., 2011), but a far less serious threat to frugivores than selective logging or hunting (Markl et al., 2012).

Although the proportion of frugivores in avian communities was not affected by fragmentation, we detected a strongly significant reduction in the size of frugivores in tropical fragments. This finding corroborates numerous studies suggesting that larger species are more extinction prone (e.g. Kattan et al., 1994; Bennett and Owens, 1997). It may arise because habitat patches are too small to accommodate large home ranges, or because fragmentation is associated with higher human populations and improved access, leading to greater pressure from hunting, which disproportionately targets larger species. The synergistic effects of land-use change and hunting tends to exterminate populations of larger species from tropical fragments (Peres, 2001), and may apply particularly to tropical frugivores simply because many of them are large and sought after as game species (e.g. guans, toucans, hornbills, etc.). The disappearance of large-bodied frugivores highlights the importance of considering functional traits, including body size, as analyses focusing on raw or proportional species richness detected no impacts of fragmentation on tropical frugivores.

4.1. Implications for ecosystem processes

We have shown that the effects of fragmentation on functional groups of birds are most extreme in the tropics, largely coinciding with rainforest regions where deforestation and fragmentation reach their peak (Achard et al., 2002). The implication of these effects on ecosystems is unclear, particularly as rare species make up a greater proportion of tropical communities, suggesting that functional redundancy may be elevated in comparison with temperate communities (Petchey et al., 2007). While this implies that many species lost from tropical forest fragments may play a relatively minor functional role, an opposing viewpoint is that increased specialisation to microhabitats and trophic niches leads to greater complementarity in tropical systems, regardless of species rarity (Rosenberg, 1997; Walker, 2006; Tobias et al., 2013). From this

perspective, the complex architecture of tropical food-webs makes them vulnerable to disruption by fragmentation.

Very few studies have investigated the functional implications of fragmentation, and those that do have tended to focus on life-history traits with uncertain implications (e.g. Barbaro and van Halder, 2009). In this study, we have focused on feeding guilds with direct links to the functioning of ecosystems. For example, insectivorous birds provide an important service through the regulation of phytophagous insects (Sekercioglu, 2006a,b). Previous work confirms that avian insectivores reduce herbivory on tropical forest trees, and that increasing herbivory by experimentally excluding insectivores leads to reductions in plant growth and rates of photosynthesis (Van Bael et al., 2003; Mooney et al., 2010). Moreover, high species richness and functional diversity of insectivores is associated with reduced leaf damage and improved agricultural yield in agroforestry systems (Philpott et al., 2009). The pervasive decline of forest-dependent insectivores with tropical fragment size fits a pattern reported previously (Sekercioglu et al., 2002; Barlow et al., 2006), and supports the view that the loss of specialised insect predators may have major long-term impacts on plant diversity and biogeochemical cycling in human-modified tropical forests (Tobias et al., 2013).

The loss of frugivores from tropical forests has been shown to reduce dispersal distances and recruitment of large-seeded tree species (Sekercioglu, 2006a; Terborgh et al., 2008; Sethi and Howe, 2009; Wotton and Kelly, 2011), many of which are important for maintaining the complex vegetation structure and dark understorey associated with rainforest. Although our results confirm that avian frugivores are relatively insensitive to forest fragmentation, in line with previous research (Willis, 1979; Markl et al., 2012), the pervasive decline we detect in large-bodied frugivores in tropical fragments has potentially critical implications for long-term ecosystem function. Notably, such frugivores are associated with the dispersal of larger seeds (Galetti et al., 2013), and thus the decline in frugivore size after fragmentation may lead to the decline or extinction of large-seeded trees, with implications for the composition and functioning of fragmented tree communities (Sekercioglu, 2006a). Moreover, the loss of key agents of seed dispersal will theoretically reduce the potential for forest restoration when fragments are reduced in size.

4.2. Limitations of our approach

Although we deal with the possibility of 'extinction filters' in temperate birds by comparing fragments with continuous forests, our analyses ignore a range of factors influencing the outcome of land-use change. For example, we do not consider the timing and duration of habitat isolation, or the history of land-use cover underlying current habitat configurations, factors that can influence present-day patterns of biodiversity occurring in fragments (Brooks et al., 1999; Ferraz et al., 2003; Martensen et al., 2012; Ewers et al., 2013). It is therefore possible that we have underestimated extinction in younger or larger fragments, both of which are more frequent in the tropics, and perhaps yet to repay their 'extinction debt' (Tilman et al., 1994). However, we have drawn our extensive dataset from both old and recent fragmentation events at all latitudes (Supplementary data 1), suggesting that fragment history does not explain our results. Moreover, we do not focus on measures of species richness per se, but rather the extent to which fragmentation affects the proportion of different feeding guilds in a community, and we are not aware that any link has been identified as yet between fragment history and the ecological structure of communities (e.g. Krauss et al., 2010). Exploring this relationship may be a fruitful target for future studies.

A related issue is that, by focusing exclusively on species occurrence data, we may overlook changes in abundance, which rank

among the most stochastic and unpredictable responses to fragmentation (MacNally, 2007). Shifts in abundance can be influential given that species occurring in small fragments may survive in such low numbers as to be 'functionally extinct' (Galetti et al., 2013; Tobias et al., 2013). The species richness of a guild may thus be artificially inflated by species that are rare or transient, contributing little to ecosystem function in small fragments. Clearly, it is important to move beyond the simplistic framework of species occurrence and patch size to explore the implications of an array of relevant factors, such as species abundance, fragment age and isolation (Laurance et al., 2011), and habitat heterogeneity within fragments (Andrén, 1994). However, these questions are currently difficult to tackle in a global framework as the datasets required are not currently available. There is a critical need for long-term, standardised monitoring studies in forest fragments, particularly through large-scale experimental studies (e.g. Ewers et al., 2011; Laurance et al., 2011).

4.3. Implications for land-use management and conservation strategies

The loss of species from forest fragments is a longstanding issue of central importance for biodiversity conservation and management (Fahrig and Merriam, 1994), including reserve design (Burkey, 1989). This is particularly true in tropical areas with rapidly growing economies such as Southeast Asia and the Brazilian Amazon, where land-use change is fragmenting natural habitat rapidly (Lepers et al., 2005). By pooling data from across a large number of fragments, we have shown that fragmentation has relatively little impact on the functional structure of bird communities in the temperate zone, where efforts to conserve ecosystem function can potentially succeed even in patchy habitats. In contrast, our results indicate that fragmentation changes the balance of functional traits, and removes key functional components, from tropical communities. These findings highlight the effect of land-use change on trophic processes (Valladares et al., 2006) and add weight to calls for maximising reserve size and connectivity in the tropics (Laurance, 2005; Laurance et al., 2011). In particular, the decline of dispersal-limited species emphasises the importance of implementing strategies to promote dispersal and connectivity across the non-forest matrix. Management interventions enforcing the retention of vegetation corridors and encouraging mosaics of secondary regrowth in deforested landscapes would help to minimise the deleterious impacts of fragmentation, and allow species to recolonize fragments after local extinctions (Gascon et al., 1999; Gillies et al., 2011; Laurance et al., 2011).

We are cautious in making inferences about the size of habitat patches required to conserve biodiversity and ecosystem function because so much depends on local conditions, and in any case our analyses are based on fragment size categories that are too broad to be directly informative. However, our results suggest that tropical forest patches should be maintained above 1000 ha where possible, and that the functioning of smaller habitat patches in agroforestry systems will be improved if they can be maintained above 100 ha because they otherwise suffer a disproportionate loss of species controlling insect herbivory. We note that these estimates relate to the maintenance of basic ecosystem function; much larger patches of tropical forest may be required to conserve populations of particular threatened or sensitive species (Laurance, 2005). Clearly, conservation efforts in fragmented tropical environments should also aim to reduce hunting pressure and maintain sufficient patch size for large frugivores. Finally, our analyses suggest that policy interventions focused on land-use and biodiversity management are always worthwhile given that even tiny forest fragments retain a relatively full set of ecosystem functions, offering hope that fragmented tropical landscapes can be successfully managed and restored.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2013.11.024.

References

Achard, F., Eva, H.D., Stibig, H.J., Mayaux, P., Gallego, J., Richards, T., Malingreau, J.P., 2002. Determination of deforestation rates of the world's humid tropical forests. Science 297, 999–1002.

Anderson, S.H., Kelly, D., Ladley, J.J., Molloy, S., Terry, J., 2011. Cascading effects of bird functional extinction reduce pollination and plant density. Science 331, 1068–1071.

Andrén, H., 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71, 355–366.

Balmford, A., 1996. Extinction filters and current resilience: the significance of past selection pressures for conservation biology. Trends Ecol. Evol. 11, 193–196.

Banks-Leite, C., Ewers, R.M., Metzger, J.P., 2012. Unravelling the drivers of community dissimilarity and species extinction in fragmented landscapes. Ecology 93, 2560–2569.

Barbaro, L., van Halder, I., 2009. Linking bird, carabid beetle and butterfly life-history traits to habitat fragmentation in mosaic landscapes. Ecography 32, 321–333.

Barlow, J., Peres, C.A., Henriques, L.M.P., Stouffer, P.C., Wunderle, J.M., 2006. The responses of understorey birds to forest fragmentation, logging and wildfires: an Amazonian synthesis. Biol. Conserv. 128, 182–192.

Beier, P., Drielen, M.V., Kankam, B.O., 2002. Avifaunal collapse in West African forest fragments. Conserv. Biol. 16, 1097–1111.

Belmaker, J., Şekercioğlu, C.H., Jetz, W., 2011. Global patterns of specialization and coexistence in bird assemblages. J. Biogeogr. 39, 193–203.

Bennett, P.M., Owens, I.P.F., 1997. Variation in extinction risk among birds: chance or evolutionary predisposition? Proc. Roy. Soc. Lond. Ser. B: Biol. Sci. 264, 401–408.

Brooks, T.M., Pimm, S.L., Oyugi, J.O., 1999. Time lag between deforestation and bird extinction in tropical forest fragments. Conserv. Biol. 13, 1140–1150.

Burkey, T.V., 1989. Extinction in nature reserves: the effect of fragmentation and the importance of migration between forest fragments. Oikos 55, 75–81.

Crooks, K.R., 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. Conserv. Biol. 16, 488–502.

De la Vega, X., Grez, A.A., Simonetti, J.A., 2012. Is top-down control by predators driving insect abundance and herbivory rates in fragmented forests? Austral Ecol. 37, 836–844.

Donoso, D.S., Grez, A.A., Simonetti, J.A., 2004. Effects of forest fragmentation on the granivory of differently sized seeds. Biol. Conserv. 115, 63–70.

Dunning, J.B., 2008. CRC Handbook of Avian Body Masses, second ed. CRC Press, Boca Raton, Florida.

Dynesius, M., Jansson, R., 2000. Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. Proc. Nat. Acad. Sci. 97, 9115–9120.

Ewers, R.M., Didham, R.K., Fahrig, L., Ferraz, G., Hector, A., Holt, R.D., Kapos, V., Reynolds, G., Sinun, W., Snaddon, J.L., Turner, E.C., 2011. A large-scale forest fragmentation experiment: the Stability of altered forest ecosystems project. Philos. Trans. Roy. Soc. Lond. B 366, 3292–3302.

Ewers, R.M., Didham, R.K., Pearse, W.D., Lefebvre, V., Rosa, I.M.D., Carreiras, J.M.B., Lucas, R.M., Reuman, D.C., 2013. Using landscape history to predict biodiversity patterns in fragmented landscapes. Ecol. Lett. 16, 1121–1233.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Syst. 34, 487–515.

Fahrig, L., Merriam, G., 1994. Conservation of fragmented populations. Conserv. Biol. 8, 50–59.

Ferraz, G., Russell, G.J., Stouffer, P.C., Bierregaard, R.O., Pimm, S.L., Lovejoy, T.E., 2003. Rates of species loss from Amazonian forest fragments. Proc. Nat. Acad. Sci. USA 100, 14069–14073.

Ferraz, G., Nichols, J.D., Hines, J.E., Stouffer, P.C., Bierregaard, R.O., Lovejoy, T.E., 2007. A large scale deforestation experiment: effects of patch size and isolation on Amazon birds. Science 315, 238–241.

Fuller, E., 2002. Extinct birds. In: del Hoyo, J., Elliott, A., Sargatal, J. (Eds.), The Handbook of the Birds of the World, Jacamars to Woodpeckers, vol. 7. Lynx Edicions, Barcelona, pp. 11–68.

Galetti, M., Guevara, R., Côrtes, M.C., Fadini, R., Von Matter, S., Leite, A.B., Labecca, F., Ribeiro, T., Carvalho, C.S., Collevatti, R.G., Pires, M.M., Guimarães, P.R., Brancalion, P.H., Ribeiro, M.C., Jordano, P., 2013. Functional extinction of birds drives rapid evolutionary changes in seed size. Science 340, 1086–1090.

Gascon, C., Lovejoy, T.E., Bierregaard, R.O., Malcolm, J.R., Stouffer, P.C., Vasconcelos, H.L., Laurance, W.F., Zimmerman, B., Tocher, M., Borges, S., 1999. Matrix habitat and species persistence in tropical forest remnants. Biol. Conserv. 91, 223–229.

Gillies, C.S., Beyer, H.L., St Clair, C.C., 2011. Fine-scale movement decisions of tropical forest birds in a fragmented landscape. Ecol. Appl. 21, 944–954.

Godfray, H.C., Beddington, J.R., Crute, I.R., Haddad, L., Lawrence, D., Muir, J.F., Pretty, J., Robinson, S.K., Thomas, S.M., Toulmin, C., 2010. Food security: the challenge of feeding 9 billion people. Science 327, 812–818.

Gonzalez-Gomez, P.L., Estades, C.F., Simonetti, J.A., 2006. Strengthened insectivory in a temperate fragmented forest. Oecologia 148, 137–143.

Gray, M.A., Baldauf, S.L., Mayhew, P.J., Hill, J.K., 2007. The response of avian feeding guilds to tropical forest disturbance. Conserv. Biol. 21, 133–141.

Hadfield, J.D., 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. J. Stat. Softw. 33, 1–22.

Hanski, I., 1999. Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. Oikos 87, 209–219.

Janzen, D.H., 1967. Why mountain passes are higher in the tropics. Am. Nat. 101, 233–249.

Kattan, G.H., Alvarez-López, H., Giraldo, M., 1994. Forest fragmentation and bird extinctions: San Antonio eighty years later. Conserv. Biol. 8, 138–146.

Kissling, W.D., Sekercioglu, C.H., Jetz, W., 2012. Bird dietary guild richness across latitudes, environments and biogeographic regions. Glob. Ecol. Biogeogr. 3, 328–340.

Krauss, J., Bommarco, R., Guardiola, M., Heikkinen, R.K., Helm, A., Kuussaari, M., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Pöyry, J., Raatikainen, K.M., Sang, A., Stefanescu, C., Teder, T., Zobel, M., Steffan-Dewenter, I., 2010. Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. Ecol. Lett. 13, 597–605.

Laurance, W.F., 2005. When bigger is better: the need for Amazonian megareserves. Trends Ecol. Evol. 20, 645–648.

Laurance, S.G.W., Stouffer, P.C., Laurance, W.F., 2004. Effects of road clearings on movement patterns of understory rainforest birds in central Amazonia. Conserv. Biol. 18, 1099–1109.

Laurance, W.F., Camargo, J.L.C., Luizao, R.C.C., Laurance, S.G., Pimm, S.L., Bruna, E.M., Stouffer, P.C., Williamson, G.B., Benitez-Malvido, J., Vasconcelos, H.L., van Houtan, K.S., Zartman, C.E., Boyle, S.A., Didham, R.K., Andrade, A., Lovejoy, T.E., 2011. The fate of Amazonian forest fragments: a 32-year investigation. Biol. Conserv. 144, 56–67.

Lees, A.C., Peres, C.A., 2006. Rapid avifaunal collapse along the Amazonian deforestation frontier. Biol. Conserv. 133, 198–211.

Lees, A.C., Peres, C.A., 2008. Avian life-history determinants of local extinction risk in a hyper-fragmented neotropical forest landscape. Anim. Conserv. 11, 128–137.

Lees, A.C., Peres, C.A., 2009. Gap-crossing movements predict species occupancy in Amazonian forest fragments. Oikos 118, 280–290.

Lens, L., Dongen, S.V., Norris, K., Githiru, M., Matthysen, E., 2002. Avian persistence in fragmented rainforest. Science 298, 1236–1238.

Lepers, E., Lambin, E.F., Janetos, A.C., DeFries, R., Achard, F., Ramankutty, N., Scholes, R.J., 2005. A synthesis of information on rapid land-cover change for the period 1981–2000. Bioscience 55, 115–124.

Lewis, O.T., Ewers, R.M., Lowman, M.D., Malhi, Y., 2013. Conservation of tropical forests: maintaining ecological integrity and resilience. In: Macdonald, D.W., Willis, K.J. (Eds.), Key Topics in Conservation Biology. John Wiley & Sons, pp. 222–235.

Lindenmayer, D.B., Cunningham, R.B., Donnelly, C.F., Nix, H., Lindenmayer, B.D., 2002. Effects of forest fragmentation on bird assemblages in a novel landscape context. Ecol. Monogr. 72, 1–18.

Lundberg, J., Moberg, F., 2003. Mobile link organisms and ecosystem functioning: implications for ecosystem resilience and management. Ecosystems 6, 87–98.

MacNally, R., 2007. Use of the abundance spectrum and relative-abundance distributions to analyze assemblage change in massively altered landscapes. Am. Nat. 170, 319–330.

Markl, J.S., Schleuning, M., Forget, P.M., Jordano, P., Lambert, J.E., Traveset, A., Wright, S.J., Böhning-Gaese, K., 2012. Meta-analysis of the effects of human disturbance on seed dispersal by animals. Conserv. Biol. 26, 1072–1081.

Martensen, A.C., Ribeiro, M.C., Banks-Leite, C., Prado, P.I., Metzger, J.P., 2012. Associations of forest cover, fragment area, and connectivity with Neotropical understory bird species richness and abundance. Conserv. Biol. 26, 1100–1111.

McLaughlin, D.W., 2011. Land, food, and biodiversity. Conserv. Biol. 25, 1117–1120.

Meyer, C.F.J., Fründ, J., Lizano, W.P., Kalko, E.K.V., 2008. Ecological correlates of vulnerability to fragmentation in Neotropical bats. J. Appl. Ecol. 45, 381–391.

Mooney, K.A., Gruner, D.S., Barber, N.A., van Bael, S.A., Philpott, S.M., Greenberg, R., 2010. Interactions among predators and the cascading effects of vertebrate insectivores on arthropod communities and plants. Proc. Nat. Acad. Sci. USA 107, 7335–7340.

Moore, R.P., Robinson, W.D., Lovette, I.J., Robinson, T.R., 2008. Experimental evidence for extreme dispersal limitation in tropical forest birds. Ecol. Lett. 11, 960–968.

Murcia, C., 1995. Edge effects in fragmented forests: implications for conservation. Trends Ecol. Evol. 10, 58–62.

Murphy, G.E., Romanuk, T.N., 2012. A meta-analysis of community response predictability to anthropogenic disturbances. Am. Nat. 180, 316–327.

Naeem, S., Li, S., 1997. Biodiversity enhances ecosystem reliability. Nature 390, 507–509.

Naeem, S., Duffy, J.E., Zavaleta, E., 2012. The functions of biological diversity in an age of extinction. Science 336, 1401–1406.

Newbold, T., Scharlemann, J.P.W., Butchart, S.H.M., Sekercioglu, C.H., Alkemade, R., Booth, H., Purves, D.W., 2013. Ecological traits affect the response of tropical forest bird species to land-use intensity. Proc. Roy. Soc. B: Biol. Sci. 280.

Norton, M.R., Hannon, S.J., Schmiegelow, F.K.A., 2000. Fragments are not islands: patch versus landscape perspectives on songbird presence and abundance in a harvested boreal forest. Ecography 23, 209–223.

Peres, C.A., 2001. Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates. Conserv. Biol. 15, 1490–1505.

Petchey, O.L., Evans, K.L., Fishburn, I.S., Gaston, K.J., 2007. Low functional diversity and no redundancy in British avian assemblages. J. Anim. Ecol. 76, 977–985.

Philpott, S.M., Soong, O., Lowenstein, J.H., Pulido, A.L., Lopez, D.T., Flynn, D.F.B., DeClerk, F., 2009. Functional richness and ecosystem services: bird predation on arthropods in tropical agroecosystems. Ecol. Appl. 19, 1858–1867.

Poisot, T., Mouquet, N., Gravel, D., 2013. Trophic complementarity drives the biodiversity–ecosystem functioning relationship in food webs. Ecol. Lett.

R Development Core Team, 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Robinson, G.R., Holt, R.D., Gaines, M.S., Hamburg, S.P., Johnson, M.L., Fitch, H.S., Martinko, E.A., 1992. Diverse and contrasting effects of habitat fragmentation. Science 257, 524–526.

Robinson, S.K., Thompson, F.R., Donovan, T.M., Whitehead, D.R., Faaborg, J., 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267, 1987–1990.

Rosenberg, K.V., 1997. Ecology of dead-leaf foraging specialists and their contribution to Amazonian bird diversity. Ornithological Monogr. 48, 673–700.

Rosenzweig, M.L., 1995. Species Diversity in Space and Time. Cambridge University Press, Cambridge.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., 2000. Global biodiversity scenarios for the year 2100. Science 287, 1770–1774.

Salisbury, C.L., Seddon, N., Cooney, C.R., Tobias, J.A., 2012. The latitudinal gradient in dispersal constraints: ecological specialisation drives recent diversification in tropical birds. Ecol. Lett. 15, 847–855.

Schemske, D.W., Mittelbach, G.G., Cornell, H.V., Sobel, J.M., Roy, K., 2009. Is there a latitudinal gradient in the importance of biotic interactions? Ann. Rev. Ecol. Evol. Syst. 40, 245–269.

Sekercioglu, C.H., 2006a. Ecological significance of bird populations. In: del Hoyo, J., Elliott, A., Christie, D.A. (Eds.), Handbook of the Birds of the World, vol. 11. Lynx Edicions, Barcelona, pp. 15–51.

Sekercioglu, C.H., 2006b. Increasing awareness of avian ecological function. Trends Ecol. Evol. 21, 464–471.

Sekercioglu, C.H., 2012. Bird functional diversity and ecosystem services in tropical forests, agroforests and agricultural areas. J. Ornithol. 153, 153–161.

Sekercioglu, C.H., Ehrlich, P.R., Daily, G.C., Aygen, D., Goehring, D., Sandí, R.F., 2002. Disappearance of insectivorous birds from tropical forest fragments. Proc. Nat. Acad. Sci. 99, 263–267.

Sekercioglu, C.H., Daily, G.C., Ehrlich, P.R., 2004. Ecosystem consequences of bird declines. Proc. Nat. Acad. Sci. 101, 18042–18047.

Sethi, P., Howe, H.F., 2009. Recruitment of hornbill-dispersed trees in hunted and logged forests of the Indian Eastern Himalaya. Conserv. Biol. 23, 710–718.

Sisk, T., Haddad, N.M., Ehrlich, P.R., 1997. Bird assemblages in patchy woodlands: modeling the effects of edge and matrix habitats. Ecol. Appl. 7, 1170–1180.

Skoczylas, D.R., Muth, N.Z., Niesenbaum, R.A., 2007. Contribution of insectivorous avifauna to top down control of Lindera benzoin herbivores at forest edge and interior habitats. Acta Oecologica 32, 337–442.

Stratford, J.A., Robinson, W.D., 2005. Gulliver travels to the fragmented tropics: geographic variation in mechanisms of avian extinction. Front Ecol. Environ. 3, 91–98.

Terborgh, J., Nunez-Iturri, G., Pitman, N.C.A., Cornejo Valverde, F.H., Alvarez, P., Swamy, V., Pringle, E.G., Paine, C.E.T., 2008. Tree recruitment in an empty forest. Ecology 89, 1757–1768.

Thomas, C.D., 2000. Dispersal and extinction in fragmented landscapes. Proc. Roy. Soc. Lond. Ser. B: Biol. Sci. 267, 139–145.

Tilman, D., May, R.M., Lehman, C.L., Nowak, M.A., 1994. Habitat destruction and the extinction debt. Nature 371, 65–66.

Tobias, J.A., Gamarra-Toledo, V., Garcia-Olaechea, D., Pulgarin, P.C., Seddon, N., 2011. Year-round resource defence and the evolution of male and female song in suboscine birds: social armaments are mutual ornaments. J. Evol. Biol. 24, 2118–2138.

Tobias, J.A., Sekercioglu, C.H., Vargas, F.H., 2013. Bird conservation in tropical ecosystems: challenges and opportunities. In: MacDonald, D., Willis, K. (Eds.), Key Topics in Conservation Biology 2. John Wiley & Sons, London, pp. 258–276.

Turner, I.M., 1996. Species loss in fragments of tropical rain forest: a review of the evidence. J. Appl. Ecol. 33, 200–209.

Valladares, G., Salva, A., Cagnolo, L., 2006. Habitat fragmentation effects on trophic processes of insect-plant food webs. Conserv. Biol. 20, 212–217.

Van Bael, S.A., Brawn, J.D., Robinson, S.K., 2003. Birds defend trees from herbivores in a Neotropical forest canopy. Proc. Nat. Acad. Sci. USA 100, 8304–8307.

Van Bael, S.A., Philpott, S.M., Greenberg, R., Bichier, P., Barber, N.A., Mooney, K.A., Gruner, D.S., 2008. Birds as predators in tropical agroforestry systems. Ecology 89, 928–934.

Van Nouhyus, S., 2005. Effects of habitat fragmentation at different trophic levels in insect communities. Ann. Zool. Fenn. 42, 433–447.

Vandewalle, M., Bello, F., Berg, M.P., Bolger, T., Dolédec, S., Dubs, F., Feld, C.K., Harrington, R., Harrison, P.A., Lavorel, S., Silva, P.M., Moretti, M., Niemela, J., Santos, P., Sattler, T., Sousa, J.P., Sykes, M., Vanbergen, A.J., Woodcock, B.A., 2010. Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. Biodivers. Conserv. 19, 2921–2947.

Walker, J.S., 2006. Resource use and rarity among frugivorous birds in a tropical rain forest on Sulawesi. Biol. Conserv. 130, 60–69.

Watson, J.E.M., Watson, A.W.T., Paull, D., Freudenberger, D., 2003. Woodland fragmentation is causing the decline of species and functional groups of birds in southeastern Australia. Pacific Conserv. Biol. 8, 261–270.

Watson, J.E.M., Whittaker, R.J., Freudenberger, D., 2005. Bird community responses to habitat fragmentation: how consistent are they across landscapes? J. Biogeogr. 32, 1353–1370.

Wilcove, D.S., McClellan, C.H., Dobson, A.P., 1986. Habitat fragmentation in the temperate zone. In: Soule, M.E. (Ed.), Conservation Biology: the Science of Scarcity and Diversity. Sinauer Associates, Sunderland, MA, pp. 237–256.

Willis, E.O., 1979. The composition of avian communities in remanescent woodlots in southern Brazil. Papeis Avulsos Zool. 33, 1–25.

Willis, E.O., Oniki, Y., 1978. Birds and army ants. Annu. Rev. Ecol. Syst. 9, 243–263.

Wotton, D.M., Kelly, D., 2011. Frugivore loss limits recruitment of large-seeded trees. Proc. Roy. Soc. B: Biol. Sci. 278, 3345–3354.

Yong, D.L., Qie, L., Sodhi, N.S., Koh, L.P., Peh, K.S.H., Lee, T.M., Lim, H.C., Lim, S.L.H., 2011. Do insectivorous bird communities decline on land-bridge forest islands in Peninsular Malaysia? J. Trop. Ecol. 27, 1–14.