'Islands' in an island: multiscale effects of forest fragmentation on lowland forest birds in Taiwan

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ABSTRACT

Intensive agricultural developments and increasing human population has caused severe lowland-forest loss and fragmentation in the western coastal plain in Taiwan over the past centuries. The goal of this study is to explore the multiscale impacts of forest fragmentation on species richness and community composition of lowland-forest birds in Taiwan. At a regional scale, Island Biogeography Theory was applied to examine area and isolation effects on species richness of lowland-forest birds using bird data derived from Breeding Bird Survey Taiwan in 2009 and 2010. I also investigate the differential responses of two functional groups (forest specialists and generalists) to area and isolation effects Furthermore, I examine the relative influences of environmental variables at regional, landscape and local scales on avian community indices and composition in northern Taiwan with a hierarchical multiscale approach. Finally, species vulnerable to forest fragmentation and the ecological traits associated with specie vulnerability to forest fragmentation were identified.

Only forest specialist species responded to the regional-scale area and isolation effects. The species richness of forest specialists increased with the size of forest islands, and the community similarity of forest specialist species declined with increasing the distance from the sources of immigrants. Structurally isolated forests may not function as real habitat patches from the view of forest generalists because of their flexibility in utilizing the non-forest matrix. After accounting for the influences of environmental variables at other spatial scales, the regional-scale isolation effect still played a key role in determining avian community composition based on the presence/absence data set. But local-scale forest condition also explained a considerable amount of variability in the presence/absence data set. The regional-scale isolation effect, however, didn't show significant influences on community composition based on the abundance data set. In contrast, the landscape-scale variables explained the largest amount of variability in the abundance data set at the entire community level. There were six bird species (*Parus varius, Dicrurus aeneus, Treron sieboldii, Pericrocotu solaris, Erporniszan tholeuca and Alcippe brunnea*) whose occurrence and abundance were both vulnerable to forest fragmentation. Habitat specialization was the ecological traits most strongly associated with their vulnerability.

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CHAPTER 1. INTRODUCTION

Habitat fragmentation occurs when a contiguous habitat is broken into small pieces, isolated from each other by a non-habitat matrix (Wilcove et al. 1998). There have been numerous studies examining the effects of habitat fragmentation on species richness patterns (Krauss et al. 2003, Watling and Donnelly 2006), population persistence (Lens et al. 2002, Korfanta et al. 2012) and reproductive success (Wilcove 1985, Stephens et al. 2004) across a variety of taxonomic groups over the past decades. Habitat fragmentation can either diminish suitable habitats for organisms through breaking contiguous habitats into smaller fragments (Andrén 1996), or impede the inter-patch movements of organisms because of an unfavorable matrix surrounding the habitat patch(Desrochers and Hannon 1997), resulting in high local extinction risk (Brown and Kodric-Brown 1977, Şekercioḡlu et al. 2002). The direction and strength of impacts of habitat fragmentation, however, depend on the spatial scales studied (Wiens 1989), matrix type (Gobeil and Villard 2002, Brotons et al. 2003) and the species of concern (Krauss et al. 2003, Devictor et al. 2008).

Habitat loss and fragmentation is well recognized as one of the primary threats for global biodiversity(Wilcove et al. 1998).The impacts of habitat fragmentation could possibly become worse under the scenario of climate change in the future (Mantyka-pringle et al. 2012), especially for insular ecosystems where species usually have small populations and limited geographic distribution range, and are vulnerable to human-altered environments. Therefore, understanding and predicting the responses of organisms to habitat fragmentation play a key role in successful habitat-based conservation management.

Taiwan is a tropical island located in the western Pacific Ocean. The Tropic of Cancer passes through the mid part of Taiwan. Therefore, Taiwan has subtropical and tropical climate types in the northern and southern parts respectively. Beyond the coastal plain and gently rolling hills on the west, the central and eastern montane landscapes occupy almost two-thirds of Taiwan. The rugged topography has resulted in diverse vegetation zones along the altitudinal gradient, from the tropical *Ficus-Machilus* forests in the lowlands to alpine vegetation at the high-elevation areas > 3,600m (Su 1992). Because of the combination of a complicated climate and diverse habitats, Taiwan harbors a variety of bird species. There are 601 bird species recorded in Taiwan (Ruan et al. 2012). Furthermore, the geographic isolation of Taiwan results in high avian endemism. Nearly 15% of the resident bird species in Taiwan are endemic (Liu et al. 2010).

Taiwan was primarily covered by pristine forests in the seventeenth century before the Chinese settlement (Keliher 2003). The combination of intensive agricultural developments and increasing human population has caused severe lowland-forest loss in the western coastal plain over the past centuries. Currently, more than 90% of the population inhabits the western coastal plain (Taiwan Directorate-General of Budget, Accounting and Statistics, http:\\dgbas.gov.tw). The majority of lowland forest was converted into orchard, tobacco or tea plantations, paddy fields, pastures or urbanized areas. Currently, forest habitat occupies only 20% of the lowland areas where elevation < 500m (Forestry Bureau 1995). The lowland forests remaining on hills or mountains are mostly secondary forests regenerated from abandoned agricultural lands or forestry plantations over the last decades. These lowland forests are severely fragmented, surrounded by agricultural lands and urbanized areas.

Several studies have investigated the impacts of forest loss or fragmentation on species richness (Lin 2010), community structure(Pei and Sun 1998, Cheng 2002), nest success (Chen 1995) and population genetics(Lin and Wang 2008) in Taiwan. At a regional scale, Pei and Sun (1998) and Cheng (2002) both documented that a lack of a source of immigrants due to large-scale isolation of forest habitat was a key determinant for lowland-forest avian communities in Taiwan. By studying the impacts of landscape and vegetation structure on species richness of birds in a fragmented forest landscape, Lin (2010) concluded that diversity of habitat patches, vertical foliage structure, and floristic composition were important factors for sustaining higher avian biodiversity in fragmented environments at a local scale. Lin and Wang (2008) who investigated the landscape genetics of Spiny Taiwan Niviventer (*Niviventerconinga*) in middle Taiwan demonstrated that the highly-developed road system and urbanized areas possibly decrease the gene flow between several local populations. Despite the evidence for negative effects of forest fragmentation on organisms, there is still little conservation protection against habitat degradation in lowland forests in Taiwan. The majority of protected areas including national parks, nature reserves, wildlife refuges and important wildlife areas are located on mid- and high-elevation areas in Taiwan. Only 15% of protected areas are in the lowlands < 1,000m elevation (Forestry Bureau 1995). Furthermore, there is no conservation network to link these lowland protected areas yet.

The lowland ecosystem of Taiwan is unique for many species. The lowlands are the biodiversity hotspots for reptiles (Ou 2007) in Taiwan because of their intolerance of cold temperature in higher elevation areas. In addition, the distribution of certain endemic bird species is limited in lowland forests; for example Formosan Magpie (*Urocissacaerulea*) primarily occurs in lowland forests < 1,000m elevation (Ko et al. 2012). Compared to other ecosystems in the higher elevation areas, the lowland biodiversity in Taiwan has been less protected and under high development pressure now. Furthermore, several endemic bird species inhabit in the lowlands of Taiwan are predicted to move upward to higher elevation areas under the scenario of climate change over the next decades(Ko 2010). The movement within a fragmented forest landscape for some species maybe impeded by unfavorable matrix surrounding the habitat patch (Desrochers and Hannon 1997). This may decrease the opportunity for lowland-forest birds to adapt to climate change in the future, impacting avian biodiversity in Taiwan.

Previous studies on forest fragmentation have identified critical environmental determinants at a given scale, and provided valuable information for specific landuse management. A single-scale study that doesn't account for the influences of other factors at coarser or finer spatial scales, however, may have limited application to practical conservation decision-making. For instance, although a regional-scale landscape connectivity was suggested from works by Pei and Sun (1998) and Cheng (2002) to sustain lowland-forest avian diversity, it is still debated because of possible confounding effects of local-scale factors (e.g. forest quality) which were not evaluated in these studies. In addition, it is still unclear which species groups or species are more vulnerable to forest fragmentation, the critical information for conservation priority decision-making when conservation resources are limited. Therefore, although the Taiwanese government has become more aware of the vulnerability of the lowland ecosystem in Taiwan, there is still no comprehensive nationwide conservation planning because of limited information.

The goal of this study is to explore the multiscale impacts of forest fragmentation on species richness and community structure of lowland-forest birds in Taiwan. The remainder of this dissertation is divided into four chapters. The second chapter reports on the effects of area and isolation on species richness of lowland-forest birds at a nationwide scale in Taiwan. Island Biogeography Theory (MacArthur and Wilson 1967) was applied to achieve this objective. In addition, I also investigated the differential responses of two functional groups to area and isolation effects. In the third chapter, I further examined the relative effects of multiscale environmental factors on avian community indices and composition in northern Taiwan by using a hierarchical multiscale approach. A variance partitioning technique (Cushman and McGarigal 2004) was employed to disentangle the relative importance of environmental factors at regional, landscape and local scales. The influences of type of response variable (presence/absence vs. abundance of birds) and species functional group (forest specialist and generalist) on the relative importance of environmental factors was also examined in this chapter. Following chapter 3, species vulnerable to forest fragmentation and ecological traits associated with species vulnerability to forest fragmentation were identified in the fourth chapter. Finally, conclusions were presented and conservation implications were made in the last chapter.

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CHAPTER 2. INFLUENCE OF HABITAT SPECIALIZATION ON MACROECOLOGICAL PATTERNS OF FOREST-DEPENDENT BIRDS IN FRAGMENTED LANDSCAPES

ABSTRACT

The response of species to area and isolation effects within fragmented landscapes is a function of ecological trait of the species concerned. I examined how habitat specialization of forest-dependent birds influences their responses to area and isolation effects within a fragmented forest landscape in Taiwan. Island biogeography theory (IBT) was applied to examine the responses of forest birds to the effects of area and isolation. I identified lowland forests remaining on hills or mountains in the western coastal plain as forest islands, isolated from each other and large continuous forests (potential sources of immigrants) by the surrounding agricultural lands and urbanized areas. Area and distance from the sources of immigrants of the forest islands were estimated using a Geographic Information System. Bird data were derived from the Breeding Bird Survey Taiwan and species were assigned as forest specialists and generalists by their forest dependency. The species-area relationship (SAR) and distance-decay in community similarity for these two species groups were evaluated, respectively.

I found a significantly positive SAR for forest specialists (P=0.014). The z-value, slope of the SAR, of forest specialists (0.421) was higher than forest generalists (0.004). Furthermore, only forest specialists showed significant distance-decay pattern in community similarity (r = -0.097, P=0.012); the similarity of community composition decreased with increasing distance from the sources of immigrants. The results indicated that the degree of habitat specialization of organisms influences their responses to habitat fragmentation. Forest specialists that highly rely on forest habitat and behaviorally resist crossing the non-forest matrix are more susceptible to forest fragmentation. Structurally, isolated forests may not function as real habitat patches from the view of forest generalists because of their flexibility in utilizing the non-forest matrix. I suggested incorporating trait-specific responses to the matrix content into future research to clarify the inconsistency of effects of habitat fragmentation.

Keywords: distance-decay, ecological trait, forest specialist, forest generalist, habitat specialization, species-area relationship (SAR)

INTRODUCTION

Habitat loss and fragmentation caused by anthropogenic activities is one of the primary threats to global biodiversity(Wilcove et al. 1998). Over the past decades, the island biogeography theory (IBT) (MacArthur and Wilson 1967), and later on, metapopulation theory (Hanski 1991)have been applied to examine the effects of area and isolation on distribution and persistence of species in fragmented landscapes. Habitat patches within human-induced fragmented landscapes are generally viewed as 'islands' which are surrounded by a non-habitat matrix considered hostile for organisms to disperse through or utilize. A growing number of studies in recent years, however, have documented that the definition of habitat patch and the degree of matrix hostility are not equivalent to all organisms (Sisk et al. 1997, Gascon et al. 1999, Krauss et al. 2003).

For species that can use the matrix for foraging or nesting, the boundary between a habitat patch and the matrix may become less obvious (Sisk et al. 1997), mediating the strength of area effect. In addition, unlike the ocean, an absolute barrier for most terrestrial organisms, the matrix is selectively permeable depending on the physical or behavioral attributes of organisms(Gobeil and Villard 2002). For instance, the functional connectivity of organisms (Kindlmann and Burel 2008) may still remain high for mobile species even in extremely structure-isolated landscapes(Andrén 1996). From the view of the species, the landscapes are still functionally continuous and the impacts of structural isolation may become ineffective. In general, species with lower dispersal ability (Hovestadt et al. 2005, Dexter 2010), narrower ecological niche (Brotons et al. 2003, Krauss et al. 2003) and lower reproduction (Ockinger et al. 2010) are more susceptible to the effects of area and isolation in fragmented landscapes.

Ecologists have become more aware that ignoring the influence of trait-specific responses on the effects of area and isolation could possibly result in inconsistent conclusions. The inconsistency may mask our understanding of the real impacts of habitat fragmentation on organisms as well as diminish conservation effectiveness. While there have been a number of studies that investigated the association between ecological traits of organisms and their responses to habitat fragmentation, the majority of the literature mainly focused on continental ecosystems in America (Sisk et al. 1997, Gascon et al. 1999, Şekercioḡlu et al. 2002), Europe (Brotons et al. 2003, Krauss et al. 2003) and Africa (Hovestadt et al. 2005). Few studies were conducted in Asia (but see Wang et al. (2009), Soga and Koike (2012)and Yu et al. (2012)), where habitat fragmentation has become an urgent conservation issue due to poor management practices and intensive developments driven by increasing population over the past decades (Li et al. 2010). Understanding how habitat specialization of organisms influences their responses to the effects of area and isolation may not only helps ecologists accumulate scientific knowledge, but also provide valuable information for habitat-based conservation management to improve the decline of global biodiversity, especially in Asia.

The aim of this study is to examine the influence of habitat specialization of forest-dependent birds on their responses to forest fragmentation in Taiwan, a montane island located in the western Pacific Ocean. The following specific question was addressed: does the differential habitat specialization between forest specialist and forest generalist birds influence their susceptibility to the effects of area and isolation in a fragmented forest landscape? Forest specialists are anticipated to be more susceptible to area and isolation effects than forest generalists.

METHODS

Study area

The rugged topography in Taiwan has resulted in diverse vegetation zones along an altitudinal gradient, from the tropical *Ficus-Machilus* forests at the lowlands to alpine vegetation at the high-elevation areas > 3,600m (Su 1992). The central and eastern montane landscapes occupy almost two-thirds of Taiwan. More than 90% of the human population inhabits the western coastal plain(Taiwan Directorate-General of Budget, Accounting and Statistics, http:\\dgbas.gov.tw). The western coastal plain was once covered by pristine forests in the seventeenth century (Keliher 2003); however, the combination of intensive agricultural developments and increasing population has resulted in severe lowland forest loss(Fig. 2.1). The lowland forests were converted to orchards, tobacco or tea plantations, paddy fields, pastures and villages. Currently, most of the lowland forests remaining on hills or mountains on the western coastal plain are secondary forests regenerated from abandoned agricultural lands or forestry plantations over the last century, surrounded by urban areas and agricultural lands.

Delineation of forest islands

Hills and mountains >50m in elevation on the western coastal plain were identified first using the Digital Terrain Model (DTM) of Taiwan. Then the land use layer derived from the third Forest Inventory of Taiwan (Forestry Bureau 1995) was used to delineate the remaining forests on these lowland hills and mountains as forest islands. I reassigned a total of seventy-four land use types to seven categories: primary forests, secondary forests, bamboos, grasslands, croplands/orchards, roads/buildings and others. The primary and secondary forests were then reclassified as ‘forest’ habitat and others as ‘non-forest’ habitat. The forest islands we identified are primarily composed of evergreen broadleaved forests at different successional stages. In total, I identified seven forest islands in this study (Fig. 2.1). The area of forest islands was calculated using ArcMap version 9.3. The areas range from 5.8 to 543.7 km^2 (Table 2.1).

Bird data

The bird data were derived from the Breeding Bird Survey Taiwan (BBS Taiwan) in 2009 and 2010. BBS Taiwan is a citizen-science project conducted to accumulate long-term and large-scale breeding bird data with a standardized protocol. Six to ten plots were set along a transect within each 1km x 1km sampling site. Point counts (Reynolds et al. 1980)were used to collect bird data at each plot. The bird surveys were conducted within 4 hours after sunrise under acceptable weather conditions(e.g., winds less than 20 km/h and no rain)(Hamel et al. 1996). Species, number and distance from observers of all bird species seen or heard within the first six minutes were recorded. Each plot was surveyed twice from March to May every year.

Only resident forest species were included for subsequent data analyses. Resident diurnal and nocturnal raptors were eliminated because of the limitation of point counts for detecting these species. Moreover, all bird species were assigned as forest specialists or forest generalists based on their forest dependency(Lin 2010). Generally, forest specialists more highly rely on forest habitats (mean occurrence in forest habitats = 88.48%) than forest generalists, while forest generalists can additionally use non-forest habitats (mean occurrence in non-forest habitats = 37.8%).

Area effect

The log-log form of the Arrhenius power model (Arrhenius 1921): $\log S = c + z^{*}\log A$, was applied to describe the species-area relationship (SAR), where S=species richness, A = forest island size, c and z are constants. Detection probabilities of species may rise with increasing sampling efforts, and observed species richness could be biased because of uneven sampling efforts in each forest island. To reduce this bias, a species accumulation curve (Colwell and Coddington 1994) was used to extrapolate the species richness for each forest island. I employed the program SPADE (Chao and Shen 2010) to perform the estimation based on the incidence (presence/absence) data. Species richness estimated by the model M(h) was chosen in this study. Model M(h) assumes that the detection probabilities are heterogeneous among species. Every visit of sampling plots is viewed as an independent sample.

A series of log-log form of the Arrhenius power models was developed for all forest bird species, forest specialists and forest generalists, respectively. Pearson correlation coefficients and p-values were used to evaluate statistical significance of the SARs. The z-values, the slopes of SARs, between forest specialists and generalists were compared. In addition, overlap in the 95% confidence intervals of z-values were also examined to assess whether there was a significant difference of the z-values between these two species groups.

Isolation effect

The environmental intolerance or higher predation risk of forest birds in the non-forest habitats (Desrochers and Hannon 1997, Stratford and Robinson 2005) may limit their movement between forest patches. The dispersal limitation could result in distance-decay in community similarity (Nekola and White 1999)within fragmented landscapes; that is, a decrease in the similarity of community composition with increasing distance from a source pool of immigrants.

Some studies have shown that the connectivity to the vast continuous lowland forests in the central montane area in Taiwan plays a critical role in shaping the community composition of forest-dependent birds in the lowland forests at a regional scale (Pei and Sun 1998, Cheng 2002). Therefore I assumed the vast lowland forests in the central part of Taiwan as the "forest mainland", a source of forest bird immigrants (Fig. 2.1). I defined the forest mainland as the lowland forests with area >500 ha and elevation lower than 1500m, where the vegetation is also dominant by evergreen broadleaved forests to reduce the vegetation variation.

In addition to the mainland-island dynamics, I also consider the possibility that the immigrants of individual forest islands may come from nearby forest islands in this study. I calculated the edge-to-edge distances of individual forest islands to the forest mainland and the nearest forest islands using ArcMap version 9.3. The Sørensen similarity index (Sørensen 1948) was used to quantify the pairwise similarities of avian community composition based on presence/absence data. There was a correlation between the area of forest islands and the distances from sources of immigrants (r =-0.64). To remove the confounding effect of area, I first regressed the similarity of avian community against the area of forest islands. Then the similarity-area residuals were plotted against the distance from the sources of immigrants to examine the distance-decay in community similarity.

The independent variables, area and distance from the sources of immigrants, were both standardized to reduce the influence of different magnitudes over which these two variables were measured (Watling and Donnelly 2006)(area: 5.37-362.01 km^2, distance: 0.99-33.16 km). If a similarity-distance relationship was detected, one-way analysis of covariance (ANCOVA) was applied to examine whether the distance-decay in community similarity depended on distance from different sources of immigrants (forest mainland or nearest forest island). All computation was performed in the R environment (R Development Core Team 2005). The ‘vegan’ package was used for the calculation of the Sørensen similarity index.

RESULTS

In total, 28,790 bird observations derived from 55 BBS Taiwan sampling sites (25 and 30 sampling sites for forest islands and forest mainland, respectively) were used in the analysis. Sampling effort was approximately proportional to the size of forest islands (Table 2.1). Based on the Clements et al. (2012) avian taxonomy system, 34 forest bird species were recorded, including 22 forest specialists and 12 forest generalists (Appendix A). The comparison of observed and estimated species richness showed that on average 90% (range from 71% to 100%, Table 2.1) of the species were detected in these forest islands. There was no correlation between the detection percentage and the size of forest islands ($r = -0.37$, $P = 0.41$).

The species-area relationship (SAR)

The species-area relationships were significant for all forest bird species and forest specialists, but not for forest generalists (Table 2.2). Species richness of forest specialists increased with increasing the size of forest islands (Fig. 2.2), while forest generalists were insensitive to forest area. The z-value for all forest bird species was 0.175, and was higher for forest specialists (0.421) than forest generalists (0.004). No overlap of 95 % confidence intervals of z-values between forest specialists and forest generalists indicated significant difference of the z-values between these two groups.

Isolation effect on community similarity

After removing the effect of area, only forest specialists showed a significant distance-decay in community similarity (*r*=-0.097, *P*=0.012, Table 2.3). The assemblage similarity of forest specialists significantly decreased with increasing distance from the sources of immigrants (Fig. 2.3). The one-way ANCOVA showed insignificance for distance type (distance from forest mainland or distance from the nearest forest island) and the interaction between distance and distance type (*P*=0.115 and 0.166 respectively, Table 2.4). That is, the slopes and intercepts of the similarity-distance regression lines on the level of distance type were not significantly different. Accordingly, the distance type has no effect on the similarity-distance relationship in this study.

DISCUSSION

I found that the degree of habitat specialization of species influences their responses to habitat fragmentation. Forest specialist species that highly rely on forest habitat and behaviorally resist crossing non-forest matrix are more susceptible to forest fragmentation. In contrast, structurally isolated forests may not function as real habitat patches from the view of forest generalists because of their flexibility in utilizing non-forest matrix.

The results of this study showed a positive species-area relationship for forest specialists, but not for forest generalists. A habitat patch suitable for a particular species is a function of not only patch size defined by landscape structure, but also species-specific response to the edge habitat or the surrounding matrix (Sisk et al. 1997, Gascon et al. 1999). The lower flexibility to use the non-forest matrix habitats by forest specialists may account for their sensitivity to the size of forest islands in this study. In comparison, a contrasting matrix surrounded the forest islands could partially provide resources for some forest generalists, such as Chinese Bamboo-Partridge (*Bambusicola thoracicus*)and Taiwan Barbet (*Megalaima nuchalis*), to survive or reproduce (Zhong 1992, Koh and Lu 2009). Under this scenario, there is likely a gradient of habitat quality from the edge of a habitat patch into the matrix for forest generalists, resulting in an insignificant SAR. The trait-specific response to area effect in this study was consistent with the findings of Brotons(2003) and Magura et al. (2008)in birds, and Krauss *et al.*(2003) in butterflies that the area effect was more influential to habitat specialists than generalists in fragmented landscapes.

In addition, the z-value of forest specialists was significantly higher than forest generalists. In a given landscape, the comparison of the z-value has been widely used to examine the relative colonization success of species from different taxonomic or functional groups among habitat patches (Rosenzweig 1995, Hovestadt and Poethke 2005, Dexter 2010). Most forest specialists in this study rarely occur in non-forest habitats. Certain species, such as Taiwan Partridge (*Arborophila crudigularis*), is particularly behaviorally reluctant to cross open-field habitats (Sun 2001). The reduction of genetic or demographic contributions of immigrants resulting from dispersal limitation may influence the population persistence within habitat patches (Brown and Kodric-Brown 1977, Lens et al. 2002), leading to the steep slope (higher z-value) of SAR.

Furthermore, the significant distance-decay pattern in community similarity of forest specialists indicated that these species primarily get their recruits from other forests. The limitation of movements within the non-forest matrix is likely the plausible underlying mechanism of the spatial pattern observed. I found that the type of immigrant source had no effect on the similarity-distance relationship for forest specialists. The result should be conservatively interpreted because of the small sample size (N=7), however, it may be possible that some nearby forest islands which harbor higher species richness could also function as a 'small mainland' (Harrison 1991), providing new colonists for other forest islands. For instance, Yang-Ming Shan (YMS), the large nearest forest island of Lin-Co Tableland (LCT), is closer to LCT (1.85 km) than the forest mainland (2.69 km). It is likely that the local populations of forest specialists in LCT receive immigrants of forest birds from YMS because of the shorter distance.

By contrast, most forest generalist species in this study were nearly found in nearly all forest islands, showing no significant spatial similarity-distance pattern. These forest generalists were either early-successional forest birds or edge species; that is, they can also use the non-forest habitats (e.g. bamboo or orchards) either for foraging or nesting. Gascon et al. (1999) concluded that the matrix-exploited species in a habitat patch is likely to receive recruits either from other habitat patches or the matrix itself, and often remains persistent populations in fragmented landscapes. The non-forest matrix may function as a potential source of immigrants for forest generalists to supply their local populations within these forest islands in our study.

Compared to the generality of area effect, the strength and direction of isolation effect depends on the species responses to the matrix surrounding habitat patches in fragmented landscapes (Watling and Donnelly 2006, Şekercioḡlu 2007, Prevedello and Vieira 2010).In this study, Ialso found that the trait-specific responses to the matrix may mask the isolation effect at the community level since a community is composed by a variety of species with distinct ecological traits. There was no isolation effect on community similarity for all forest bird species combined (Table 2.3). However, the similarity-distance pattern emerged when we considered the different responses to the non-forest matrix among forest specialists and generalists. Krauss et al. (2003)who studied the effects of habitat fragmentation on butterflies in German grassland fragments also reported that habitat isolation only negatively influenced the occurrence of particular butterfly species at the species level instead of the species richness of the entire butterfly community. I suggest incorporating trait-specific responses to the matrix content into future research to advance our understanding of isolation effects on organisms in fragmented landscapes.

CONSERVATION IMPLICATIONS

The worldwide decline of specialist species across a variety of taxonomic groups has made protection of specialist species a top conservation priority (Clavel et al. 2010). The results in this study have shown forest specialist birds in Taiwan are susceptible to the broad-scale effects of area and isolation in fragmented forest landscapes. Abundance of certain endemic specialists, such as Taiwan Partridge, is relatively low in these forest islands (F.-Y. Lin, unpublished data, 2012). Without appropriate conservation actions, small populations of these species in the forest islands may possibly suffer high local extinction due to the lack of sufficient new colonists, inevitably leading to the decline of lowland avian biodiversity. From a long-term perspective, current forest management in Taiwan which is primarily focused on enhancing local forest quality, however, probably provides insufficient protection to these forest specialist birds. The findings in this study support incorporating landscape connectivity enhancement into the current framework of forestry management in Taiwan. Corridors generally facilitate the movements of focal species between habitat patches at population level (Gilbert-Norton et al. 2010). In addition, management of the surrounding matrix could be conducted alongside corridors to enhance landscape connectivity (Castellon and Sieving 2006). Increasing the structure similarity between matrix and habitat patches such as cultivation with shade trees or complex vertical-structure agriculture (Raman 2006), as well as the presence of stepping-stone trees (Gillies et al. 2011) could be used as a general guideline.

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Table 2.1.Characteristics of the forest islands identified in this study.

Id	Name	Area (km^2)	No. of sampling sites	Observed species richness			Estimated species richness[1]						Detection percentage (%)[2]
				All species	Forest specialist	Forest generalist	All species	Standard error	Forest specialist	Standard error	Forest generalist	Standard error	
YMS	Yang-ming Shan	543.7	11	26	16	10	29.0	1.7	19.0	1.6	10.0	0.0	89.66%
LCT	Lin-co Tableland	248.9	4	21	11	10	29.4	3.3	22.6	4.0	10.0	0.0	71.43%
FBM	Huo-yan Shan	135.5	2	17	7	10	18.3	1.1	8.6	1.2	10.0	0.0	92.90%
BGS	Ba-gua Shan	163.5	4	19	8	11	19.0	0.0	8.5	0.7	11.0	0.0	100.00%
DGS	Da-gong Shan	8.7	2	15	5	10	15.6	0.8	5.6	0.7	10.0	0.0	96.15%
JS	Jade Shan	12.3	1	11	2	9	11.4	0.6	2.0	0.0	9.5	0.7	96.49%
FSD	Fon-shan Dam	5.8	1	13	3	10	14.1	0.7	3.8	0.7	10.5	0.7	92.20%

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[1] Species accumulation curve (Colwell & Coddington, 1994) was used to extrapolate the true species richness for each forest island. Species richness estimated by the M(h) in the program SPADE (Chao and Shen 2010) was chosen in this study.

[2] Detection percentage =(observed species richness of all species / estimated species richness of all species) x100.

Table 2.2. Species-area relationships for all forest species, forest specialists and forest generalists. The area of forest islands and the estimated species richness were both log-transformed

Category	Z-value (slope)			*F*	R^2	*P*-value
	Estimator	Lower 95% C.I	Upper 95% C.I.			
All species	0.175	0.057	0.294	14.390	0.742	0.013
Forest specialists	0.421	0.129	0.714	13.750	0.733	0.014
Forest generalists	0.004	-0.026	0.034	0.110	0.022	0.754

Table 2.3. Distance-decay in community similarity for all forest species, forest specialists and forest generalists. Here, the residuals of similarity-area regression were regressed against distance of the sources of immigrants to remove the confounding effect of area.

	Estimator	*F*	R^2	*P*-value
All species	-0.040	2.000	0.143	0.183
Forest specialists	-0.097	8.713	0.421	0.012
Forest generalists	0.011	1.328	0.100	0.272

Table 2.4.One-way ANCOVA was used to examine whether the distance-decay in community similarity of forest specialists depended on the type of distance from sources of immigrants (forest mainland or the nearest forest island).There was insignificance for distance type and the interaction between distance from the sources of immigrants and distance type. That is, the distance type has no effect on the distance-decay in community similarity of forest specialists.

Source	DF	Sum of Square	Mean of square	*F*	*P*-value
Model 1:					
Distance	1	0.340	0.340	30.578	0.001
Type	1	0.036	0.036	3.250	0.102
Distance * Type	1	0.025	0.025	2.234	0.166
Error	10	0.111	0.011		
Total	13	0.512			
Model 2:					
Distance	1	0.340	0.340	27.493	0.001
Type	1	0.036	0.036	2.922	0.115
Error	11	0.012	0.012		
Total	13	0.389			

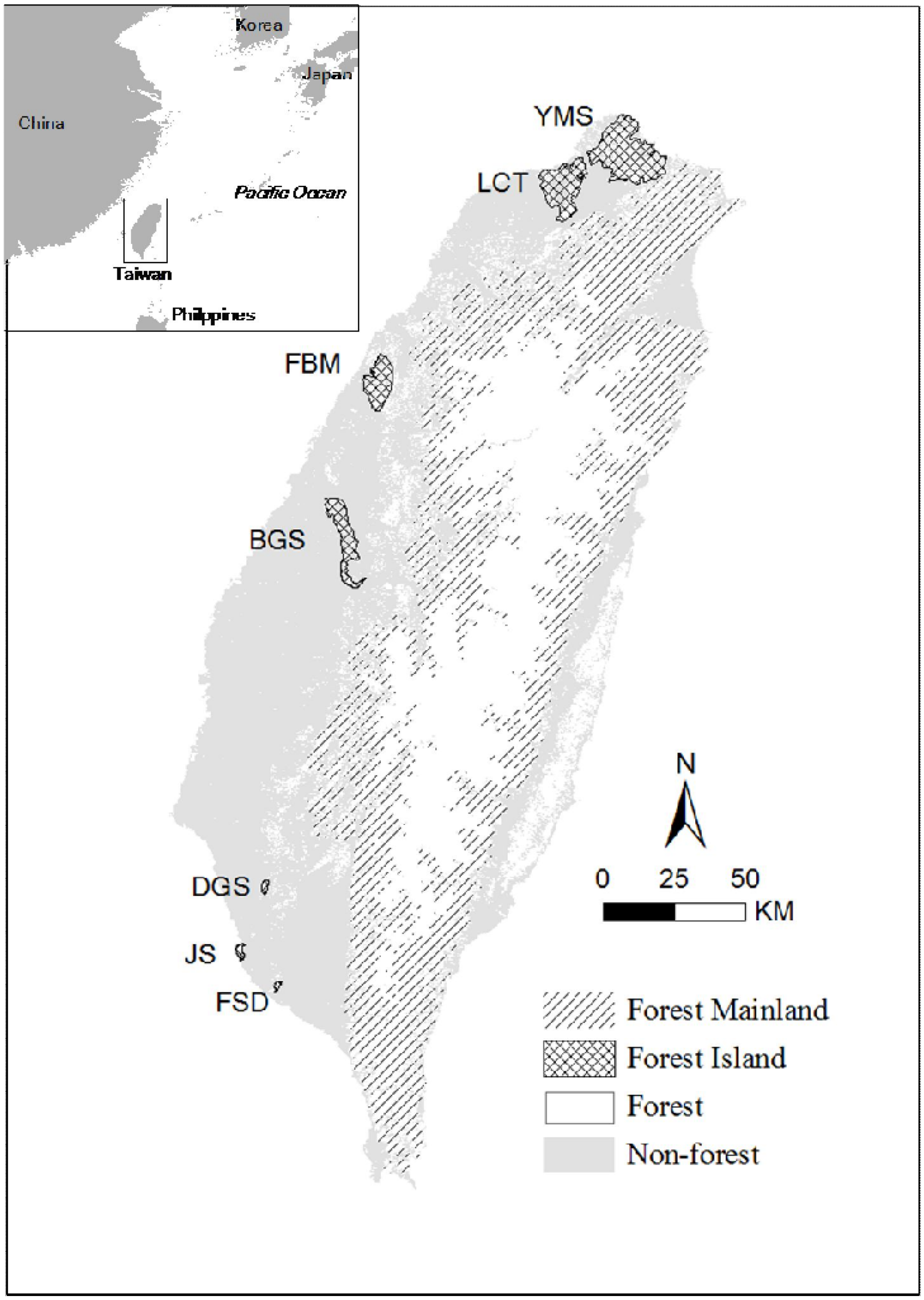

Figure 2.1. Location of the study area in Taiwan. The forest islands on the western coastal plain and the large continuous forest on the central montane area (forest mainland) were shown.

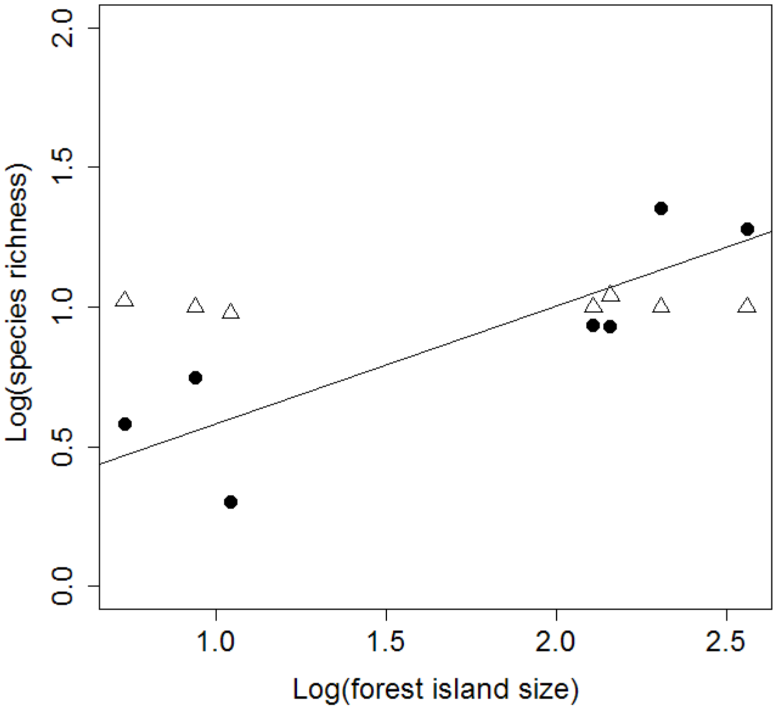

Figure 2.2. Species-area relationships for forest specialists (black dot) and forest generalists (hollow triangle). Species richness of forest specialists increased with the size of forest island (solid line: logS= 0.162 + 0.421 * logA, *P=0.014*), while forest generalists were insensitive to the size of the forest island (*P*=0.754).

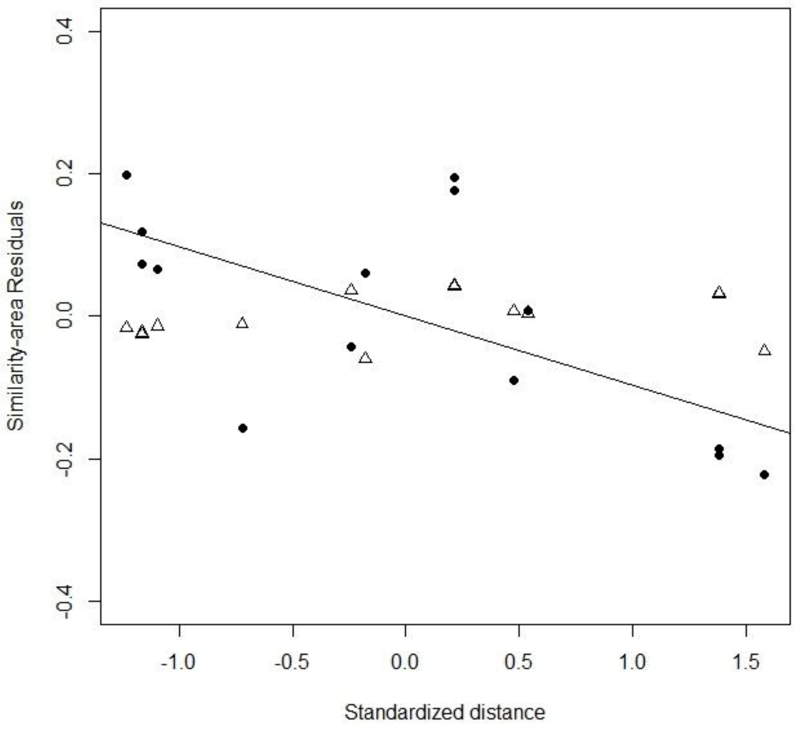

Figure 2.3. Distance-decay pattern in community similarity for forest specialists (black dot) and forest generalists (hollow triangle). To remove the effect of area, the similarity-area residual was used as the dependent variable to examine the relationship between community similarity and distance from the sources of immigrants. Only the similarity of forest specialist assemblage significantly decreased with increasing distance from the sources of immigrants (solid line: Y = 0.128 - 0.097 *X, *P*=0.012).

CHAPTER 3. MULTISCALE EFFECTS OF HABITAT FRAGMENTATION ON DIVERSITY AND ABUNDANCE OF FOREST BIRDS IN TAIWAN

ABSTRACT

Habitat fragmentation can affect organisms through several scale-dependent ecological processes. The majority of these ecological processes often co-vary across scales, and therefore a change of phenomena at a given scale can be a product of alterations at multiple scales. Thus, for conservation management, it is critical to understand how organisms respond to multiscale factors in fragmented landscapes. In this study, I apply a hierarchical multiscale approach to examine multiscale effects of forest fragmentation on community indices and composition of lowland-forest birds in northern Taiwan. The following specific questions were addressed: (1) What are the relative influences of environmental variables at different scales to the variability of community indices and composition on community indices and composition of forest-dependant birds? (2) How does the relative influences of environmental variables at different scales vary with type of response variable and species group?

Presence/absence and relative abundance of bird species were estimated at three assemblage levels (all species, forest specialist, forest generalist) at twenty-two sampling sites. Thirty-seven environmental metrics at three spatial scales(regional-, landscape-, and local-scale) were quantified using GIS and in the field. First, I employed RandomForest (RF) to examine the important environmental determinants of community indices (species richness, richness ratio of forest specialists and abundance ratio of forest specialists). Furthermore, partial Redundancy Analysis (pRDA), a multivariate variance partitioning approach, was used to investigate the relative contributions of environmental determinants of community structure for both the presence/absence and abundance data sets.

The results showed that regional-scale (*e.g.* distance from the potential source of immigrants) and local-scale (*e.g.* tree diversity) factors played key roles in determining the presence of forest birds, while landscape-scale factors (e.g. percentage of landuse type, degree of patch shape complexity) were most important in influencing abundance at the entire assemblage level. In terms of species group, only forest specialists responded to regional-scale factors, indicating that forest specialists experienced a regional-scale dispersal limitation within a human-modified landscape more than generalists.

The findings demonstrate that community indices and structure of forest birds in fragmented landscapes are determined simultaneously by ecological processes acting at multiple scales, although their relative contributions are not equivalent. Furthermore, the relative importance of multiscale determinants shaping the avian community shifts with the type of response variable chosen and species group of concern. Thus, researchers should be aware that their results may depend on the response variables and species group chosen, and they should be cautious when applying conclusions to conservation decision-making.

Keywords: avian communities, ecological trait, forest fragmentation, multiscale, partial Redundancy Analysis (pRDA), RandomForest (RF), variance partitioning

INTRODUCTION

Habitat fragmentation can affect organisms through different scale-dependent ecological processes (Olff and Ritchie 2002), including constraints of structural isolation on inter-patch movements of individuals at a landscape scale (Hanski and Gilpin 1991, Ernest et al. 2003, Tittler et al. 2006) or through patch-scale edge effects on nest success of birds (Wilcove 1985, van Rooyen et al. 2011). The majority of these impacts often co-vary across scales. For example, loss of suitable habitat can simultaneously lead to increase in landscape isolation as well as local edge effects (Fahrig 2003). Thus, a change in phenomena observed at a given scale can be a product of habitat alterations at multiple scales. Although numerous studies have advanced our knowledge of impacts of habitat fragmentation on distribution patterns, demographic dynamics (Ernest et al. 2003, Korfanta et al. 2012) and reproductive success(Wilcove et al. 1986, Stephens et al. 2004) across a variety of taxa at given scales, little attention has been paid to how organisms respond to multiscale factors in fragmented landscapes.

Recently, a growing number of studies have provided justification for a multiscale approach which adopts the concept of hierarchy theory (Allen and Starr 1982, O'Neill 1986) to examine species-environment relationships(Grand and Cushman 2003, Cushman and McGarigal 2004a, Stephens et al. 2004, Richmond et al. 2012). This framework emphasizes the idea that broad-scale patterns or processes may constrain fine-scale ones to a certain point. Accordingly, at least two more scales beyond the focal scale, broader and finer ones, should also be considered together to provide the context and details to explain the phenomena observed at the focal scale, respectively (Turner et al. 2001). Although the conclusions regarding the relative importance of environmental determinants at different scales varied across studies, these studies overall revealed that variability at multiple scales collectively contribute to shape the species-environment relationships. In some cases, the joint effects derived from cross-scale interactions of landscape or habitat elements at different scales explained a large amount of variability (Cushman and McGarigal 2004a, Lawler and Edwards 2006, Stewart-Koster et al. 2007). The difficulty in disentangling independent effects of factors at a given scale also highlights the need of multiscale design scheme.

Although increasing attention has been given to the hierarchical multiscale approach recently, few studies have linked the scales of measurement to ecological processes (Parsons et al. 2004). Defining scales arbitrarily without consideration of the corresponding underlying mechanisms could mislead ecologists to infer patterns that are artifacts of scales instead of real dynamics (Wiens 1989). In addition, there has been relatively little research focused on the issue that multiscale effect is a function of parameters measured and the ecological traits of the species studied (Lawler and Edwards 2006, Pardini et al. 2010). For example, the relative importance of environmental determinants at multiple scales for bird-habitat associations was contingent on response variables chosen (Pearson 1993, Cushman and McGarigal 2004b). Furthermore, species with distinct ecological traits may respond differently to ecological processes acting at different scales. Some species or groups may be more affected by the amount of landscape-level suitable habitat but not by habitat patch size(Betts et al. 2006). This could result in inconsistent conclusions about the impacts of habitat fragmentation as well as lead us to make inefficient conservation decisions.

The lowland forests in Taiwan, a montane island in the western Pacific Ocean, harbor diverse endemic bird species and subspecies(Liu et al. 2010). Unfortunately, the unique insular forest ecosystem has become severely fragmented because of dense human populations and intensive developments along the west coastal plains. There have been several studies that investigated the effects of forest fragmentation on forest-dependent birds at different scales in Taiwan (Pei and

Sun 1998, Cheng 2002, Lin 2010a). At a regional-scale, Pei and Sun (1998) and Cheng (2002) both documented that a lack of a source of immigrants due to large-scale isolation of forest habitat was a key determinant for lowland-forest avian communities. By studying the impacts of landscape and vegetation structure on species richness of birds in a fragmented forest landscape, Lin (2010) concluded that diversity of habitat patchness, vertical foliage structure and floristic composition were important factors for sustaining higher avian biodiversity in fragmented environments at a local scale. These studies have identified critical determinants at a given scale and provided valuable information for landuse management, however, it is still unclear how multiscale processes derived from forest fragmentation collectively affect the lowland forest birds in Taiwan.

In this study, I apply a hierarchical multiscale approach to examine multiscale effects of forest fragmentation on community indices and structure of lowland-forest birds in northern Taiwan. The three spatial scales defined in this study, regional-scale, landscape-scale and local-scale, are linked to hypothetical ecological processes based on prior knowledge (Fig. 3.1). In addition, I also investigated the influence of type of response variable (presence/absence vs. abundance) and ecological traits (forest specialist vs. generalist) on multiscale effects of forest fragmentation. The following specific questions were addressed: (1) What are the relative influences of environmental variables at different scales on community indices and composition of forest-dependant birds? (2) How does the relative influences of environmental variables at different scales vary with type of response variable and species group?

METHODS

Study area

This study was conducted in northern Taiwan over an area of approximately 2,000 km^2. The study area lies between 24°00' N-25° 18' N and 120° 27' E-122° 00' E (Fig. 3.2). The average temperature and annual precipitation range from 16.7-23.0°C and 1283.0-4892.4 mm, respectively (Taiwan Central Weather Bureau, http://www.cwb.gov.tw/eng/index.htm). The major climate type in the study area is the summer rain climate (Su 1985), that is, precipitation is heaviest during summer but rain falls year-round. The elevation ranges from 0 to around 1,000 m, and subtropical *Machilus-Castanopsis* forest is the primary vegetation type (Su 1992).

This area was once primarily covered by pristine forests in the seventeenth century (Keliher 2003); however, the combination of intensive agricultural developments and increasing human population has resulted in severe lowland forest loss. The majority of lowland forest was converted to orchards, tobacco or tea plantations, paddy fields, pastures and urban areas. Currently, the lowland forests remaining on hills or mountains within our study area are almost all secondary forests regenerated from abandoned agricultural lands or forestry plantations over the last century. Only a minority of lowland forests near the central mountain ridge (east side of the study area) still remain pristine. Other lowland forests are severely fragmented, surrounded by agricultural lands and cities (Fig. 3.2).

Sampling design

The land use layer derived from the third Forest Inventory of Taiwan (Forestry Bureau 1995) was used to delineate the potential source of immigrants for lowland forest birds. The seventy-four cover types in the data layer were reassigned to six categories: primary forests, secondary forests, bamboo, croplands/orchards, roads/buildings and others (e.g. water body, graveyard, nursery and mines). I delineated the large primary lowland forests >500 ha with an elevation < 1,500m in the central part of Taiwan as the source of forest bird immigrants. The vegetation of the source of immigrants is primarily dominated by subtropical *Machilus-Castanopsis* forests. Twenty-two 1kmx1km sampling sites were then set at locations where lowland forest was the dominant habitat, and at a variable distance from the source of immigrants.

Bird data

Point counts (Reynolds et al. 1980) were used to collect bird data in this study. It is a dilemma to balance data accuracy and survey efficiency for a large-scale field census. A preliminary analysis showed that thirty-six samples were required to detect 90% of bird species within a 1kmx1km sampling site in the study area (Appendix B) using point counts. Thus, six plots were set along a transect with at least a 200m interval between them within each sampling site. Each plot was surveyed three times during the sampling period because of the seasonal variation of bird activity patterns (Best 1981). In addition, the detection of birds singing may also change with time of day (Robbins 1981). Thus, each plot was visited twice in each survey. Plots were numbered and sampled in order. After finishing the first round, the investigators would stop at the last point for 10 minutes, and then survey each plot again in reverse order. This resulted in a total of thirty-six samples for each site.

Bird data were collected between March and May, 2010. The bird surveys were conducted within 4 hours after sunrise under acceptable weather conditions(e.g., winds less than 20 km/h and no rain)(Hamel et al. 1996). Species and number of all bird species seen or heard within the first 6 minutes at each plot were recorded in four distance bands (0-10m, 10-25m, 50-100m and >100m). Birds recorded beyond 100m were excluded from analyses. Furthermore, only resident forest species were included for subsequent data analyses. Diurnal and nocturnal raptors were eliminated because of the limitation of point counts for these species (Hamel et al. 1996).

To reduce the bias caused by imperfect detection in abundance estimation (Archaux et al. 2012), distance sampling was applied to estimate the detection probability of each bird species (Buckland 1993). This was achieved by using the distance sampling software, DISTANCE 6.0 (Thomas et al. 2010). Program DISTANCE allows users to estimate the detection function of each species by its distance data. The detection function is then used to adjust the estimation of species density. Every visit to a plot was viewed as an independent sample. For five species whose counts were < 30 (Malaysian Night Heron (*Gorsachius melanolophus*), Taiwan Partridge (*Arborophila crudigularis*), Slaty-legged Crake (*Rallina eurizonoides*), Collared Finchbill (*Spizixos semitorques*) and White-tailed Robin (*Myiomela leucura*)), another independent data set derived from Breeding Bird Survey Taiwan (BBS Taiwan) was used to estimate their detection probability. Furthermore, I followed Lin (2010b) to exclusively assign each species to forest specialists or forest generalists based on their forest dependency. Species without enough information were defined based on my field observations.

A richness ratio of forest specialists was calculated as the number of forest specialist species divided by the total number of forest bird species at each sampling site. An abundance ratio of forest specialists was defined as summed density of forest specialist species divided by total density of all forest bird species at each sampling site.

Environmental metrics

I used thirty-seven variables to quantify the multi-scale environmental characteristics of each sampling site (Table 3.1). Environmental variables were placed into three groups which were associated with the spatial scales: regional-, landscape- and local-scale.

Regional scale environmental variables

At a regional scale, I used ArcMap version 9.3 software to calculate the nearest edge-to-edge distances from each sampling site to the source of immigrants (DIST). Altitude (ELEV) was derived from the Digital Terrain Model layer of Taiwan.

Landscape scale environmental variables

Selecting an appropriate spatial scale is a challenge for the design of multi-scaled research. Arbitrary definition of spatial scales may result in misleading conclusions as well as inefficient conservation management (Wiens 1989, Lawler and Edwards 2006). Therefore I delineated eight buffer zones (radii=0.5, 1.0, 1.5, 2.0, 2.5, 3.0, 3.5, 4.0km, respectively) from the center of sampling plots first. Then the strength of responses of birds to landscape context within each buffer zone was evaluated to determine the landscape scale in this study. The result showed that the landscape context within the radius of 2.5km buffer zone explained the largest amount of variation in the avian community, both for presence and abundance data sets (Appendix C). Thus, I defined the buffer zone within the radius of 2.5km as the landscape scale in this study.

The landscape-scale variables including landscape composition and configuration were quantified by using FRAGSTATS version 3.3 software (McGarigal and Marks 1995). The landscape composition variables were expressed as the proportion of each land cover (forest, bamboo, croplands/orchards, roads/buildings and others) within a 2.5km radius buffer zone (PLAND). Furthermore, Simpson diversity index of the proportions of the land cover (SIDI), largest patch index of forest (LPI_f) and patch density (PD) were also calculated to characterize the complexity of landscape composition. I chose several landscape configuration variables to represent shape complexity (FRAC), edge (ECON) and connectivity (PROX, ENN and CONNECT) of the landscape, which have been recognized as highly influential in shaping avian community in fragmented landscapes (Sisk et al. 1997, Uezu et al. 2005). Species respond differently to the matrix types surrounding suitable habitat patches (Raman 2006, Prevedello and Vieira 2010). Therefore, the edge segments of patches were weighted by the pairwise contrasting weights (Table 3.2). These weights represent the magnitude of edge contrast between adjacent patch types and range from 0to 1. Higher contrasting weight refers to more structure difference between a patch of a focal class and its adjacent patch of another class. For example, a patch of forest class adjacent to a patch of roads/buildings has the maximum contrasting weight that equals to 1. The structural contrast between a forest patch and other three patch types (i.e. bamboo, croplands/orchard and others) is intermediate comparing to the forest-roads/buildings contrast. Thus, I assigned contrasting weight value 0.25, 0.50 and 0.75 to represent the forest-bamboo, forest-croplands/orchard and forest-others contrasts in order. All landscape configuration variables were calculated for both forest class (suffix _f) and whole landscape level (suffix_all).

Local scale environmental variables

Following the completion of bird sampling, I measured the local-scale variables in the field. Within each 100m-radius sampling plot, four 10m x 10m quadrats were randomly set for vegetation measurement. All live and dead trees with DBH>=5cm and height >= 1.5m within quadrats were identified, and their DBH were measured. Tree density was estimated by dividing the number of live trees by area. The mean and coefficient of variance of basal area were calculated. Furthermore, I conducted a Detrended Correspondence Analysis (DCA) based on the frequency matrix of tree species pooled for each sampling site, and took the scores projected on the first (DCA1) and second axes (DCA2) to represent the tree assemblage composition. The richness and Shannon diversity index ($H= -\sum p_i \log (p_i)$, where p_i is the proportion of species i) for tree species DBH>=5cm were also calculated to provide more floristic information. Finally, the average density of shrubs was calculated by dividing the numbers of woody shrubs counted within two 2mx10m strips along the north-south and east-west directions in each quadrat by area.

I employed the point intercept sampling method (Caratti 2006) to quantify the vegetation structure at each quadrat. Vertical foliage coverage was assigned to five levels: ground litter, herb (<1m), shrub (1-2m), subcanopy (2-6m) and canopy (>6m). Twenty points were randomly selected within each quadrat, and the presence/absence of each vertical layer was estimated by investigators. The percentage of foliage coverage of each layer was then calculated separately as the number of plots where a given layer appeared divided by the total number of points. For example, if the shrub layer appears at ten points within a quadrat, then the percentage of shrub coverage is 50% (10/20). The percentage of foliage coverage for each layer was averaged for each sampling site, and then used to calculate the foliage height diversity (FHD) based on Shannon diversity index (MacArthur and MacArthur 1961). Furthermore, the maximum canopy height was estimated by a clinometer at each quadrat. All computation of local-scale variables was performed using the 'vegan' package in the R environment (R Development Core Team 2005).

Data analysis

To reduce the bias caused by multicollinearity, highly correlated environmental variables ($|r|> 0.7$) were excluded from subsequent analyses. I retained the variables which were considered more biologically meaningful for forest birds if they were highly correlated to other variables.

Identifying critical environmental variables of avian community indices

For the three community indices (species richness, richness and abundance ratio of forest specialist), RandomForest analysis (RF) was implemented to explore the relative importance of determinants at different scales. The fundamental concept of RF analysis is similar to Classification and Regression Tree (CART) (De'ath and Fabricius 2000). The response variable is repeatedly split by one single variable selected from all explanatory variables to construct a tree model. Each splitting would partition the data into two exclusive groups, each of which is as homogeneous as possible. The homogeneity of group is evaluated by Shannon-Weiner diversity index or Gini index for categorical response variables, and sum of squares about the within-group mean for numeric response variables. RF, however, bootstraps the samples to construct a variety of tree models instead of just one final model. In addition, the most determinative variable at each splitting node in RF analysis is selected from a subset of randomly chosen explanatory variables. These unique characteristics of bootstrapping and randomization make RF able to handle small sample sizes with relative larger numbers of explanatory variables and is robust against overfitting (Breiman 2001).

I followed Murphy et al. (2010) to decide which explanatory variables were influential in determining the assemblage indices in this study. As an output from RF, variable importance (I) of individual explanatory variable was calculated as the averaged increase of mean squared error (MSE) after permuting this variable over all regression tree models. If an explanatory variable is strongly associated with the response variable, random permutation would break the association and increase MSE. Then a model improvement ratio (MIR) was defined as $I/I_{\max}$for each explanatory variable for comparison. Higher MIR indicated more important explanatory variables. I then iteratively developed a series of models using the explanatory variables for which MIR was above the given threshold (from 0.1 to 1.0 in 0.1 increments). The model with the smallest MSE and largest variance explained was chosen as the best model.

Relative importance of multiscale environmental determinants of avian community structure

Variance partitioning analysis was applied to disentangle the pure and shared effects of environmental variables at different scales on the explained variation in avian community structure (Cushman and McGarigal 2002). I conducted the variance partitioning analysis using a multivariate procedure, partial Redundancy Analysis (pRDA), because our preliminary DCA showed the gradient length of the first axis was < 2 SD, indicating a somewhat linear response of the avian community to the environmental gradient (Lepš and Šmilauer 2003). The variation in avian community structure was partitioned into eight components by a series of pRDA based on the combinations of the environmental variables at three scales I defined in this study. I chose the unbiased RDA statistic R_a^2 to represent the explained fraction of variance due to its insensitivity to sample size and numbers of explanatory variables (Peres-Neto et al. 2006). I also examined the responses of species to the gradients of environmental metrics by plotting a species-environment biplot diagram. The environmental vectors were projected onto an RDA ordination. The fitted environmental variable was considered insignificant if the squared correlation coefficient (r^2) between the ordination configuration and this environmental variable was higher after the random permutation(Oksanen et al. 2012).

Presence/absence and abundance data sets were both used as response variables at the entire species, forest specialist and forest generalist assemblage levels. Abundance data were Hellinger transformed (Legendre and Gallagher 2001) into relative abundance prior to analyses. Before data analyses, I log-transformed environmental variables to improve their normality. A multivariate forward selection procedure (Blanchet et al. 2008) was used to select important environmental variables for the subsequent variance partition analysis. First, a global model including all environmental variables in each subgroup (e.g. floristic, physiognomy) was performed to test if the subgroup had an effect on the response variables. If the test showed no significant effect, the environmental variables within this subgroup would be excluded from further variable selection procedure and variance partitioning analysis. If the test showed a significant effect, the marginal contribution of each environmental variable to the variability explained in bird data set was estimated. The environmental variable with the largest contribution would be selected if the Monte Carlo permutation test for its contribution was significant. Subsequently, given the selected variable as a covariate, the conditional contributions of the remaining environmental variables to the variability explained in the bird data set were calculated. Similarly, this environmental variable with the best contribution would be selected if the permutation test for its contribution was significant. I iteratively ran this procedure until no more environmental variables had significant conditional contributions to the variability of avian community. The significance level of the variable selection procedure was set at 0.1 to avoid missing any potentially critical explanatory variables.

All statistical analyses were conducted in the R environment. RandomForest analysis was implemented with the R package 'randomForest.'The forward selection procedure and variance partition analysis were performed using the R package 'packfor' and 'vegan,' respectively.

RESULTS

In total, 12,082 bird observations of 28 forest bird species recorded in the 22 sampling sites were used in the data analysis. Among these forest bird species, there were 17 forest specialists and 11 forest generalists (Appendix D).

Critical environmental determinants of avian community indices

Distance from the source of immigrants (DIST) and canopy height (HEIGHT) were more critical environmental variables for the total species richness of forest birds than others based on MIR (Table 3.3). However, only the distance from the source of immigrants was included in the best model that explained about 16% of the variability in species richness (Table 3.4). The total species richness declined sharply when the distance from the source of immigrants exceeded approximately 5km (Fig.3.3a).

Although DIST was also the most critical determinant for the richness ratio of forest specialists, other environmental variables at landscape (PLAND_f) and local (HEIGHT and SDI) scales were influential too (Table 3.3). These four variables accounted for approximately 36.5% of the variability in the species ratio of forest specialists (Table 3.4).The species ratio of forest specialists was higher at large forest area with diverse tree species near the source of immigrants (Fig. 3.3b). It was notable that the threshold of landscape-scale forest cover for the richness ratio of forest specialists is about 70%.

In contrast, DIST was not a critical determinant of the abundance ratio of forest specialists. Only landscape- (PLAND_f, PLAND_r) and local-scale (DCA1, DENt) environmental variables were included into the best model, which accounted for 52.3% of the abundance ratio variability (Table 3.4). It indicated that the populations of forest specialists thrive at less disturbed locations covered by larger forest areas with a high density of trees (Fig. 3.3c).

Multiscale environmental determinants on avian community structure

Multivariate forward selection of important environmental variables

Twenty environmental variables were selected by the multivariate forward selection procedure (Table 3.5). More environmental variables selected for the presence of all forest bird species were shared with forest specialist species (DIST, FRAC_all, BAs and COL) than generalist species (DIST and DCA1). Distance from the source of immigrants was influential for these three assemblages. For the abundance data set, forest specialists and forest generalists both shared nine important environmental variables with the entire species assemblage.

Relative importance of environmental determinants at different spatial scales

Overall, the total amount of variability explained in the avian community based on the variance partitioning analysis was higher for the abundance data set than the presence/absence data set. The total variance of presence/absence data explained for the entire, forest specialist and forest generalist assemblages was 22.50%, 23.48% and 37.15%, respectively. The corresponding values based on abundance data were 55.79%, 47.60% and 64.19%, respectively (Table 3.6).

Environmental variables at different scales were not equally influential on the avian assemblage structure in the study area. For the presence/absence data at the entire community level, the pure regional-scale variables [R] explained the largest amount of variance (6.05%), then the pure local-scale [V] (4.44%) and the pure landscape-scale [L] (0.76%) ones in order. The regional-scale variable DIST and the local-scale variable SDI and COL showed high correlation ($|r| > 0.7$, Table 3.7) with RDA1 axis which explained the largest amount of variability in the presence of forest birds (Table 3.7). The location of species along the RDA1 axis primarily followed the gradient of the distance from the source of immigrants and local forest conditions. Several species with higher RDA1 scores, such as Grey-chinned Minivet

(*Pericrocotus solari*), Varied Tit (*Parus varius*), Taiwan Partridge and Bronzed Drongo (*Dicrurus aeneus*) preferably occur at locations close to the source patch or with higher tree diversity (Fig. 3.4). The majority of these species are forest specialists.

The relative importance of environmental variables at different scales shifted with the choice of response variables. The pure landscape-scale variables [L] contributed to the largest component of variance explained (30.39%) of the abundance data set at the entire assemblage-level, then the pure local-scale [L] (3.64%) and pure regional-scale [R] (0.62%) ones. Two landscape-scale variables, PLAND_f and PLAND_r, were highly correlated to RDA1 axis (r=-0.824 and 0.823, respectively, Table 3.7). The location of species along the RDA1 axis primarily followed the gradient of proportion of forest area and the degree of human disturbance. Several forest generalists, such as Japanese White-eye (*Zosterops japonicus*), Light-vented Bulbul (*Pycnonotus sinensis*) and Black Bulbul (*Hypsipetes leucocephalus*) thrive in more fragmented and disturbed forest landscapes resulting from human developments (Fig. 3.5). In contrast, larger forest areas are more preferred by certain forest specialists, such as Dusky Fulvetta (*Alcippe brunnea*) and Gray-cheeked Fulvetta (*Alcippe morrisonia*).

Effects of habitat specialization of species on relative importance of multiscale environmental determinants

The assemblage structure of forest specialists and generalists were both shaped simultaneously by the environmental variables at multiple scales (Fig. 3.6). The regional variables, however, were only influential on forest specialists for both presence/absence and abundance data sets (4.45% and 6.83% variance explained, respectively, Table 3.6). This indicated that forest specialists are more sensitive to regional dispersal limitation within human-modified landscapes than generalists in this study. In contrast, forest generalists highly responded to landscape-scale variables in both cases (12.08% and 41.52% variance explained for presence/absence and abundance data sets, respectively, Table 3.6).

DISCUSSION

The community indices and structure of forest bird assemblages in fragmented forest landscapes are determined simultaneously by ecological processes acting at multiple scales, although their relative contributions are not equivalent. Also, the relative importance of multiscale determinants on shaping the avian community shifts with the response variables chosen and species group. Regional-scale variables are more influential for species richness and community composition of forest birds based on presence/absence data, while landscape-scale variables influence abundance of the avian community. In terms of species groups, only forest specialists respond to regional-scale factors (*i.e.* distance from the source of immigrants).

Incorporating multiscale environmental variables greatly increased the amount of variance explained in the community indices and structure of forest-dependent birds in this study. It is also notable that relatively large amounts of variance were explained by joint components in this study even after eliminating highly correlated environmental factors ($|r| > 0.7$). This indicates that the community pattern observed at a given scale is structured by ecological processes acting at multiple scales instead of a single one, and these ecological processes are not independent of each other. The findings in this study are consistent with previous studies on avian communities (Grand and Cushman 2003, Cushman and McGarigal 2004a), demography (Richmond et al. 2012) and nest-site selection at a species-level (Lawler and Edwards 2006).

Although the avian community structure in fragmented landscapes was shaped by ecological processes acting at multiple scales, their relative contributions among scales were not equivalent. Regional-scale and local-scale factors played key roles in determining the presence of forest birds, while landscape-scale factors overrode the others for the abundance data set at the entire community level in this study. Organisms need to gather and respond to environmental information to maximize their fitness. The information available and the decision made will be different depending on how organisms perceive their environments and their species-specific life history. For instance, some species inspect habitat characteristics in a hierarchical order (Johnson 1980); that is, they respond to coarse-scale (*e.g.* geographic range) habitat heterogeneity first, then meso-scale (*e.g.* home range) and fine-scale ones in order. In contrast to top-down habitat selection, other species may show a bottom-up strategy (Kristan 2006), interacting first with the environmental characteristics at finer scale, such as floristic or vegetation structure which are directly involved in their foraging, reproduction and survival, then secondarily with other coarser-scale factors (Cushman and McGarigal 2004a). Therefore, the relative importance of multiscale determinants at a community level may vary depending on the attributes of species that compose the community as well as location-specific habitat heterogeneity and historical events (McAlpine et al. 2008).

The findings in this study provided an interesting perspective on this issue. The total species richness declined sharply after the distance from the potential source of immigrants was about >5 km (Fig.3.3a), and this regional-scale factor alone explained the largest amount of variability in the presence of forest birds (Table.3.6). A subset of species which only occurred at locations near the source patches, such as Grey-chinned Minivet and Bronzed Drongo, are forest specialists. The intolerance to non-forest habitat by forest specialists may reduce their probability of colonizing a new habitat patch in fragmented landscapes (Villard and Taylor 1994), increasing their extinction vulnerability to stochastic events or deterministic incidents (Brown and Kodric-Brown 1977, Feeley et al. 2007). This is consistent with Cheng (2002), who found that a lack of source of immigrants due to large-scale disconnection of forest habitat was a key determinant for a lowland-forest avian community in the same area. In contrast, the presence of a subset of species, such as Varied Tit, was more associated with local-scale factors, such as tree diversity and basal area of snags, so that local-scale factors also explained a certain degree of variability (Fig.3.4).

In addition, I found that the strength and the relative importance of multiscale environmental determinants on avian community indices and structure varied with the type of response variable. Compared to the presence/absence data set, the multiscale environmental metrics better described the variability in the abundance data set of forest birds(Table 3.6). Furthermore, the landscape-scale factors were more influential in determining the avian community for the abundance data set. One possible reason for the inconsistency between presence/absence and abundance data sets may lie in the nature of the data-specific source of variability. Cushman and McGarigal (2004b) have demonstrated that the variability of presence/absence data set at a community level is primarily affected by rare species rather than common species which occur almost everywhere, and is better explained by coarser-scale factors. Fine-scale variations appear to be more important in explaining the detail of abundance variability of common species. The RDA ordination results showed that the variability of species presence in the entire avian community was mainly affected by certain rare species along the gradients of distance of the source of immigrants and floristic, whereas several common species along the gradient of landscape-level forest fragmentation accounted for the variability of abundance.

For instance, species such as Taiwan Partridge, Varied Tit and Grey-chinned Minivet all occurred in less than half of the sampling sites in this study area (Appendix D). Their presence was primarily determined by the distance from the source of immigrants or forest conditions (Fig. 3.4). Sun (2001) reported that Taiwan Partridge prefer old-growth forests and avoid crossing roads for their daily movement. Its habitat preference and sensitivity to non-forest barriers may constrain this species within forest patches, reducing the possibility of inter-patch movement. In terms of species abundance, several common species such as Japanese White-eye, Light-vented Bulbul, Dusky Fulvetta, Rusty-cheeked Scimitar Babbler, and Grey-cheeked Fulvetta were influenced by the land-use composition and the degree of fragmentation (Fig. 3.5). The first three species can use a variety of habitats and adapt well to fragmented, disturbed landscapes, even urban areas (Liu et al. 2010). In contrast, although Grey-cheeked Fulvetta, Rusty-cheeked Scimitar Babbler and Dusky Fulvetta also occur in almost all of the sampling sites, they had higher density at locations with larger, less fragmented forests.

The relative contributions of multiscale determinants on avian assemblage structure also vary with species group. Only forest specialist species responded to the regional-scale distance from the source of immigrants (Fig. 3.6), while forest generalists were strongly positively related to landscape-scale factors, such as the degree of fragmentation and the percentage of building/road areas. The forest generalist species in this study were either early-successional or edge species. They might utilize the edge or non-forest habitats matrix and persist well in these habitats. Their broad habitat niche and the potential of recruitment from the surrounding matrix habitat (Gascon et al. 1999) possibly resulted in the lower sensitivity to local-scale vegetation conditions and the distance from the source of immigrants. In contrast, the behavioral avoidance of non-forest habitats by forest specialists could lead to their vulnerability to broad-scale forest fragmentation

(Gobeil and Villard 2002, Dexter 2010). My finding is consistent with Brotons and Herrando(2001), who studied the bird communities in a fragmented pine forest landscape in the Mediterranean basin and also reported a similar pattern.

CONSERVATION IMPLICATIONS

Disentangling the multiscale effects of habitat fragmentation on wildlife is critical to provide information for managers to decide the priority of conservation actions when resources are limited. The findings from this study, however, demonstrate that the perceived relative importance of ecological processes acting at multiple scales to structure avian communities in fragmented landscapes may change with the parameters measured and target species groups. Researchers should be aware of this and be cautious when providing information to managers for decision-making.

Moreover, my findings also have implications for goal-oriented conservation in this study area. Some studies have revealed that the disconnection of forest habitats was influential in determining the community structure of lowland-forest birds at a large spatial scale in Taiwan (Pei and Sun 1998, Cheng 2002, Huang 2004). Single-scale research, however, may underestimate the effects of other environmental factors at different scales on the pattern observed, such as the degree of local forest fragmentation or location-specific vegetation conditions. Thus, there is still a debate on the value of increasing regional-scale connectivity in Taiwan. My multiscale approach study revealed that the presence of several endemic forest specialist species (*e.g*. Taiwan Partridge) is strongly associated with regional-scale connection of forest habitat and local-scale vegetation attributes. I suggested that it is necessary to enhance large-scale connectivity as well as local forest quality if the goal is to improve biodiversity of lowland-forest birds in northern Taiwan. Nevertheless, if the goal of management is to secure the persistence of existing local populations, preserving the amount of forest habitat (*e.g.* > 70%) and mitigating the degree of forest fragmentation may be practical guidelines.

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Table 3.1. Summary of the environmental metrics used in this study. Thirty-seven environmental variables at three spatial scales, regional-, landscape-, and local-scale, were quantified at 22 sampling sites using GIS and field measurements.

Scales	Variables	Description (unit)	Mean	C.V.
Regional-scale:	DIST	Nearest edge-to-edge distance from a sampling site to the source of immigrants (km)	14.96	0.757
	ELEV	Altitude (m)	451.45	0.344
Landscape-scale:				
Landscape Composition	PLAND_f	Percentage of forest area (%)	66.00	0.247
	PLAND_b	Percentage of bamboo area (%)	4.00	1.768
	PLAND_c	Percentage of orchard/cropland area (%)	7.00	0.813
	PLAND_o	Percentage of others area (%)	16.00	0.669
	PLAND_r	Percentage of road/building area (%)	5.00	0.920
	LPI_f	Largest Patch Index of forest (%)	62.00	0.358
	SIDI	Simpson's Diversity Index	0.46	0.310
	PD	Patch density (# /100ha)	1.46	0.357
Landscape Configuration	FRAC_f	Fractal dimension index of forest class	1.08	0.030
	FRAC_all	Fractal dimension index for whole landscape	1.03	0.006
	ECON_f	Edge contrasting for forest class (%)	2.00	1.281
	ECON_all	Edge contrasting for whole landscape (%)	37.50	0.237
	PROX_f	Proximity index for forest class	62.73	1.034
	PROX_all	Proximity index for whole landscape	13.75	0.920
	ENN_f	Euclidean nearest neighbor for forest class (m)	239.84	164.64
	ENN_all	Euclidean nearest neighbor for whole landscape (m)	585.34	156.89
	CONNEC_f	Connectance index for forest class (%)	1.20	3.101
	CONNEC_all	Connectance index for whole landscape (%)	0.30	1.814
Local-scale:				
Floristic	RICH	Species richness of trees DBH>=5cm	48.68	0.261
	DENt	Density of trees DBH>=5cm (# /m^2)	0.26	0.487
	DENb	Density of bushes height>=50cm (# /m2)	1.44	0.505
	BAt	Mean basal area of trees DBH>=5cm (m2/ha)	55.51	0.467
	BAt_cv	CV of basal area of trees DBH>=5cme	0.51	0.446
	BAs	Mean basal area of snag DBH>=5cm (m2/ha)	4.46	0.421
	SDI	Shannon diversity index of tree species DBH>=5cm	2.84	0.097
	DCA1	Site scores of DCA 1	-0.11	4.977
	DCA2	Site scores of DCA 2	0.05	8.036
	VOL	Volume of logs length>=2m (m^3/ha)	10.00	1.011
Physiognomy	HEIGHT	Maximum canopy height (m)	12.15	0.185
	COca	Coverage of canopy (%)	0.78	0.136
	COsub	Coverage of sub-canopy (%)	0.86	0.091
	COb	Coverage of shrub (%)	0.62	0.187
	COh	Coverage of herb (%)	0.55	0.324
	COl	Coverage of litter (%)	0.92	0.074
	FHD	Foliage height diversity index, calculating Shannon diversity index for vegetation structure	0.42	0.174

Table 3.2. Edge contrast weights for each pairwise combination of land-use types. Higher contrasting weight refers to more difference between a patch of focal class and its adjacent patch of another class.

Patch type	Forest	Bamboo	Croplands/Orchard	Others	Roads/Buildings
Forest	0.0				
Bamboo	0.25	0.00			
Croplands/Orchard	0.50	0.25	0.00		
Others	0.75	0.50	0.25	0.00	
Roads/Buildings	1.00	0.50	0.50	0.25	0.00

Table 3.3. Variable importance (I) from RandomForest analysis for three community indices (total species richness, richness ratio of forest specialist and abundance ratio of forest specialist.)For comparison, the original value of variable importance for each explanatory variable was scaled by the maximum value of variable importance(I/ I_{max}) as model improvement ratio (MIR).

Environmental Variables[1]	Total species richness		Richness ratio of forest specialist		Abundance ratio of forest specialist	
	Variable Importance (I)[2]	Model Improvement Ratio (MIR)	Variable Importance (I)[2]	Model Improvement Ratio (MIR)	Variable Importance (I)[2]	Model Improvement Ratio (MIR)
DIST	1.762	1.000	0.0024	1.000	0.0000	0.008
HEIGHT	0.584	0.332	0.0006	0.262	0.0003	0.061
PLAND_f	0.142	0.081	0.0009	0.365	0.0044	1.000
COh	0.090	0.051	0.0000	0.001	-0.0002	0.000
PLAND_c	0.081	0.046	-0.0001	0.000	-0.0002	0.000
BAt_cv	0.074	0.042	0.0000	0.008	0.0003	0.078
DENt	0.064	0.036	0.0000	0.000	0.0033	0.753
PLAND_b	0.043	0.024	0.0000	0.016	0.0001	0.022
ECON_all	0.042	0.024	0.0000	0.000	0.0003	0.058
SDI	0.022	0.013	0.0005	0.202	0.0004	0.097
BAs	0.019	0.011	0.0000	0.007	0.0004	0.100
ELEV	0.018	0.010	0.0000	0.011	0.0000	0.000
DCA1	0.018	0.010	0.0001	0.037	0.0038	0.850
PD	0.003	0.002	0.0000	0.000	0.0006	0.139
CON_all	0.001	0.000	0.0000	0.014	0.0000	0.000
CON_f	-0.002	0.000	0.0000	0.000	0.0000	0.002
FHD	-0.009	0.000	0.0001	0.046	-0.0002	0.000
PLAND_r	-0.017	0.000	0.0000	0.000	0.0030	0.665
COca	-0.021	0.000	0.0000	0.019	0.0000	0.007
COsub	-0.039	0.000	0.0000	0.004	-0.0001	0.000
DCA2	-0.068	0.000	-0.0001	0.000	0.0000	0.000
COb	-0.083	0.000	0.0000	0.003	-0.0001	0.000

[1] Description of important environmental variables whose MIR>=0.1. DIST: nearest edge-to-edge distance from a sampling site to the source of immigrants; HEIGHT: maximum canopy height; PLAND_f: percentage of forest area; SDI: Shannon diversity index of tree species DBH>=5cm; DCA1: site scores of DCA1 based on tree species composition; DENt: density of trees DBH>=5cm; PD: patch density; BAs: mean basal area of snag DBH>=5cm.

[2] Calculated as the increase in mean squared error (MSE) after permuting the variable across all tree models. Permuting an irrelevant variable could possibly result in a slight decrease in MSE by chance, leading to a negative value of variable importance(Strobl et al. 2009). Therefore, I set MIR as zero (no importance) for the environmental variables with negative variable importance, and eliminated them from the subsequent model selection analysis.

Table 3.4. The best models for total species richness, richness ratio of forest specialists and abundance ratio of forest specialists based on RandomForest analysis. A series of models were iteratively developed using the explanatory variables for which Model Improvement Ratio (MIR) was above the given threshold (from 0.1 to 1.0 in 0.1 increments). The model with the smallest mean squared error (MSE) and largest variance explained was chosen as the best model (bold mark).

Response Variable	MIR threshold	Model[1]	Mean Squared Error	% Variance Explained
Total species richness				
	0.1	DIST+HEIGHT	5.522	11.05
	0.2	DIST+HEIGHT	5.522	11.05
	0.3	DIST+HEIGHT	5.522	11.05
	0.4	**DIST**	**5.198**	**16.27**
	0.5	DIST	5.198	16.27
	0.6	DIST	5.198	16.27
	0.7	DIST	5.198	16.27
	0.8	DIST	5.198	16.27
	0.9	DIST	5.198	16.27
Species ratio of forest specialist				
	0.1	**DIST+PLAND_f+HEIGHT+SDI**	**0.007**	**36.49**
	0.2	DIST+PLAND_f+HEIGHT+SDI	0.007	36.49
	0.3	DIST+PLAND_f	0.008	25.54
	0.4	DIST	0.011	0.00
	0.5	DIST	0.011	0.00
	0.6	DIST	0.011	0.00
	0.7	DIST	0.011	0.00
	0.8	DIST	0.011	0.00
	0.9	DIST	0.011	0.00
Abundance ratio of forest specialist				
	0.1	PLAND_f+DCA1+DENt+PLAND_r+PD+BAs	0.019	40.27
	0.2	**PLAND_f+DCA1+DENt+PLAND_r**	**0.015**	**52.26**
	0.3	PLAND_f+DCA1+DENt+PLAND_r	0.015	52.26
	0.4	PLAND_f+DCA1+DENt+PLAND_r	0.015	52.26
	0.5	PLAND_f+DCA1+DENt+PLAND_r	0.015	52.26
	0.6	PLAND_f+DCA1+DENt+PLAND_r	0.015	52.26
	0.7	PLAND_f+DCA1+DENt	0.016	49.59
	0.8	PLAND_f+DCA1	0.017	46.14
	0.9	PLAND_f	0.022	30.24

[1] Description of important environmental variables. DIST: nearest edge-to-edge distance from a sampling site to the source of immigrants; HEIGHT: maximum canopy height; PLAND_f: percentage of forest area; SDI: Shannon diversity index of tree species DBH>=5cm; DCA1: site scores of DCA1 based on tree species composition; DENt: density of trees DBH>=5cm; PD: patch density; BAs: mean basal area of snag DBH>=5cm.

Table 3.5. Results of multivariate forward selection for choosing important environmental variables. Presence/absence and abundance data sets were both used as response variables at the entire forest species, forest specialist and forest generalist assemblage levels. The number indicated adjusted R^2 for each selected variable. The p value of Monte Carlo permutation test for significant contribution (<0.1) of environmental variables to the variability explained in bird data sets was shown within the parentheses.

Scale	Selected Environmental Variables	Presence/Absence			Abundance		
		Entire species	Forest Specialist	Forest Generalist	Entire Species	Forest Specialist	Forest Generalist
Regional-scale:	DIST	0.1261 *(0.001)*	0.1442 *(0.001)*	0.07896 *(0.024)*	0.0785 (*0.026*)	0.0674 (*0.038*)	
	ELEV			0.0783 *(0.025)*	0.0448 (*0.081*)	0.0782 (*0.035*)	
Landscape-scale:							
Landscape Composition	PLAND_f	0.0821*(<0.001)*			0.0435 (*0.015*)		0.2559 (*<0.001*)
	PLAND_b			0.0488 *(0.061)*	0.0653 (*0.012*)	0.0801 (*0.008*)	0.0299 (*0.094*)
	PLAND_c				0.0310 (*0.049*)		0.0889 (*0.006*)
	PLAND_r			0.1841 (*0.001*)	0.2523 (*0.001*)	0.2501 (*0.002*)	0.0356 (*0.059*)
	PD			0.0425 (*0.083*)	0.0434 (*0.018*)		0.0624 (*0.013*)
Landscape Configuration	FRAC_all	0.0488 *(0.025)*	0.0463 *(0.029)*		0.1521 (*0.001*)	0.0475 (*0.047*)	0.1537 (*0.002*)
	ECON_all			0.0670 (*0.031*)	0.0704 (*0.011*)	0.0475 (*0.045*)	0.0707 (*0.019*)
	PROX_f						
	ENN_all			0.1494 (*0.003*)	0.0358 (*0.061*)	0.1505 (*0.003*)	0.0452 (*0.047*)
Local-scale:							
Floristic	DENt				0.0349 (*0.097*)		
	DENb						0.0635 (*0.046*)
	BAt_cv			0.0616 (*0.046*)			0.0521 (*0.052*)
	BAs	0.0305 *(0.061)*	0.0966 *(0.003)*				
	SDI	0.0891 *(0.002)*				0.1043 (*0.015*)	
	DCA1	0.0307 *(0.035)*		0.1170 (*0.004*)	0.1023 (*0.022*)	0.0790 (*0.033*)	0.1106 (*0.011*)
	DCA2		0.0351 *(0.057)*				
	VOL				0.0652 (*0.034*)	0.0540 (*0.044*)	
Physiognomy	COl	0.0858 *(0.003)*	0.1151 *(0.001)*				

Table 3.6. Percentage of variance explained by different components based on the combinations of the environmental variables at regional, landscape and local scales.

Component of variation	Presence/Absence			Abundance		
	Entire Species	Forest Specialist	Forest Generalist	Entire Species	Forest Specialist	Forest Generalist
(1) Pure regional-scale [R]	6.05%	4.45%	0.00%	0.62%	6.83%	0.00%
(2) Pure landscape-scale [L]	0.76%	2.20%	12.08%	30.39%	20.81%	41.52%
(3) Pure local-scale [V]	4.44%	6.81%	3.79%	3.64%	0.00%	12.09%
(4) Shared regional- and landscape-scale [RL]	0.91%	0.39%	8.04%	4.55%	0.00%	0.00%
(5) Shared landscape- and local-scale [LV]	4.72%	0.05%	5.55%	9.44%	12.81%	10.58%
(6) Shared regional- and local-scale [RV]	3.55%	7.59%	1.38%	1.03%	0.70%	0.00%
(7) Shared regional-, landscape- and local-scale [RLV]	2.08%	2.00%	7.12%	6.13%	10.80%	0.00%
(8) Unexplained [Res]	77.50%	76.52%	62.85%	44.21%	52.40%	35.81%
Total explained	22.50%	23.48%	37.15%	55.79%	47.60%	64.19%

Table 3.7. Percentage of variance explained by the first three Redundancy analysis (RDA) axes, and the correlation coefficients between environmental variables and the first three RDA axes.

Response variable	Selected environmental variable[1]	RDA1	RDA2	RDA3
Presence/absence	Percentage of variance explained	20.92%	9.83%	7.23%
	DIST	-0.827	0.462	0.048
	PLAND_f	0.650	0.313	0.603
	FRAC_all	-0.579	-0.039	-0.296
	SDI	0.718	0.273	-0.052
	DCA1	0.083	0.625	0.600
	BAs	0.613	0.401	-0.460
	COl	-0.723	0.083	0.360
Abundance	Percentage of variance explained	41.39%	15.68%	8.29%
	DIST	0.254	0.083	0.791
	ELEV	-0.351	-0.245	0.300
	PLAND_f	-0.824	-0.100	-0.042
	PLAND_c	0.014	-0.707	-0.298
	PLAND_b	0.317	-0.279	0.013
	PLAND_r	0.823	0.133	-0.003
	PD	0.308	-0.303	0.239
	ECON_all	-0.555	-0.121	0.486
	FRAC_all	0.658	0.139	0.039
	ENN_all	-0.609	0.337	0.012
	DENt	-0.444	0.386	0.243
	DCA1	-0.520	0.023	0.426
	VOL	-0.434	-0.072	-0.398

[1] Description of important environmental variables that have high correlation ($|r| > 0.7$) with the first three RDA axes. DIST: nearest edge-to-edge distance from a sampling site to the source of immigrants; SDI: Shannon diversity index of tree species DBH>=5cm; COl: coverage of litter; PLAND_f: percentage of forest area; PLAND_r: percentage of roads/buildings area.

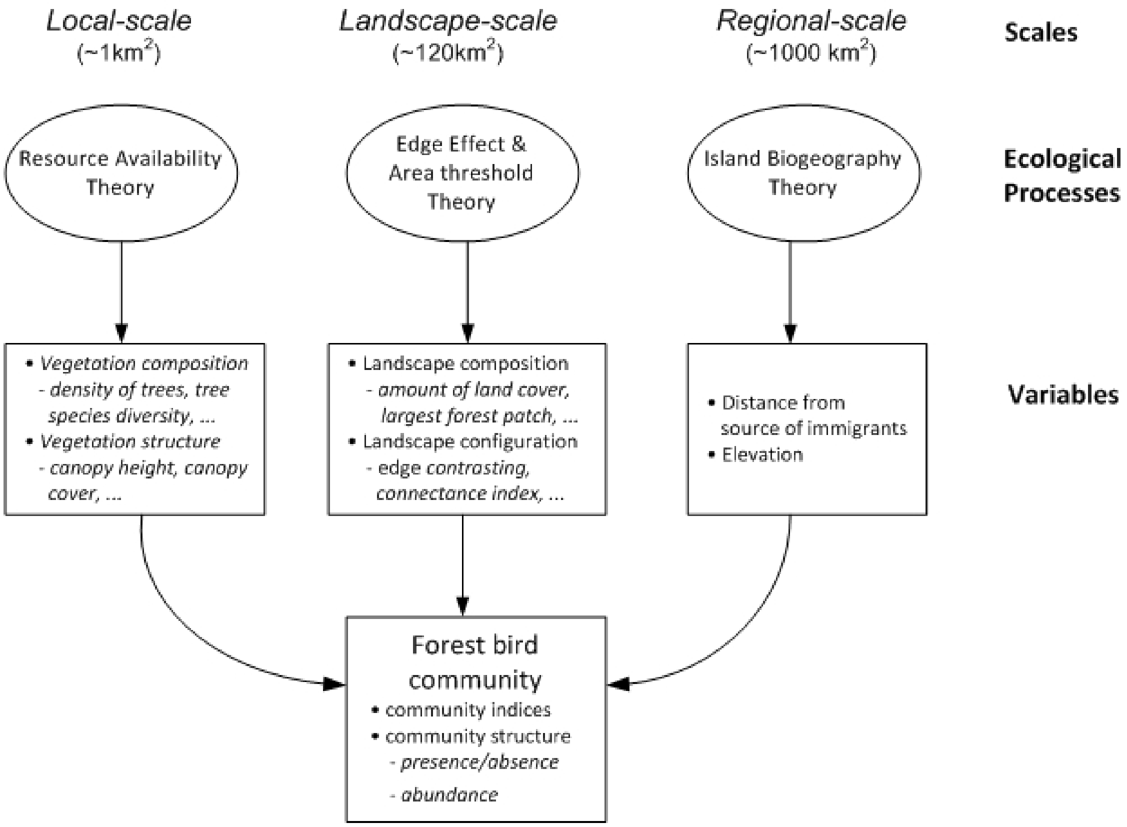


Figure 3.1. Multiscale conceptual model of the effects of forest fragmentation on community indices and composition of forest birds in fragmented lowland forest landscape of northern Taiwan.

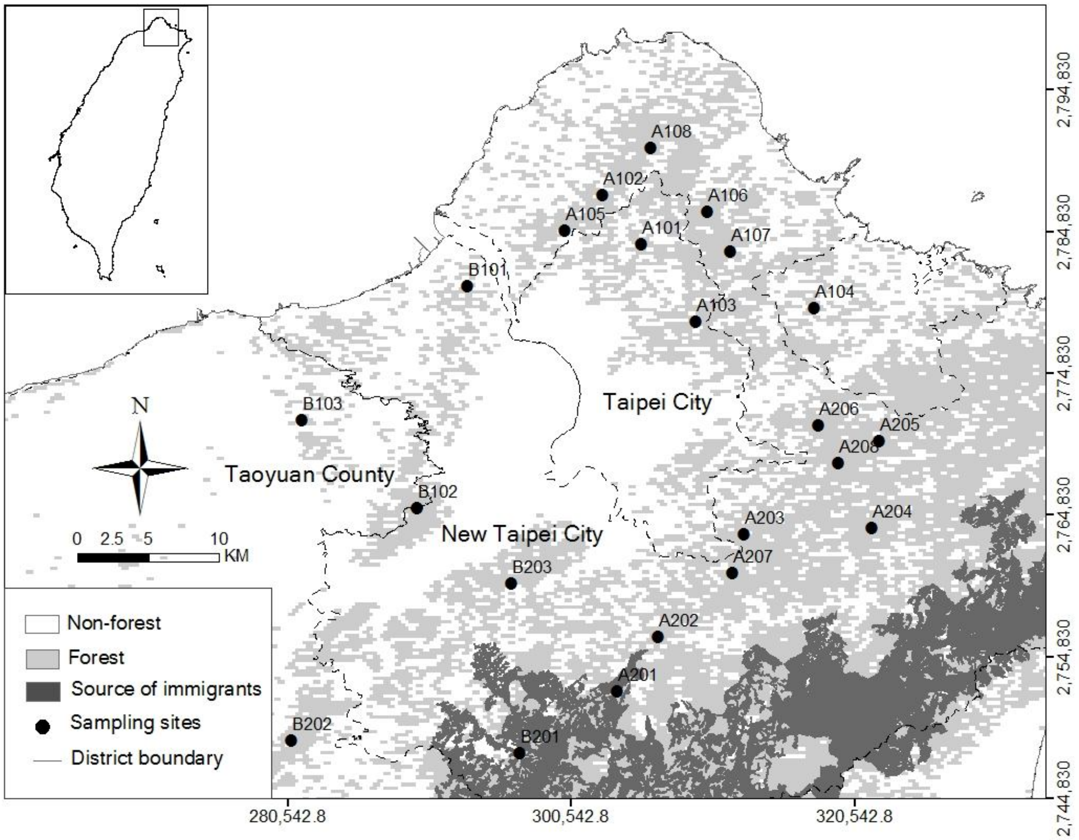
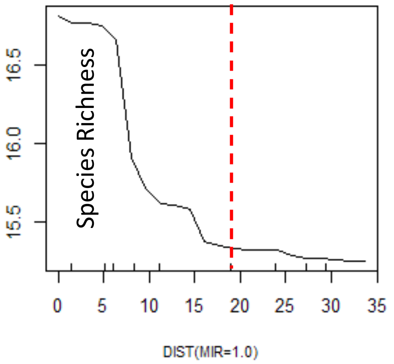


Figure 3.2. Map of study area. This study was conducted in northern Taiwan over an area 2,000 km^2. Dark dots represent the 1kmx1km sampling sites. Light gray refers to forest habitat, while white is non-forest habitat. The coordinate system shown in this map is Universal Transverse Mercator (UTM) system.

(a)



(b)

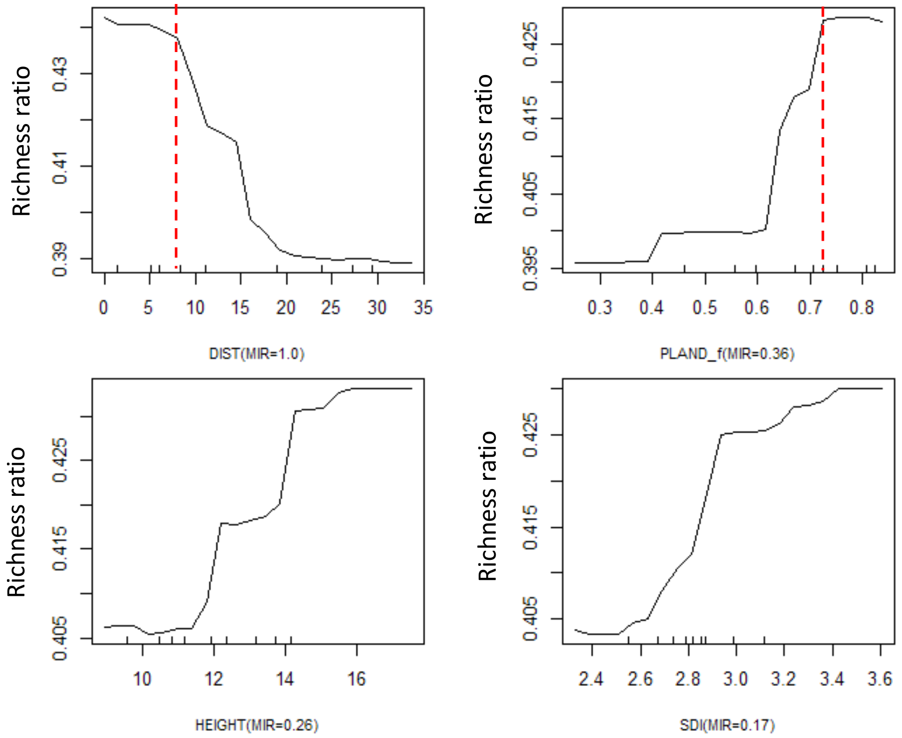


Figure 3.3. Smoothed partial plots for the critical environmental varibles for three community indices: (a) total species richness, (b) richness ratio of forest specialist species, and (c) abundance ratio of forest specialist species based on the RandomForest analyses. The dashed lines indicate the threshold value of the determinants for these indices.

(c)

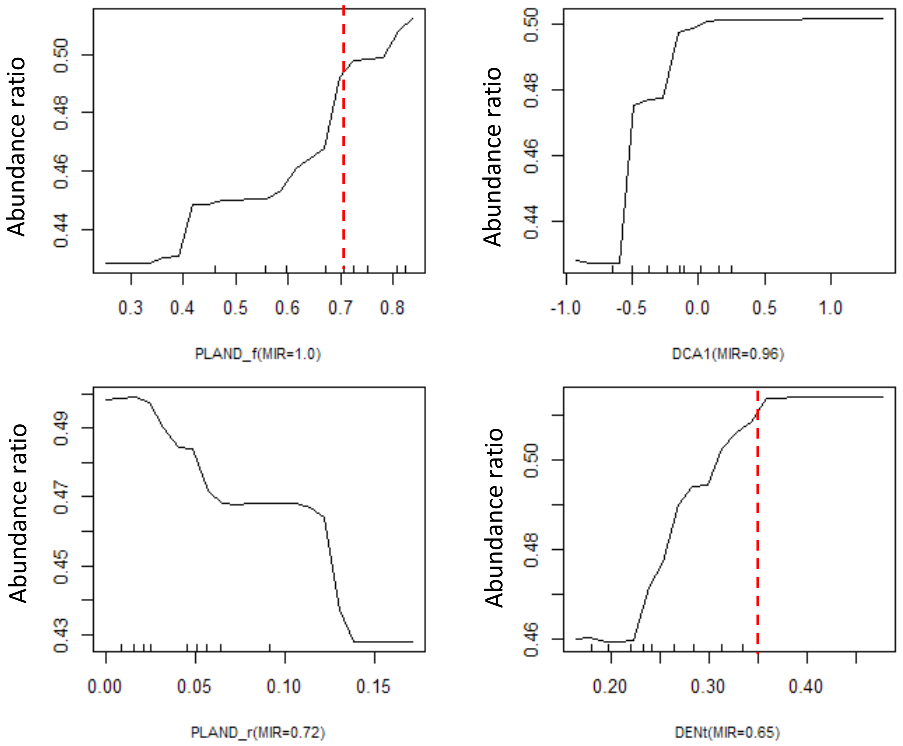


Figure 3.3. Continued.

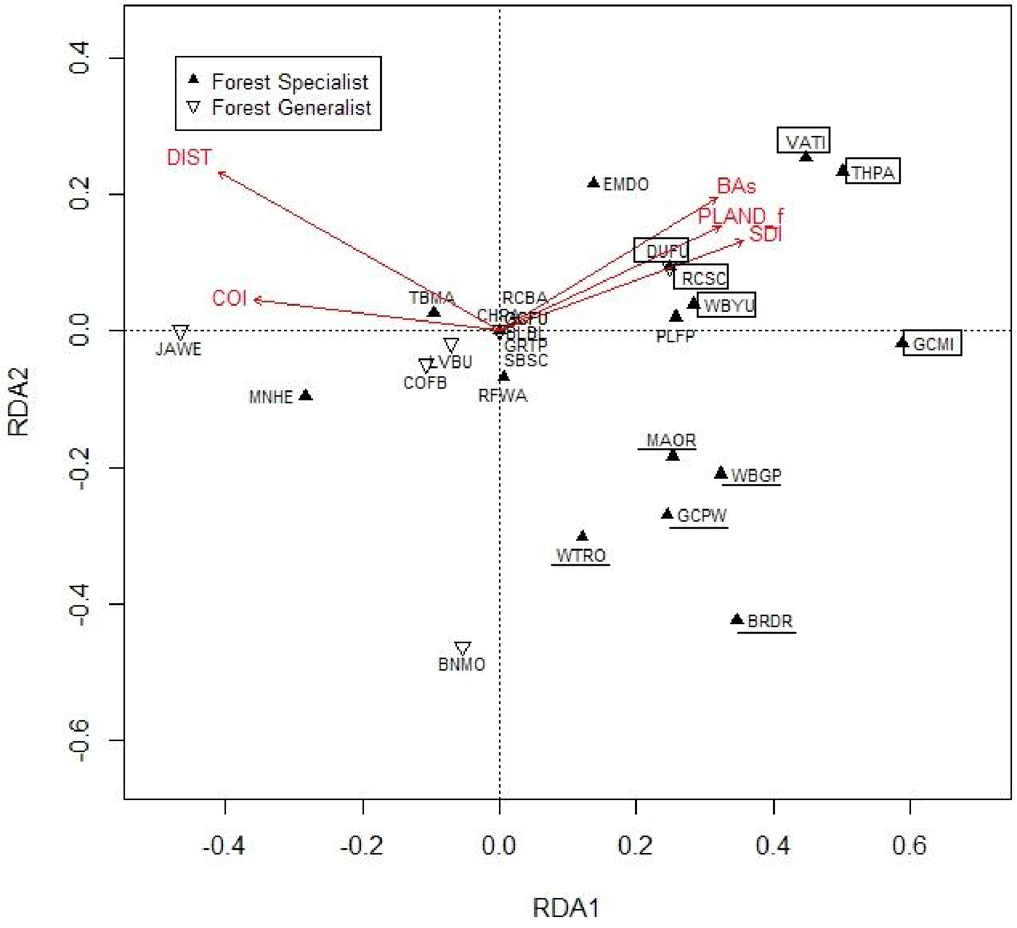


Figure3.4. Species–environment biplot for the presence/absence data set, based on a Redundancy analysis (RDA) method. Only environmental variables with significant permutation test (*P* <0.01)were shown. Underline indicate distance-sensitive species, while solid-line boxes are vegetation-sensitive species. See Appendix D for abbreviation of bird species.

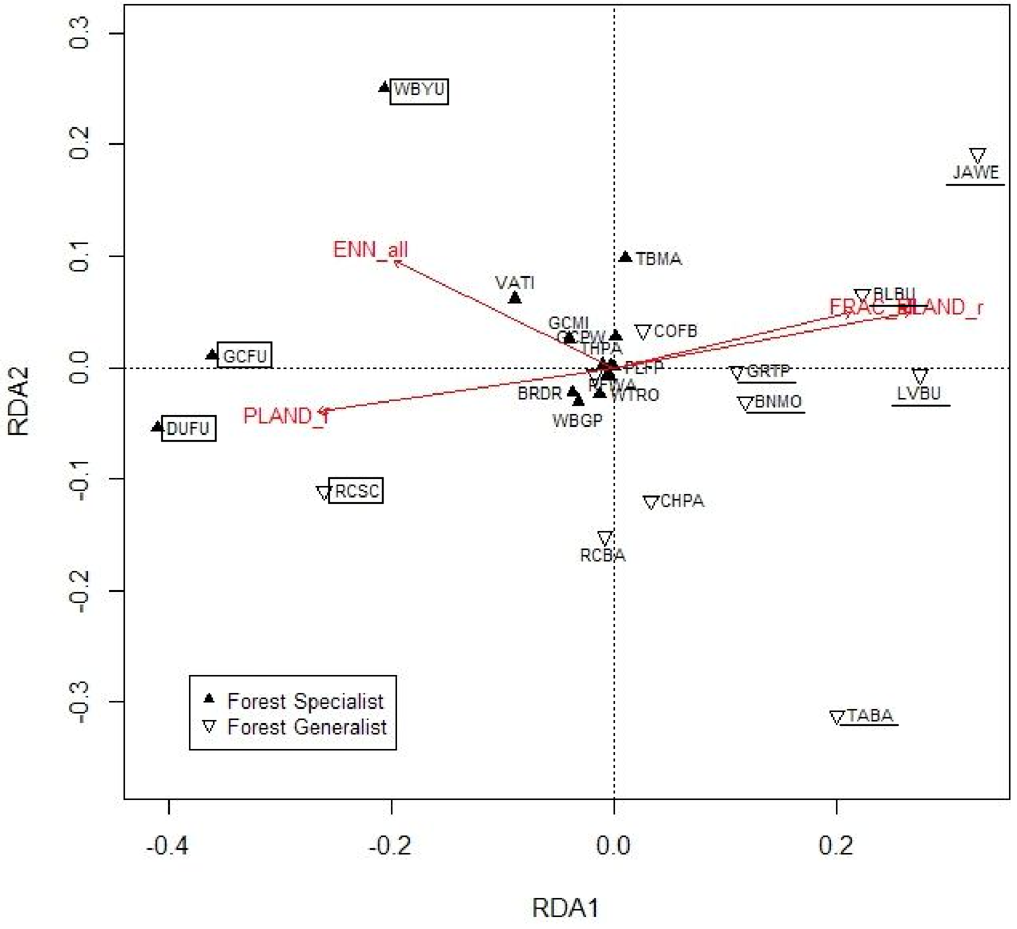


Figure3.5. Species–environment biplot for the abundance data set, based on a Redundancy analysis (RDA) method. Only environmental variables with significant permutation test (*P* <0.01)were shown. Underline indicate forest generalist specie that favor more fragmented and disturbed areas resulting from human-caused developments, while solid-line boxes are several common forest specialist species limited to locations with large amount of forest area. See Appendix D for abbreviation of bird species.

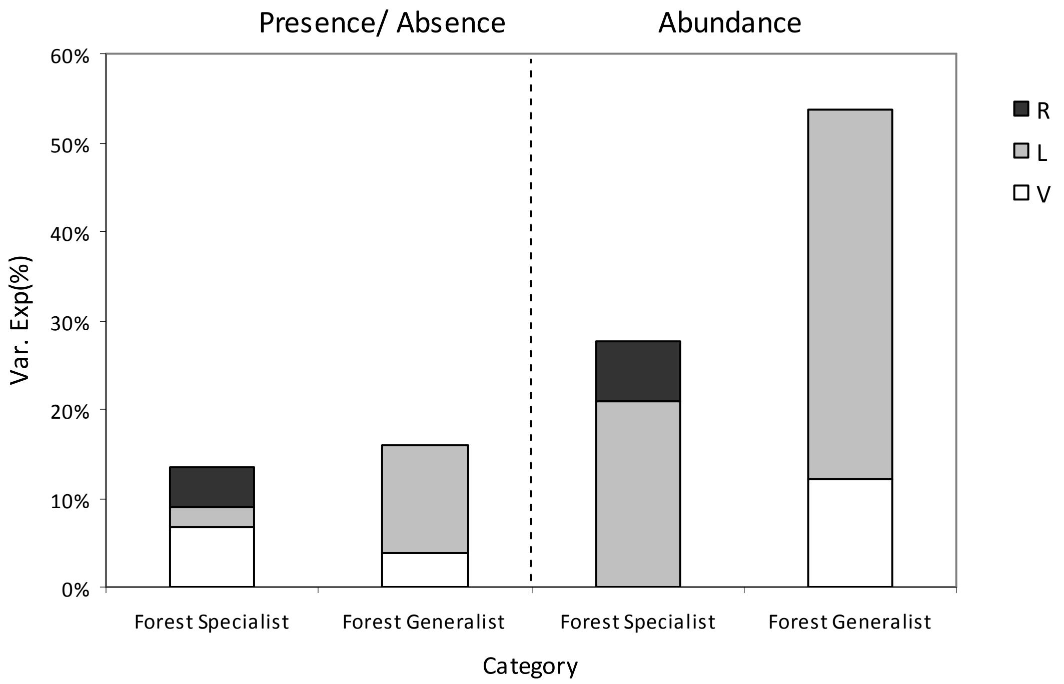


Figure 3.6. Results of variance partitioning for presence/absence and abundance data sets at forest specialist and generalist assemblages. (R: regional-scale, L: landscape-scale, V: local-scale variables)

CHAPTER 4. ECOLOGICAL TRAITS ASSOCIATED WITH THE VULNERABILITY OF FOREST BIRDS TO FOREST FRAGMENTATION

ABSTRACT

Understanding and predicting the associations between ecological traits and species vulnerability to habitat fragmentation could encourage ecologists to investigate mechanisms underlying effects of habitat fragmentation as well as provide crucial information for wildlife conservation. The aim of this study is to examine the trait-vulnerability relationship for lowland-forest birds in north Taiwan. The species vulnerable to fragmentation, and the ecological traits associated with species-specific vulnerability to fragmentation will be identified.

The responses of species to multiscale effects of forest fragmentation (regional-, landscape-, and local-scale) were quantified to represent their vulnerability to fragmentation. Two fragmentation vulnerability indices, V_p and V_a, were estimated for each species by using presence/absence and abundance data sets, respectively, as the species matrix in Redundancy Analysis. I evaluated nine ecological traits including habitat specialization, flight capacity, diet, foraging location, mixed-flocking behavior, nest type, nesting location, clutch size and body mass for all 27 bird species based on information from literature or measurement of museum specimens. RandomForest analysis was used to investigate the important ecological traits associated with species vulnerability to fragmentation.

The bird species analyzed in this study exhibited considerable variation among the two fragmentation vulnerability indices. However, there were seven species (*Pericrocotus solaris*, *Parus varius*, *Dicruru aeneus*, *Treron sieboldii*, *Erpornis zantholeuca*, *Alcippe brunnea* and *Pomatorhinus erythrogenys*) ranked in the top ten of vulnerable species based on each index. High vulnerability to fragmentation was associated most strongly with habitat specialization. Forest specialists tend to be absent or less abundant in fragmented landscapes than forest generalists. In addition to habitat specialization, foraging location of birds also has an effect on species prevalence in fragmented landscapes, while the vulnerability of species abundance to fragmentation is negatively associated with the flight capacity of species.

Keywords: ecological trait, fragmentation vulnerability index, forest fragmentation

INTRODUCTION

Species do not respond to habitat fragmentation in the same way. Certain species are adversely impacted by habitat fragmentation, and may go extinct from fragmented landscapes (Şekercioḡlu et al. 2002, Kirika et al. 2008). In contrast, some species benefit from habitat fragmentation and become prevalent in fragmented landscapes (Devictor et al. 2008). This may cause a decrease of global biodiversity as well as functional homogeneity due to the replacement of vulnerable species by species benefitted by fragmentation (Clavel et al. 2010). Accordingly, identifying species or species groups vulnerable to habitat fragmentation is critical for make conservation priority, especially when resources are limited.

Several reviews and meta-analyses have shown that the species-specific responses to habitat fragmentation were associated with the ecological traits of species of concern (Henle et al. 2004, Sodhi et al. 2004, Ockinger et al. 2010, Newbold et al. 2013). For example, habitat fragmentation appears to influence the persistence of some foraging guilds over others. Understory insectivores and larger frugivores are more extinction-prone in small habitat fragments because of their dietary specialization (Şekercioḡlu et al. 2002, Arriaga-Weiss et al. 2008, Sigel et al. 2010). In addition, species with specialized habitat requirements are more vulnerable to habitat fragmentation . Generally, specialists, sedentary species, insectivores, ground inhabitants and large-bodied species are less likely to occur and less abundant in fragmented habitats (Henle et al. 2004, Sodhi et al. 2004). The analysis of ecological traits associated with species vulnerability to habitat fragmentation could assist in developing a more mechanistic understanding of community ecology as well as identification of functional groups sensitive to fragmentation to be targeted for conservation concern (Kleyer et al. 2012).

The aim of this study was to examine the association between ecological traits and species vulnerability to forest fragmentation for lowland-forest birds in north Taiwan. I expected to: (1)

identify the species vulnerable to fragmentation; and (2) determine the ecological traits associated with species-specific vulnerability to fragmentation. The vulnerability of species to habitat fragmentation could be estimated by a variety of approaches. Patch occupancy (Wang et al. 2009) and ratio of species abundance in fragments to unfragmented controls (Davies et al. 2000) are commonly used to quantify the vulnerability to fragmentation. Patch occupancy could be biased if species-specific characteristics are not accounted for (Thornton et al. 2010). Rare or patchily-distributed species may be categorized as more vulnerable to fragmentation than abundant or evenly distributed species due to their presence in fewer fragments, although they maybe not really sensitive to habitat fragmentation.

Furthermore, these patch-based approaches may make it difficult to quantitatively investigate the relationships between the degree of habitat fragmentation and the magnitude of responses of organisms (Fahrig 2003). For example, the comparison of the species' abundance in habitat fragments and unfragmented controls can show the extinction proneness of species within a fragmented landscape. However, this approach doesn't allow ecologists to identify the causal environmental characteristics (e.g. area or edge effect) and the strength of the effects on organisms of concern, which is critical information for habitat-based conservation management. In this study, a multivariate method was used to quantify the responses of forest birds to influential environmental gradients within a fragmented landscape to represent their vulnerability to forest fragmentation.

METHODS

Study area

This study was conducted in northern Taiwan over an area of approximately 2,000 km^2. The study arealies between 24°00' N-25° 18' N and 120° 27' E-122° 00' E (Fig. 3.2). The average temperature and precipitation range from 16.7-23.0°C and 1283.0-4892.4 mm, respectively (Taiwan Central Weather Bureau, http://www.cwb.gov.tw/eng/index.htm). The major climate type in the study area is the summer rain climate(Su 1985), that is, precipitation is heaviest during summer but rain falls year-round. The elevation on the study area ranges from 0 to around 1,000 m, and the subtropical *Machilus-Castanopsis* forest is the primary vegetation type (Su 1992).

This area was once primarily covered by pristine forests in the seventeenth century (Keliher 2003); however, the combination of intensive agricultural developments and increasing human population has resulted in severe lowland forest loss. The majority of lowland forest was converted to orchards, tobacco or tea plantations, paddy fields, pastures and urban areas. Currently, the lowland forests remaining on hills or mountains within our study area are almost all secondary forests regenerated from abandoned agricultural lands or forestry plantations over the last century. Only a minority of lowland forests near the central mountain ridge (east side of the study area) remain pristine. Other lowland forests are severely fragmented, surrounded by agricultural lands and cities.

Ecological traits of species

Information on nine ecological traits was collected for all 27evaluated bird species from the literature or by measurement of museum specimens. I considered habitat specialization, flight capacity, diet, foraging location, mixed-flocking behavior, nest type, nesting location, clutch size and body mass (Table 4.1). These ecological traits were selected because they are commonly hypothesized to influence vulnerability to habitat fragmentation for birds based on ecological mechanisms such as niche specialization (Devictor et al. 2008, Hinsley et al. 2009), foraging habits (Sodhi et al. 2004, Arriaga-Weiss et al. 2008), nest predation risk (Newmark and Stanley 2011)and dispersal limitation(Lens et al. 2002, Şekercioḡlu et al. 2002).

Each species was exclusively assigned to forest specialists or forest generalists based on their forest dependency by following Lin (2010). Generally, forest specialists rely more on forest habitats than forest generalists (mean occurrence in forest habitats = 88.48% and 62.2% respectively), while the majority of forest generalists also can usea variety of non-forest habitats such as orchards or urbanized areas. Diet and foraging location data were derived fromShiu (2003) and modified based on my field observations. I assigned each species to one of three diet (herbivores, insectivores and omnivores) and foraging groups (species feed on ground, shrub and canopy). Data on nest type, nesting location and clutch size, mixed-flocking behavior were based on Liu et al. (2010). Clutch sizes published as a range in Liu et al. (2010) was averaged in this study. However, the clutch size of Grey-chinned Minivet (*Pericrocotus solaris*) andChinese Bamboo Partridge (*Bambusicola thoracicus*) used in this study were from (Yao 2008). Finally, body mass data were taken from Nieh (1999).

Wing morphology is a good indicator of flight capacity for bird species (Monkkonen 1995, Egbert and Belthoff 2003). Wing morphology of 342 bird specimens from the National Museum of Nature Science, Research Museum at Academia Sinica and Museum of Zoology at National Taiwan University were measured. I measured the distance from the carpal joint (wrist) of the right wing to the distal end of the outermost secondary feather (a) and wing tip (b), respectively(Fig. E1, Appendix E). Then wing aspect ratio, known as b/a was calculated to represent the flight capacity of birds. Left wings were measured when right wings were damaged or absent from the specimen (n=33). Every specimen was measured twice and then averaged to reduce the measurement error (Table E1, Appendix E). The wing data of White-tailed Robin (*Cinclidium leucurum*) were from the project Monitoring Avian Productivity and Survival in Taiwan (MAPS Taiwan) because of a lack of specimen sources.

Vulnerability to fragmentation

The responses of species to multiscale effects of forest fragmentation were quantified to represent their vulnerability to fragmentation in this study. To achieve this goal, I applied Redundancy Analysis (RDA) to estimate the species scores along the environmental gradients within the fragmented forest landscape in the study area to represent species vulnerability to fragmentation. RDA was chosen because a preliminary Detrended Correspondence Analysis (DCA) showed the gradient length of the first axis was less than 2 standardized deviation, indicating a somewhat linear relationship between bird species and environmental variations (Lepš and Šmilauer 2003). Details on the collection of bird data and environmental metrics were described in the Methods section in Chapter 3.

Two fragmentation vulnerability indices, V_p and V_a, were calculated for each species by using presence/absence and abundance data sets as the species matrix in RDA. Abundance data were Hellinger transformed (Legendre and Gallagher 2001) into relative abundance prior to analyses. Before data analyses, I log-transformed all environmental variables to improve their normality. A multivariate forward selection procedure (Blanchet et al. 2008)was used to select important environmental variables for the subsequent analysis (see the description in the Method section in Chapter 3 for details). The environmental vectors were projected onto the RDA ordination, and their significance was assessed by random permutations. The fitted environmental variable was considered significant if the squared correlation coefficient (r^2) was higher for the observed data than the permuted one (Oksanen et al. 2012).The forward selection procedure and RDA analysis were performed using the R package 'packfor' and 'vegan,' respectively.

Data analysis

First, simple regressions were developed to preliminarily explore the associations between species vulnerability to fragmentation and individual ecological traits. Dummy coding was used to create k-1 dichotomous variables that contained the information of a categorical variable with k levels in the R environment (R Development Core Team 2005).

Furthermore, I implemented RandomForest analysis (RF) to examine the relative importance of determinants at different scales. Similar to the concept of Classification and Regression Tree (CART) (De'ath and Fabricius 2000), RF analysis repeatedly split the response variable into two exclusive homogeneous groups by a single critical variable selected from a subset of randomly chosen explanatory variables. The homogeneity of group is evaluated by the Shannon-Weiner diversity index or Gini index for categorical response variables, and sum of squares about the within-group mean for numeric response variables. RF, however, bootstraps the samples to construct a series of tree models instead of just one. The unique characteristics of bootstrapping and randomization make RF able to handle small sample sizes with relative larger numbers of explanatory variables and is robust against overfitting (Breiman 2001). The correlations between ecological traits were tested. Traits with significant correlations ($P<0.01$) were eliminated from the subsequent analysis when a pair had a high correlation. I retained the ecological trait that was more commonly recognized to associate with the vulnerability to habitat fragmentation for forest birds.

I followed Murphy et al. (2010) to decide which ecological traits were influential in determining the vulnerability of species to fragmentation. As an output from RF, variable importance (I) of individual explanatory variable was calculated as the averaged increase of mean squared error (MSE) after permuting this variable over all regression tree models. If a explanatory variable is strongly associated with the response variable, random permutation would break the association and increase MSE. Then a model improvement ratio (MIR) was defined as I/ Imax for each explanatory variable for comparison. Higher MIR indicated more important explanatory variables. I then iteratively developed a series of models using the explanatory variables for which MIR was above the given threshold (from 0.1 to 1.0 in 0.1 increments). The model with the smallest MSE and largest variance explained was chosen as the best model. RandomForest analysis was implemented with the R package 'randomForest.'

RESULTS

Species vulnerability to fragmentation

The first RDA axis alone explained about 21% and 41% variability in presence/absence and abundance of birds respectively (Table 4.2), which was more than half of the total variation explained by the first three axes. Therefore, species scores along the RDA1 axis were used to represent species vulnerability to fragmentation. For presence/absence data, the regional-scale variable DIST and the local-scale variables SDI (*r*=-0.827 and 0.718 respectively, Table 4.2) were highly correlated to the RDA1 axis. That is, the location of species along the RDA1 axis primarily followed the gradient of distance from the source of immigrants and local tree diversity(Fig. 4.1). Accordingly, species with higher fragmentation vulnerability index (Vp) tend to occur at locations with higher tree diversity and close to the source patch. For the abundance data set, two landscape-scale variables, percentage of forest (PLAND_f) and roads/buildings (PLAND_r) showed high correlations to the first RDA1 axis (*r*=-0.824 and 0.823, respectively,

Table 4.2). Species with lower RDA1 score were more abundant at locations with higher proportion of forest and less human disturbance (Fig. 4.2). In order to avoid confusion, I multiplied the original RDA1 score by -1 to represent the fragmentation vulnerability index of species for the abundance data set (Va), with higher values representing greater vulnerability.

The 27 bird species analyzed in this study exhibited considerable variation among these two fragmentation vulnerability indices (Table 4.3). However, there were several species that showed consistency. For example, seven species, (Grey-chinned Minivet, Varied Tit (*Parus varius*), Bronzed Drongo (*Dicruru saeneus*), White-bellied Pigeon (*Treronsi eboldii*),White-bellied Yuhina (*Erporniszan tholeuca*),Dusky Fulvetta (*Alcippe brunnea*)and Rusty-cheeked Scimitar Babbler (*Pomatorhinus erythrogenys*)) were both ranked in the top ten of vulnerable species based on these two fragmentation vulnerability indices. In addition, Japanese White-eye (*Zosterops japonicus*) showed the least vulnerability to forest fragmentation for both. Notably, Vp has limited power to distinguish species that showed moderate vulnerability to fragmentation (vulnerability rank=15). They all have the same value of Vp.

Ecological traits associated with species vulnerability to fragmentation

Habitat specialization of species was significantly associated both with vulnerability Vp ($F_{1,26}$=8.461, *P*=0.007, Fig. 4.3) and Va ($F_{1,26}$=8.606, *P*=0.007, Fig. 4.4). Forest specialists were more sensitive to forest fragmentation than forest generalists. For abundance data, there was also some evidence of association between the species vulnerability to fragmentation and foraging location and diet of birds based on *p* values (*P*=0.052 and *P*=0.066, Fig. 4.4). Three ecological traits, nest type, nesting location and mixed-flocking behavior, were significantly associated with other ecological traits (*P*<0.01, Table 4.4). These variables were eliminated from the subsequent analysis.

Habitat specialization was the most important trait to determine species vulnerability to fragmentation based on the variable importance (Table 4.5). The best model including habitat specialization and foraging location explained the largest amount of variability in the vulnerability index Vp (16.96%, Table 4.6). Forest specialists that forage on the ground or canopy were more vulnerable to fragmentation (Fig. 4.5a). For the vulnerability index Va, the combination of habitat specialization and flight capacity could explained the largest amount of variability (38.71%, Table 4.6). Forest fragmentation was more influential to forest specialists than forest generalists (Fig. 4.5b). Furthermore, species with lower flight capacity were more sensitive to fragmentation. The relationship between the vulnerability index Va and flight capacity of birds was non-linear.

DISCUSSION

For the bird species studied in a fragmented forest landscape in northern Taiwan, high vulnerability to fragmentation was associated most strongly with habitat specialization. Forest specialists tend to be absent or less abundant in fragmented landscapes than forest generalists. In addition to habitat specialization, foraging location of birds also had an effect on species presence in fragmentation landscapes, while sensitivity based on abundance of species was positively associated with their flight capacity.

In this study, species categorized as the most vulnerable species to forest fragmentation based on both their presence and abundance are forest specialists, except Rusty-cheeked Scimitar Babbler. The fact that habitat specialists are more vulnerable to habitat fragmentation than habitat generalists has been reported in the literature (Devictor et al. 2008). The narrow habitat requirements of habitat specialists make them very sensitive to the shrinking of suitable habitat

(Andrén 1996). These species usually have lower abundance in small habitat fragments compared to the large continuous control sites. In addition, the behavioral resistance of habitat specialists to crossing unfavorable matrix may limit their inter-patch movement (Desrochers and Hannon 1997, Gobeil and Villard 2002). This dispersal limitation could reduce the rescue effect (Brown and Kodric-Brown 1977), influencing their persistence in a fragmented landscape (Şekercioḡlu et al. 2002). Therefore, habitat specialists tend to disappear faster from fragments, and show less prevalence than habitat generalists in severely fragmented landscapes.

Foraging location was also associated with the presence of species in fragmented landscapes in this study. Ground and canopy foragers are more vulnerable to fragmentation than shrub foragers. One possible explanation for the vulnerability of ground foragers to fragmentation is their intolerance of unstable microhabitat (Stratford and Robinson 2005). In this study, two ground insectivores, the (Dusky Fulvetta and Rusty-cheeked Scimitar Babbler that showed high vulnerability to fragmentation prefer dense and moist understory of forests (Liu et al. 2010). The microhabitat (e.g. temperature and moisture) is relatively stable in the understory of dense tropical forests compared to temperate forests. Stratford and Robinson (2005) pointed out that birds inhabiting the understory of tropical forests have evolved to adapt to a stable microhabitat, and may be less physiologically tolerant to microhabitat change caused by forest fragmentation.

Dispersal plays a key role in population dynamics in a fragmented landscape (Hanski and Gilpin 1991). Immigrants could reduce extinction rate of local population in a habitat fragment by their demographic or genetic contributions (Brown and Kodric-Brown 1977), influencing population persistence within a fragmented landscape. Species with low dispersal capacity are more vulnerable to habitat fragmentation than mobile species (Lens et al. 2002, Henle et al. 2004, Ockinger et al. 2010). In this study, flight capacity, an ecological trait linked to dispersal ability, did not show a significant association with species-specific vulnerability to fragmentation alone (Fig. 4.4). The combination of habitat specialization and flight capacity, however, explained the largest amount of variation in bird abundance within the fragmented landscape in the study area. It is possible that the relationship between dispersal capacity and vulnerability to fragmentation is non-linear. Furthermore, dispersal success of species within a fragmented landscape depends on not only their flight capacity, but also their behavioral responses to an unfavorable matrix. For example, Van Houtan et al. (2007) who analyzed capture-recapture data of birds in Brazil reported that species that disappeared from small fragments largely reduced their dispersal distance after forest fragmentation. These species, however, were good dispersers before fragmentation, implying that not mobility *per se* but the change of mobility resulting from their responses to deforested gaps determine their persistence in a fragmented landscape.

The findings from this study provide several conservation implications. First, fragmentation vulnerability indices evaluated at occurrence (Vp) and population levels (Va) can provide information for goal-oriented conservation management. For example, if the conservation goal is to increase or sustain lowland-forest avian biodiversity, species such as the Grey-cheeked Minivet, Taiwan Partridge, and Bronzed Drongo should be considered as conservation priorities. Regional-scale connectivity as well as local forest quality should be enhanced to allow these vulnerable species to dispersal and establish their populations in fragmented landscapes. In addition, it is notable that the top five species vulnerable to forest fragmentation at a population level are common forest birds in the lowland forest of Taiwan, except *Parus varius*. They occurred at > 80% of the sampling units in the study area. The vulnerability of these species populations to fragmentation could possibly be underestimated because of their prevalence. For example, although *Alcippe morrisonia* occurred at all sampling sites in the study area, they are more abundant at locations where the proportion of forest cover is high and less fragmented. The loss of forest cover and an increase of isolation could have adverse effects on their local populations. Accordingly, it is critical to maintain high proportion of forest cover in a fragmented landscape to secure the population persistence of these species.

Finally, the influential ecological traits associated with species vulnerability to fragmentation slightly vary with different fragmentation vulnerability indices. Habitat specialization, however, is strongly associated with species vulnerability to fragmentation regardless of the type of vulnerability index. The finding supports the global decline of specialist species because of habitat degradation (Clavel et al. 2010). There are several forest specialists whose occurrence and population are both vulnerable to fragmentation should be concerned. These species could possibly be used as indicator species that serve as an early warning indicator of environmental changes or use to monitor the effectiveness of conservation managements(Lindenmayer et al. 2000).

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Table 4.1. Nine ecological traits used in this study were collected for all 27 bird species from literature or measurement of museum specimens.

Variable	Variable Type	Description	Mean	S.D.
h_spec	Category	Habitat specialization. Forest specialists or forest generalists	—	—
diet	Category	Diet. Insectivore, omnivore or herbivore	—	—
loc_F	Category	Foraging location. Ground, brush or above brush	—	—
loc_N	Category	Nesting location. Ground, brush or above brush	—	—
type_N	Category	Nesting type. Open-cup nests, disk-like nests or cavity	—	—
clutch.size	Numeric	Average number of eggs laid in each clutch	3.57	1.06
flight capacity	Numeric	Average wing aspect ratio	1.24	0.14
weight	Numeric	Average body weight (g)	82.26	109.37
mflock	Category	Mixed foraging flock behavior either in breeding or non-breeding seasons. Yes or no	—	—

Table 4.2. Percentage of variance explained by the first three Redundancy analysis (RDA) axes and the correlation coefficients between environmental variables and the first three RDA axes.

Species matrix	Selected environmental variables[1]	RDA1	RDA2	RDA3
Presence/absence	Perecntage of variance explained	20.92%	9.83%	7.23%
	DIST	-0.827	0.462	0.048
	PLAND_f	0.650	0.313	0.603
	FRAC_all	-0.579	-0.039	-0.296
	SDI	0.718	0.273	-0.052
	DCA1	0.083	0.625	0.600
	BAs	0.613	0.401	-0.460
	COl	-0.723	0.083	0.360
Abundance	Perecntage of variance explained	41.39%	15.68%	8.29%
	DIST	0.254	0.083	0.791
	ELEV	-0.351	-0.245	0.3
	PLAND_f	-0.824	-0.1	-0.042
	PLAND_c	0.014	-0.707	-0.298
	PLAND_b	0.317	-0.279	0.013
	PLAND_r	0.823	0.133	-0.003
	PD	0.308	-0.303	0.239
	ECON_all	-0.555	-0.121	0.486
	FRAC_all	0.658	0.139	0.039
	ENN_all	-0.609	0.337	0.012
	DENt	-0.444	0.386	0.243
	DCA1	-0.520	0.023	0.426
	VOL	-0.434	-0.072	-0.398

[1] Description of important environmental variables that have high correlation ($|r| > 0.7$) with the first three RDA axes. DIST: nearest edge-to-edge distance from a sampling site to the source of immigrants; SDI: Shannon diversity index of tree species DBH>=5cm; COl: coverage of litter; PLAND_f: percentage of forest area; PLAND_r: percentage of roads/buildings area.

Table 4.3.Two vulnerability indices to fragmentation (Vp and Va) were estimated based on the species scores along the first axis of Redundancy Analysis (RDA) by using presence/absence and abundance data of birds, respectively. The original fragmentation vulnerability indices were transformed into a ranking for comparison. Lower ranking refers to relatively higher vulnerability to fragmentation.

Scientific name	Presence/absence		Abundance	
	Vulnerability index (Vp)	Vulnerability Rank	Vulnerability index (Va)	Vulnerability Rank
Pericrocotussolaris	0.5879	1	0.0405	6
Arborophilacrudigularis	0.5008	2	0.0108	11
Parusvarius	0.4482	3	0.0888	5
Dicrurusaeneus	0.3469	4	0.0369	7
Treronsieboldii	0.3241	5	0.0323	8
Erporniszantholeuca	0.2837	6	0.2061	4
Dicaeumminullum	0.2585	7	-0.0004	17
Oriolustraillii	0.2538	8	0.0062	13
Alcippebrunnea	0.2482	9	0.4101	1
Pomatorhinuserythrogenys	0.2482	10	0.2601	3
Dendrocoposcanicapillus	0.2449	11	-0.0017	18
Chalcophapsindica	0.1372	12	0.0029	15
Myiomelaleucura	0.1209	13	0.0126	10
Abroscopusalbogularis	0.0060	14	-0.0004	16
Alcippemorrisonia	0.0000	15	0.3607	2
Pomatorhinusruficollis	0.0000	15	0.0170	9
Stachyrisruficeps	0.0000	15	0.0081	12
Dendrocittaformosae	0.0000	15	-0.1100	22
Hypsipetesleucocephalus	0.0000	15	-0.2230	25
Megalaimanuchalis	0.0000	15	-0.2004	24
Bambusicolathoracicus	0.0000	15	-0.0325	21
Hypothymisazurea	-0.0537	16	-0.1174	23
Pycnonotussinensis	-0.0714	17	-0.2747	26
Urocissacaerulea	-0.0970	18	-0.0098	19
Spizixossemitorques	-0.1068	19	-0.0258	20
Gorsachiusmelanolophus	-0.2836	20	0.0035	14
Zosteropsjaponicus	-0.4669	21	-0.3257	27

Table 4.4.Significance of relationships between ecological traits (*P* value). Chi-square was used to test the associations between six categorical ecological traits (h_spec, diet,loc_F, type_N, loc_N and mflock). Relationships between categorical and continuous variables, and correlations between three continuous variables (flight capacity, clutch.size and weight) were tested by one-way ANOVA and Pearson's correlation test respectively.

Variable	h_spec	diet	loc_F	type_N	loc_N	mflock	clutch.size	flight capacity	weight
h_spec									
diet	0.275								
loc_F	0.438	0.115							
type_N	0.407	0.004	0.064						
loc_N	0.076	0.413	0.003	0.049					
mflock	1.000	0.103	0.003	0.050	0.329				
clutch.size	0.779	0.442	0.889	0.042	0.300	0.645			
flight capacity	0.023	0.788	0.115	0.127	<0.001	0.487	0.845		
weight	0.470	0.024	0.029	<0.001	0.312	0.009	0.643	0.309	

Table 4.5. Variable importance (*I*) from RandomForest analysis and model improvement ratio (MIR) for two vulnerability indices. Model improvement ratio was defined as I/ Imax for each explanatory variable.

Response variable	Explanatory variable	Variance Importance (I)*	Model Improvement Ratio (MIR)
Vulnerability Index Vp	h_spec	0.0149	1.0000
	flight capacity	0.0020	0.1332
	loc_F	0.0002	0.0148
	diet	0.0001	0.0066
	weight	-0.0013	0.0000
	clutch.size	-0.0020	0.0000
Vulnerability Index Va	h_spec	0.0082	1.0000
	flight capacity	0.0044	0.5354
	loc_F	0.0017	0.2017
	diet	0.0016	0.2003
	weight	0.0011	0.1364
	clutch.size	-0.0005	0.0000

* Calculated as the increase in mean squared error (MSE) after permuting the variable across all tree models. Permuting an irrelevant variable could possibly result in a slight decrease in MSE by chance, leading to a negative value of variable importance(Strobl et al. 2009). Therefore, I set MIR as zero (no importance) for the environmental variables with negative variable importance, and eliminated them from the subsequent model selection analysis.

Table 4.6. The best models based on RandomForest analysis. A series of models were iteratively developed using the explanatory variables for which normalized variable importance was above the given threshold (from 0.1 to 1.0 in 0.1 increments). The model with the smallest mean squared error (MSE) and largest variance explained was chosen as the best model (bold).

Response variable	Threshold	Model	MSE	% variance explained
Vulnerability Index Vp	>0.0	h_spec+ loc_F+mobility+diet	0.0507	5.24%
	>0.1	**h_spec+ loc_F**	**0.0444**	**16.96%**
	> 0.2	h_spec	0.0464	13.29%
	> 0.3	h_spec	0.0464	13.29%
	> 0.4	h_spec	0.0464	13.29%
	> 0.5	h_spec	0.0464	13.29%
	> 0.6	h_spec	0.0464	13.29%
	> 0.7	h_spec	0.0464	13.29%
	> 0.8	h_spec	0.0464	13.29%
	> 0.9	h_spec	0.0464	13.29%
Vulnerability Index Va	>0.0	h_spec+mobility+loc_F+diet+weight	0.0190	28.71%
	>0.1	h_spec+mobility+loc_F+diet+weight	0.0187	29.67%
	> 0.2	h_spec+mobility+loc_F+diet	0.0182	31.52%
	> 0.3	**h_spec+mobility**	**0.0163**	**38.71%**
	> 0.4	h_spec+mobility	0.0163	38.71%
	> 0.5	h_spec+mobility	0.0163	38.71%
	> 0.6	h_spec	0.0233	12.56%
	> 0.7	h_spec	0.0233	12.56%
	> 0.8	h_spec	0.0233	12.56%
	> 0.9	h_spec	0.0233	12.56%

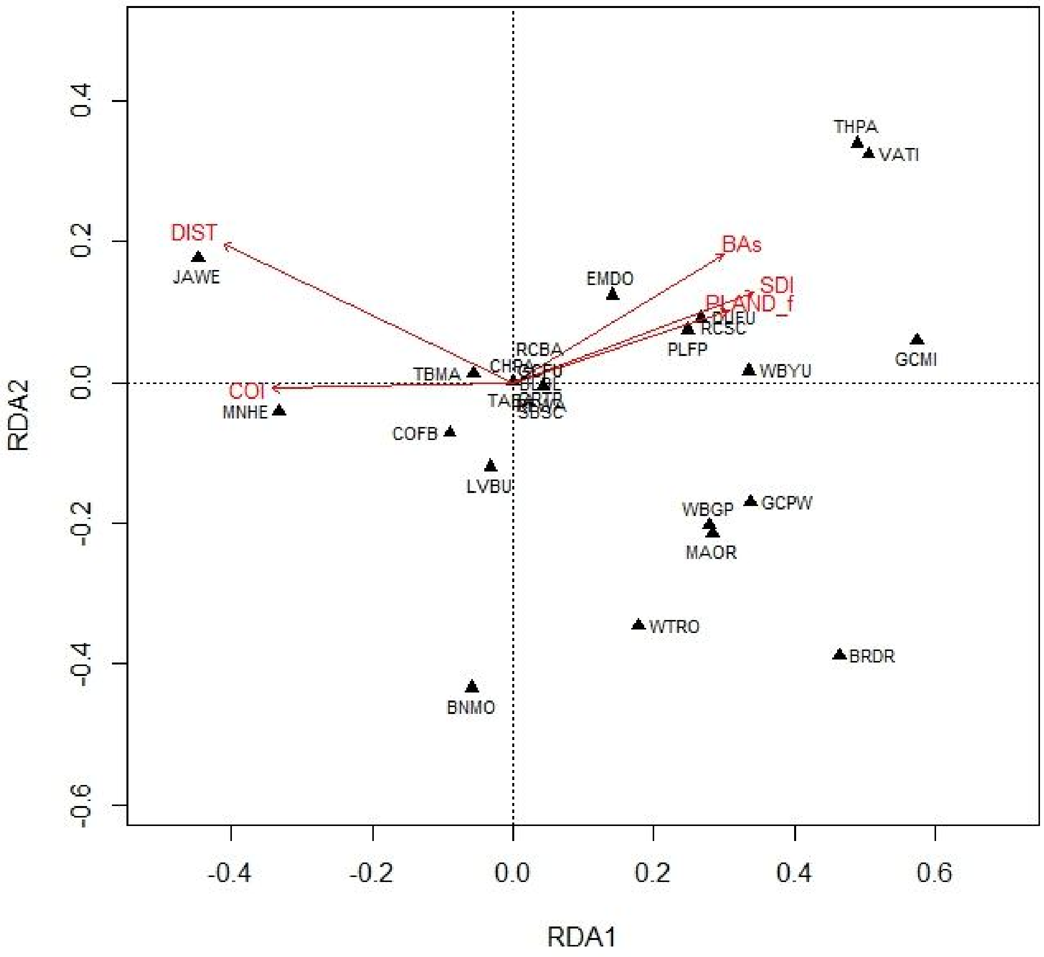

Figure 4.1. Species–environment biplot for the presence/absence data set, based on a Redundancy analysis (RDA) method. Only environmental variables with significant permutation test ($P<0.01$) were shown. See Appendix F for abbreviation of bird species.

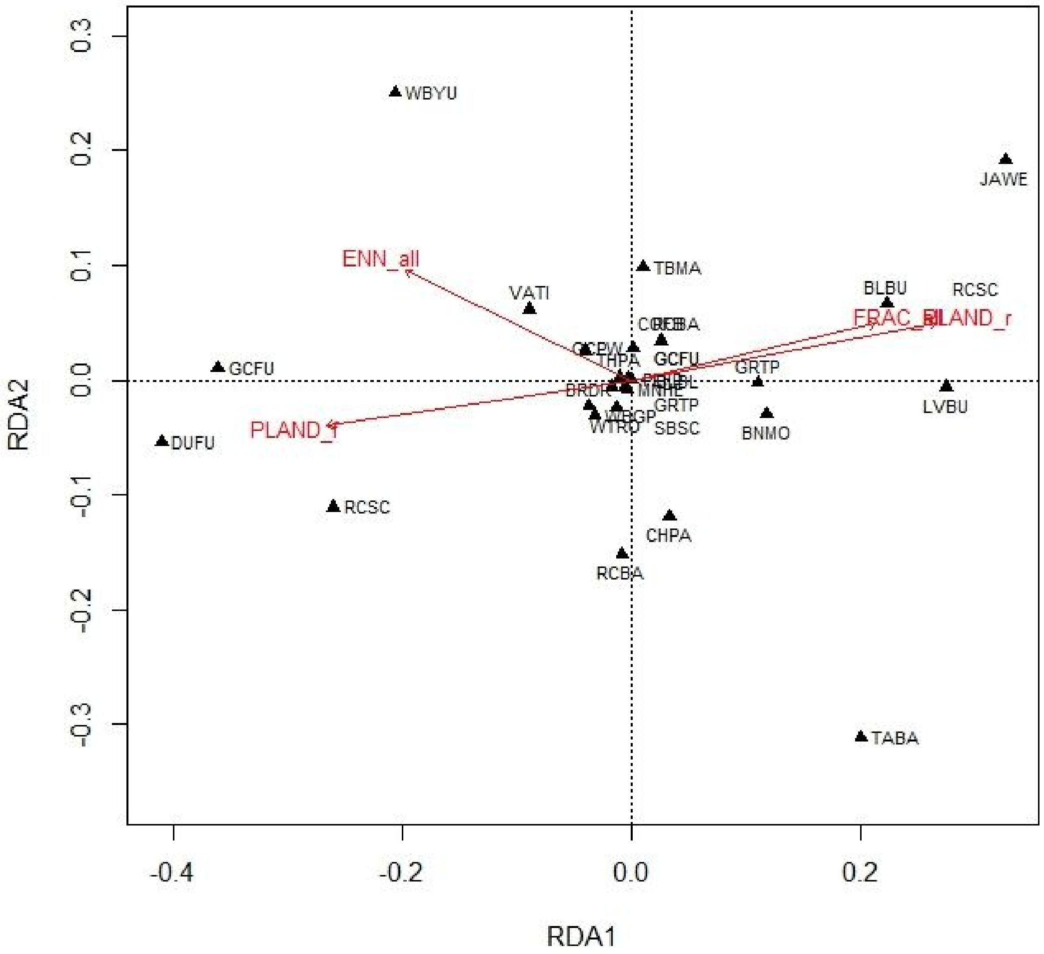

Figure 4.2. Species–environment biplot for the abundance data set, based on a Redundancy analysis (RDA) method. Only environmental variables with significant permutation test (*P*<0.01) were shown. See Appendix F for abbreviation of bird species.

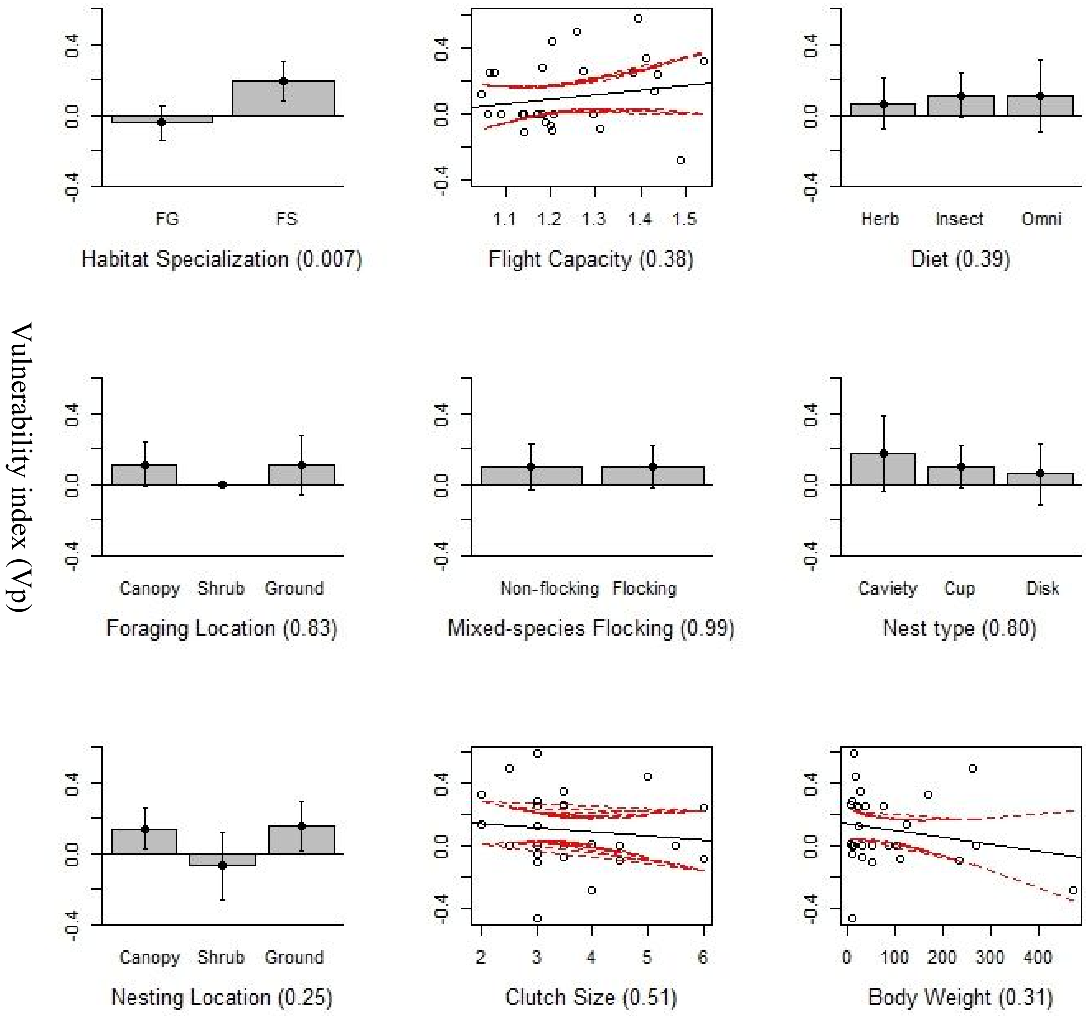

Figure 4.3. Associations between fragmentation vulnerability index (Vp) and ecological traits. The value in the parenthesis is the p value. Standardized errors and 95% confidence intervals were shown.

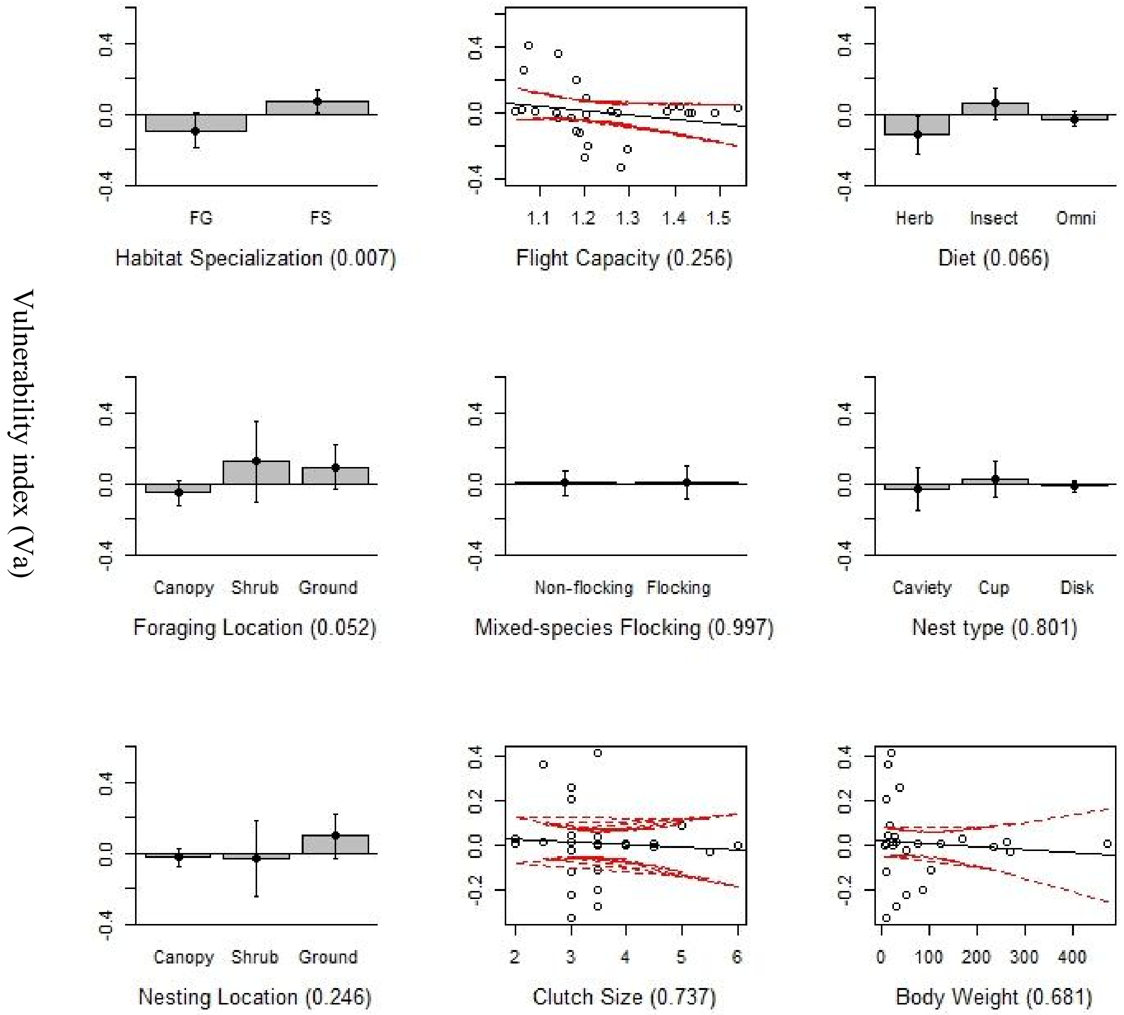

Figure 4.4. Associations between fragmentation vulnerability index (Va) and ecological traits. The value in the parenthesis is the p value. Standardized errors and 95% confidence intervals were shown.

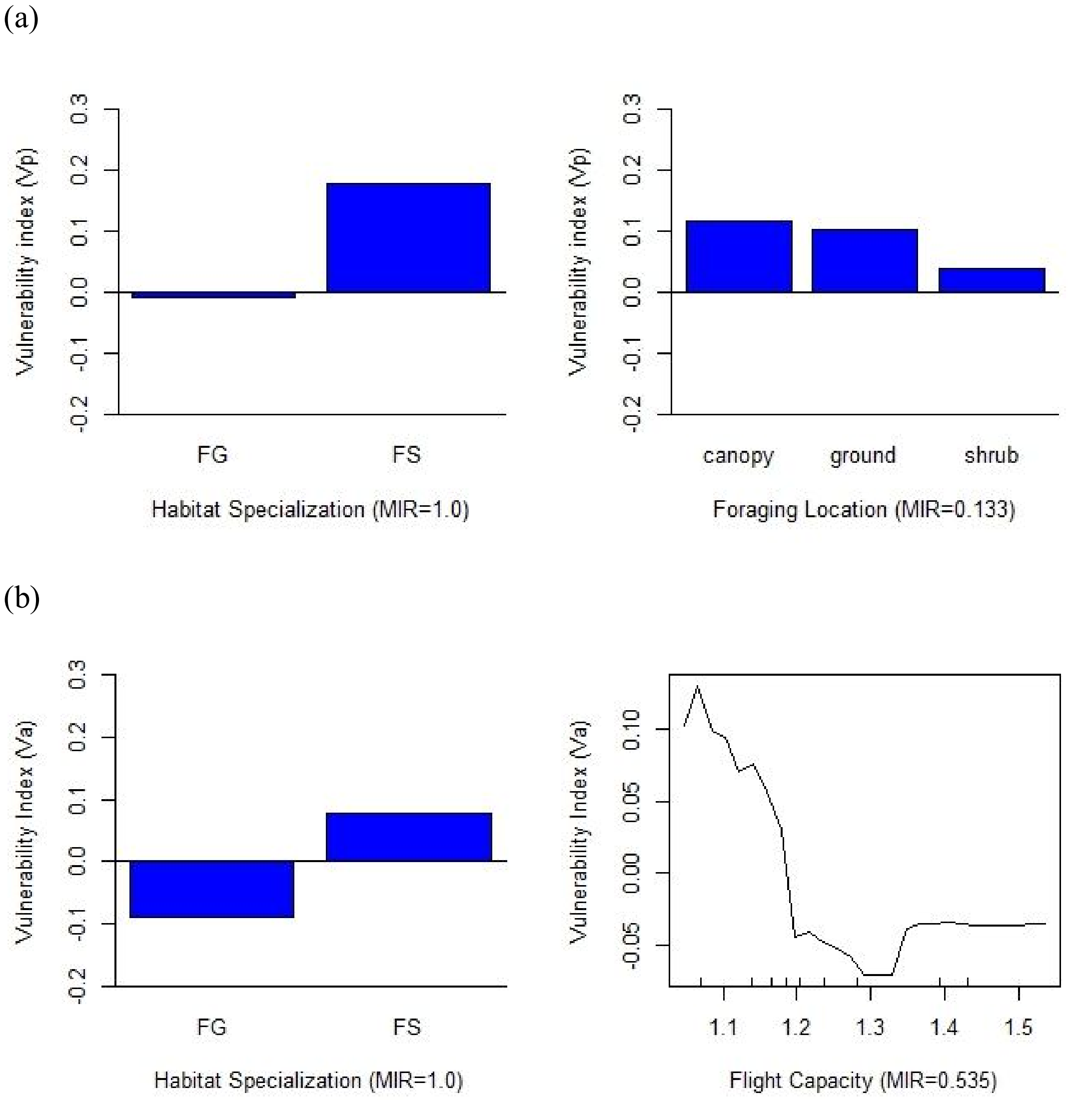

Figure 4.5. Marginal effects of critical ecological traits included in the best models on two fragmentation vulnerability indices(a) Vp, and (b) Va. For a categorical variable, the predicted mean vulnerability index for each level (e.g. forest specialist and generalist) was shown. In contrast, a smooth curve was plotted for the predicted a relationship between the vulnerability to fragmentation and a continuous variable (e.g. flight capacity).

CHAPTER 5. CONCLUSIONS AND CONSERVATION IMPLICATIONS

OVERVIEW

Lowland-forest fragmentation in the western coastal plain in Taiwan affects forest-dependent birds at different spatial scales and depends on species characteristics. At a nationwide scale, total species richness increased with the size of forest 'islands' remaining on the lowland hills. And species richness declined sharply when the distance from the potential sources of immigrants exceeded a threshold, after accounting for other environmental factors at landscape and local scales. Forest specialists were more vulnerable to the broad-scale area and isolation effects than forest generalists. Structurally isolated forests may not function as real habitat patches from the view of forest generalists because of their flexibility in utilizing the non-forest matrix.

The analysis at a community level also showed that the broad-scale isolation effect played a key role in determining the community structure based on the presence/absence data set. But it is notable that local-scale forest condition explained a considerable amount of variability in the presence/absence data set too. Certain species, such as Grey-chinned Minivet (*Pericrocotus solaris*) and Bronzed Drongo (*Dicrurus aeneus*) primarily limited to locations near potential sources of immigrants and with higher tree diversity. Habitat specialization and foraging location are the species traits associated with vulnerability to forest fragmentation based on the presence/absence data. The combination of the dispersal limitation of forest specialists within a fragmented landscape and specialized foraging requirements could possibly influence their colonization success of new forest fragments, which is a process involving both dispersal success as well as successful establishment (Hovestadt and Poethke 2005).

The broad-scale isolation effect, however, didn't show significant influences on community structure based on the abundance data set. In contrast, the landscape-scale factors explained the largest amount of variability in the abundance data set at the entire community level in this study. Several species' abundance such as Dusky Fulvetta (*Alcippe brunnea*), Grey-cheeked Fulvetta (*Alcippe morrisonia*) and Rusty-cheeked Scimitar Babbler (*Pomatorhinusery throgenys*) are very sensitive to the amount of forest area and distance from nearest neighboring habitat patch within a fragmented landscape. A large forest area can support more individuals of forest-dependent species, especially the ones who highly rely on forest habitat. In addition, the distance from the nearest neighboring habitat patch could influence the inter-patch movement of species in a fragmented landscape, especially for those that are less mobile. It was not surprising that habitat specialization and flight capacity are the species traits strongly associated with their vulnerability to forest fragmentation.

Analysis at different data resolutions may reflect the underlying mechanisms acting on avian community structure at different scales. Most species vulnerable to the amount of forest area and degree of connectivity at a landscape scale were common species that occurred at > 80% of the sampling sites in the study area. Their vulnerability to forest fragmentation could be underestimated because of their prevalence in the study area. It appeared that the presence/absence data may not be able to provide detailed enough information to reflect the responses of species' populations to landscape-scale environmental determinants. In contrast, the majority of species whose occurrence was sensitive to broad-scale isolation effects had a relatively limited distribution and were less abundant in the study area. At the community-level analyses, the variability in abundance was possibly not large enough to reflect their responses to the broad-scale effects of isolation. Caution should be used when interpreting the results and providing information to managers for conservation decision-making.

Finally, I found habitat specialization of species plays a key role in determining species richness patterns, community structure and species-level vulnerability to forest fragmentation within the fragmented forest landscape in this study. Specialization in forest habitats may constrain these species within forest fragments as well as limit their dispersal in a fragmented forest landscape. This finding supports the global decline of specialist species because of habitat degradation (Clavel et al. 2010).There are six forest specialist species (*Parus varius*, *Dicrurus aeneus*, *Treron sieboldii*, *Pericrocotus solaris*, *Erpornis zantholeuca* and *Alcippe brunnea*) whose occurrence and abundance are both vulnerable to effects of forest fragmentation acting at different scales. Among these species, the first three are endemic subspecies in Taiwan.

CONSERVATION IMPLICATIONS

The findings in this study could contribute to avian conservation in Taiwan. At a nationwide scale, the preservation of lowland forests islands remaining on the hills and enhancement of the connection among forest islands and the potential source of immigrants in the nearby Central Mountain Ridge should contribute to conservation of lowland forest avian biodiversity in Taiwan. Corridors generally facilitate the movements of species between habitat patches at a population level (Gilbert-Norton et al. 2010). However, conservation becomes a challenge at a community level because of the distinct requirements of multiple species that compose a community. Forest specialist species are more vulnerable to broad-scale isolation effects. Future research should focus on understanding their habitat selection and modeling least cost paths (Adriaensen et al. 2003) to provide information on the potential locations of corridors.

Furthermore, management of the surrounding matrix could be conducted alongside corridors to enhance landscape connectivity (Castellon and Sieving 2006). Increasing the similarity of vegetation structure between the matrix and forest patches, such as cultivation with shade trees or complex vertical-structure agriculture (Raman 2006), as well as the presence of stepping-stone trees (Gillies et al. 2011)could be possible strategies, especially in mid and southern Taiwan where agriculture land is the dominant land use. In addition to broad-scale connections, the findings in this multiscale study also support efforts to improve local forest conditions, since several forest specialists may have specific requirements to support local populations once they reach a new forest fragment. Nevertheless, if the goal of management is to secure the persistence of existing local populations, preserving the greatest amount of forest habitat(e.g. > 70%) and mitigating the degree of forest fragmentation may be practical guidelines.

There are several species whose occurrence and abundance are both vulnerable to forest fragmentation and should be a top priority for conservation. In addition, these species could be designated as indicator species to monitor the effect of forest fragmentation in the future. Currently, there are several citizen-science projects conducted to accumulate long-term and large-scale bird data in Taiwan, such as the Breeding Bird Survey Taiwan (BBS Taiwan) and Monitoring Avian Productivity and Survival in Taiwan (MAPS Taiwan). Data derived from these projects could be used to monitor the population change for these vulnerable species.

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Appendix A Attributes and presence/absence of forest bird species analyzed in this study

Family	Scientific name[1]	English name[1]	Forest dependency (%) [2]	Category[2]	Forest Island							Forest Mainland
					YMS	LCT	FBM	BGS	DGS	JS	FSD	
Ardeidae	*Gorsachiusmelanolophus*	Malaysian Night Heron	–	FS	+	+		+	+			+
Phasianidae	*Arborophilacrudigularis*	Taiwan Partridge	–	FS	+		+					+
	Bambusicolathoracicus	Chinese Bamboo-Partridge	63.81%	FG	+	+	+	+	+	+	+	+
Columbidae	*Chalcophapsindica*	Emerald Dove	–	FS		+		+	+	+	+	+
	Columba pulchricollis	Ashy Wood-Pigeon	–	FS								+
	Treronsieboldii	White-bellied Pigeon	–	FS	+	+		+				+
Megalaimidae	*Megalaimanuchalis*	Taiwan Barbet	73.78%	FG	+	+	+	+	+	+	+	+
Picidae	*Dendrocoposcanicapillus*	Grey-capped Woodpecker	81.25%	FS	+	+	+	+	+		+	+
Campephagidae	*Pericrocotussolaris*	Grey-chinned Minivet	87.72%	FS	+							+
Dicruridae	*Dicrurusaeneus*	Bronzed Drongo	80.25%	FS	+			+				+
Oriolidae	*Oriolustraillii*	Maroon Oriole	–	FS								+
Corvidae	*Dendrocittaformosae*	Grey Treepie	73.28%	FG	+	+	+	+	+		+	+
	Urocissacaerulea	Formosan Magpie	88.24%	FS	+	+	+					+
Paridae	*Parusmonticolus*	Green-backed Tit	100.00%	FS		+						+
	Parusvarius	Varied Tit	95.24%	FS	+							+
Pellorneidae	*Schoeniparusbrunnea*	Dusky Fulvetta	79.37%	FS	+			+				+
	Alcippemorrisonia	Grey-cheeked Fulvetta	81.90%	FS	+	+	+	+	+	+		+
Leiothrichidae	*Heterophasiaauricularis*	White-eared Sibia	97.72%	FS	+	+	+					+
Timaliidae	*Pomatorhinuserythrogenys*	Rusty-cheeked Scimitar Babbler	65.97%	FG	+		+	+	+	+		+
	Pomatorhinusruficollis	Streak-breasted Scimitar Babbler	65.81%	FG	+	+	+	+	+	+	+	+
	Stachyridopsisruficeps	Rufous-capped Babbler	73.96%	FG	+	+	+	+	+	+	+	+
Vireonidae	*Erporniszantholeuca*	White-bellied Erpornis	82.42%	FS	+	+	+	+	+			+
Pycnonotidae	*Hypsipetesleucocephalus*	Black Bulbul	71.41%	FG	+	+	+	+	+	+	+	+
	Pycnonotussinensis	Light-vented Bulbul	47.14%	FG	+	+	+	+	+	+	+	+
Pycnonotidae	*Pycnonotustaivanus*	Styan's Bulbul	–	FG								+

Appendix A Continued.

Family	Scientific name[1]	English name[1]	Forest dependency (%) [2]	Category[2]	Forest Island							Forest Mainland
					YMS	LCT	FBM	BGS	DGS	JS	FSD	
Pycnonotidae	*Spizixossemitorques*	Collared Finchbill	46.15%	FG		+		+			+	+
Muscicapidae	*Myophonusinsularis*	Formosan Whistling-Thrush	85.29%	FS	+	+						+
	Cinclidiumleucurum	White-tailed Robin	88.10%	FS	+	+						+
	Phoenicurusfuliginosus	Plumbeous Redstart	–	FS								+
	Niltavavivida	Vivid Niltava	100.00%	FS								+
Turdidae	*Turduspoliocephalus*	Island Thrush	–	FS			+					
Cettiidae	*Abroscopusalbogularis*	Rufous-faced Warbler	91.27%	FS							+	+
Monarchidae	*Hypothymisazurea*	Black-naped Monarch	64.26%	FG	+	+	+	+	+	+	+	+
Zosteropidae	*Zosteropsjaponicus*	Japanese White-eye	47.39%	FG	+	+	+	+	+	+	+	+

[1] Taxonomy, scientific names, and English names follow Clement et al. (2012).

[2] All bird species were assigned as forest specialists (FS) or forest generalists (FG), based on their forest dependency (Lin, 2010). Species without enough information were defined by the authors’ field observations

Appendix B Preliminary analysis to determine sample size

I selected a 1km x 1km sampling site, where vegetation composition and structure are relatively homogeneous. Twelve sampling points were evenly set at a 200m interval within this sampling site. Point counts were used to collect bird data in February, 2009.Each sampling plot was visited six times. The bird surveys were conducted within 4 hours after sunrise under acceptable weather conditions. All birds seen or heard within a radius of 100m at each plot during the first 6 minutes were recorded. Only resident forest species were included in subsequent analyses.

EstimateS program (Colwell 2005) was applied to generate a sample-based species accumulation curve. Each visit to sampling points was viewed as an independent sample. There was a total of sixty-nine samples in this study. The average expected number of accumulative species with 95% confidence intervals was estimated for each sample size ranging from 1 to 69 by conducting1000 randomizations without replacement. This procedure eliminates the effect of the order in which samples are sequentially added to the analysis and simultaneously smoothes the species accumulation curve by averaging over randomizations. The number of total forest species recorded in this sampling site was used as 100% to convert the average expected number of accumulative species to a percentage of accumulative species.

Fig.B1 shows the sample-based species accumulation curve. The percentage of accumulative species increased with sample size. Eighteen and thirty-six sampling points were needed to reach 80% and 90% of detection of total forest bird species within a 1km x 1km sampling site, respectively. The number of points required to increase detection by 5% after 90% increased greatly to fifty-two sampling points.

Sample size should be determined by the objective of the research as well as available survey effort. The aim of this study was to examine the effects of forest fragmentation on community indices and structure of lowland forest birds. It is critical to record as many species as possible to avoid skipping species which are rare, but vulnerable to forest fragmentation. Detection of 90% of total species is likely a compromise between our study objective and available survey effort since the effort needed to reach 95% of detection increases disproportionately. Therefore, I set 90% detection as the threshold to determine our sample size of point counts within a 1km^2 sampling site in this study.

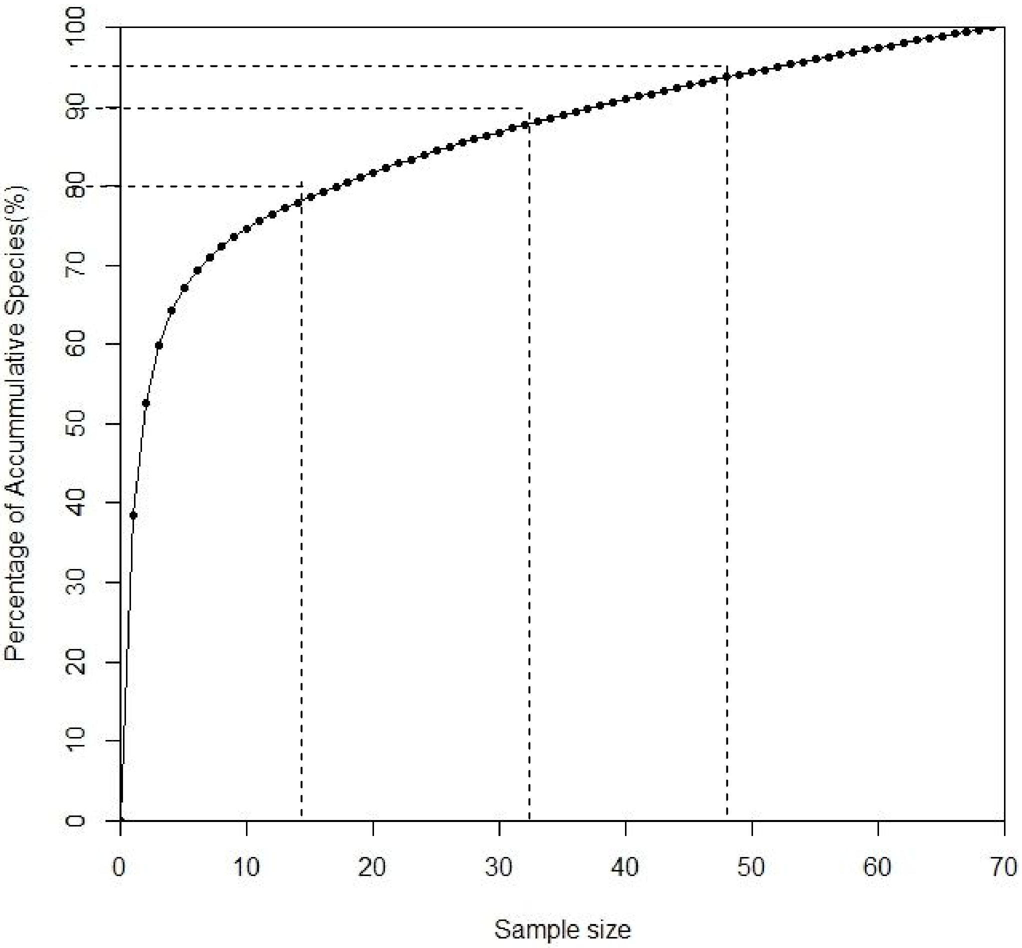

Figure B.1 Sample-based species accumulation curve. The percentage of accumulative species increased with sample size. Eighteen and thirty-six sampling points were needed to reach 80% and 90% of detection of total forest bird species within a 1 km^2 sampling site, respectively. The number of points required to increase detection by 5% after 90% increased greatly to fifty-two points.

Appendix C Selection of landscape scale

Eight concentric buffer zones (radii=0.5, 1.0, 1.5, 2.0, 2.5, 3.0, 3.5, 4.0km, respectively) from the center of sampling plots were delineated. The amount of variation of avian community explained by the landscape context within each buffer zone was evaluated to decide the landscape scale in this study. Thirty-seven landscape characteristics were quantified (Table 3.1) by using FRAGSTATS version 3.3 software (McGarigal and Marks 1995). We calculated the pairwise Pearson correlation coefficients (*r*) and retained those variables which we considered more biologically meaningful for forest birds if they were highly correlated to other variables ($|r| > 0.7$). Before data analyses, all environmental variable were log-transformed to improve their normality. I employed Canonical Correspondence Analysis (CCA) to examine the spatial variations of avian community composition for both presence/absence and abundance data sets. Abundance data were Hellinger transformed (Legendre and Gallagher 2001) into relative abundance prior to analyses. The forward selection procedure in CANOCO (Lepš and Šmilauer 2003) was conducted to select important environmental variables, and the total amount of spatial variance of avian community composition explained by these variables was calculated.

Fig.C1 showed the variation of avian community explained by landscape characteristics within different concentric buffer zones. For the presence/absence data set, the landscape context within the radius of 1.0km (27.02%, p=0.005) and 2.5km (25.54%, p=0.005) buffer zone explained the most variation of avian community composition. On the other hand, the landscape context within the radius of 2.5km (25.54%, p=0.005) buffer zone explained the largest amount of variation of avian community composition for the abundance data set (52.98%, p=0.005). Thus, we chose the buffer zone within the radius of 2.5km as the landscape scale in this study.

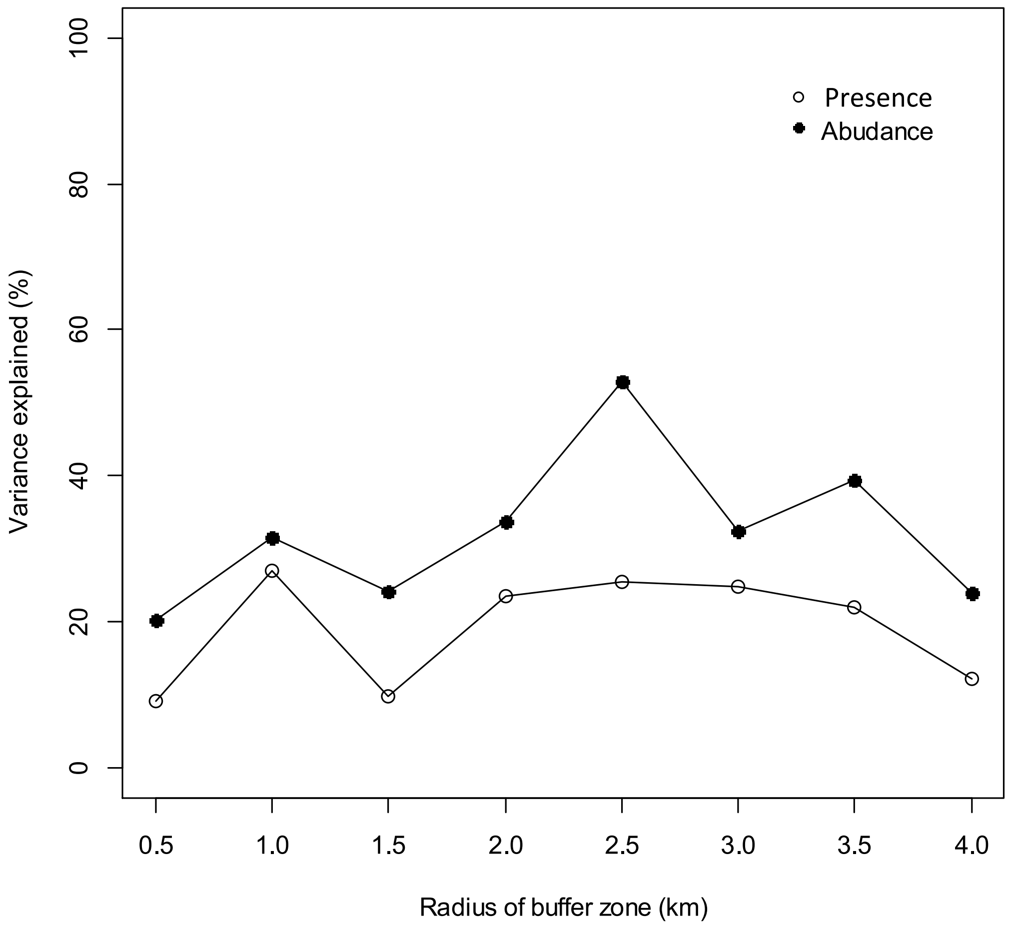

Figure C1.The variation of avian community explained by landscape characteristics within different concentric buffer zones. For the presence/absence data set, the landscape context within the radius of 1.0km and 2.5km buffer zone explained the most variation of avian community composition. The landscape context within the radius of 2.5km buffer zone explained the largest amount of variation of avian community composition for the abundance data set.

Appendix D Abbreviation, forest specialization and occupancy of forest bird species analyzed in this study

Family[1]	Scientific name[1]	English name[1]	Abbreviation	Forest dependency (%) [2]	Category [2]	Occupany[3]
Ardeidae	*Gorsachiusmelanolophus*	Malaysian Night Heron	MNHE	–	FS	55%
Phasianidae	*Arborophilacrudigularis*	Taiwan Partridge	THPA	–	FS	41%
	Bambusicolathoracicus	Chinese Bamboo Partridge	CBPA	63.81%	FG	100%
Rallidae	*Rallinaeurizonoides*	Slaty-legged Crake	SLCR	–	FS	9%
Columbidae	*Chalcophapsindica*	Emerald Dove	EMDO	–	FS	18%
	Treronsieboldii	White-bellied Pigeon	WBGP	–	FS	36%
Megalaimidae	*Megalaimanuchalis*	Taiwan Barbet	TABA	73.78%	FG	100%
Picidae	*Dendrocoposcanicapillus*	Grey-capped Woodpecker	GCPW	81.25%	FS	27%
Campephagidae	*Pericrocotussolaris*	Grey-chinned Minivet	GCMI	87.72%	FS	36%
Dicruridae	*Dicrurusaeneus*	Bronzed Drongo	BRDR	80.25%	FS	27%
Oriolidae	*Oriolustraillii*	Maroon Oriole	MAOR	–	FS	14%
Corvidae	*Dendrocittaformosae*	Grey Treepie	GRTP	73.28%	FG	100%
	Urocissacaerulea	Taiwan Blue Magpie	TBMA	88.24%	FS	86%
Paridae	*Parusvarius*	Varied Tit	VATI	95.24%	FS	45%
Pellorneidae	*Alcippebrunnea*	Dusky Fulvetta	DUFU	79.37%	FS	86%
	Alcippemorrisonia	Grey-cheeked Fulvetta	GCFU	81.90%	FS	100%
Timaliidae	*Pomatorhinuserythrogenys*	Rusty-cheeked Scimitar Babbler	RCSC	65.97%	FG	86%
	Pomatorhinusruficollis	Streak-breasted Scimitar Babbler	SBSB	65.81%	FG	100%
	Stachyrisruficeps	Rufous-capped Babbler	RCBA	73.96%	FG	100%
Vireonidae	*Erpornis zantholeuca*	White-bellied Yuhina	WBYU	82.42%	FS	82%
Pycnonotidae	*Hypsipetesleucocephalus*	Black Bulbul	BLBU	71.41%	FG	100%
	Pycnonotussinensis	Light-vented Bulbul	LVBU	47.14%	FG	86%
	Spizixossemitorques	Collared Finchbill	COFB	46.15%	FG	5%

Appendix D Continued

Family[1]	Scientific name[1]	English name[1]	Abbreviation	Forest dependency (%) [2]	Category[2]	Occupany[3]
Muscicapidae	*Myiomelaleucura*	White-tailed Robin	WTRO	88.10%	FS	14%
Cettiidae	*Abroscopusalbogularis*	Rufous-faced Warbler	RFWA	91.27%	FS	5%
Dicaeidae	*Dicaeumminullum*	Plain Flowerpecker	PLFP	–	FS	68%
Monarchidae	*Hypothymisazurea*	Black-napped Monarch	BNMO	64.26%	FG	9%
Zosteropidae	*Zosteropsjaponicus*	Japanese White-eye	JAWE	47.39%	FG	59%

[1] Taxonomy, scientific names, and English names follow Clements et al. (2012).

[2] All bird species were assigned as forest specialists (FS) or forest generalists (FG), based on their forest dependency (Lin 2010). Species without enough information were defined by the authors' field observations.

[3] Percentage of sampling sites one species occurs in our study area

Appendix E Measurement of flight capacity of bird species

There are many different approaches to estimate the flight capacity of birds. Using capture-recapture data to quantify the dispersal distance of birds is a ideal way to evaluate their flight capacity in the real nature world (Van Houtan et al. 2007). This approach, however, is high-cost and it is not easy to accumulate a large enough sample size for estimation of dispersal distance, especially for rare or less abundant species. Wing morphology has been known a good indicator of flight capacity for birds and bats (Wainwright and Reilly 1994, Monkkonen 1995). In this study, I measured the wing aspect ratio of species of concern to evaluate their potential flight capacity.

Wing morphology of 342 bird specimens from the National Museum of Nature Science, Research Museum at Academia Sinica and Museum of Zoology at National Taiwan University were measured. I measured at least 10 specimen for all species except *Dendrocopos canicapillus, Parus varius, Myiomela leucura* and *Dicaeum minullum* because of limited availability (Table E1). In addition, the wing data of *Myiomela leucura* was from the project Monitoring Avian Productivity and Survival, Taiwan (MAPS Taiwan).

Then wing aspect ratio, defined as a ratio of the distance from the carpal joint to the distal end of the first secondary feather (a) to the length of wing tip (b), was measured (Fig. E1). Left wings were measured only when right wings were damaged or absent from the specimen (n=33). Each specimen except Malaysian Night Heron (*Gorsachius melanolophus*) was repeatedly measured twice by me to reduce the measurement error caused by different investigators. T-tests showed no significant difference between two repeated measurements (Table E1) for all species except Black Bulbul (*Hypsipetes leucocephalus*) guaranteed the consistent measurements by the same person. Mean of wing aspect ratio was used to represent the flight capacity for each bird species. Higher wing aspect ratio refers to better flight capacity, and *vice versa*

Table E1. Sample size, mean and standard deviation of wing aspect ratio of bird species in this study. All specimens were measured twice by the same person. T-test was used to evaluate if any significant difference between two repeated measurements of each specimen. Bold marker refers to $P<0.05$.

Family	Scientif name	Sample size	Mean	SD	T-test
Ardeidae	*Gorsachiusmelanolophus*	10	1.4878	0.2734	--
Phasianidae	*Arborophilacrudigularis*	10	1.2563	0.0704	0.751
	Bambusicolathoracicus	12	1.1719	0.0581	0.153
Columbidae	*Chalcophapsindica*	18	1.4284	0.1297	0.583
	Treronsieboldii	13	1.5371	0.0011	0.446
Megalaimidae	*Megalaimanuchalis*	12	1.2067	0.3381	0.344
Picidae	*Dendrocoposcanicapillus*	7	1.4383	0.0013	0.870
Campephagidae	*Pericrocotussolaris*	16	1.3948	0.0541	0.425
Dicruridae	*Dicrurusaeneus*	12	1.4104	0.0527	0.794
Oriolidae	*Oriolustraillii*	10	1.3832	0.0006	0.484
Corvidae	*Dendrocittaformosae*	14	1.1812	0.2074	0.376
	Urocissacaerulea	22	1.2034	0.0006	0.076
Paridae	*Parusvarius*	9	1.2040	0.0193	0.891
Pellorneidae	*Alcippebrunnea*	15	1.0741	0.0002	0.701
	Alcippemorrisonia	15	1.1421	0.0710	0.945
Timaliidae	*Pomatorhinuserythrogenys*	13	1.0630	0.0721	0.979
	Pomatorhinusruficollis	15	1.0618	0.0002	0.277
	Stachyrisruficeps	15	1.0897	0.0356	0.625
Vireonidae	*Erporniszantholeuca*	14	1.1833	0.0006	0.058
Pycnonotidae	*Hypsipetesleucocephalus*	12	1.2934	0.1131	**0.016**
	Pycnonotussinensis	13	1.2013	0.0005	0.773
	Spizixossemitorques	10	1.1405	0.0668	0.083
Muscicapidae	*Myiomelaleucura*	7	1.0460	0.1725	--
Cettiidae	*Abroscopusalbogularis*	13	1.1373	0.0002	0.628
Dicaeidae	*Hypothymisazurea*	13	1.1899	0.0583	0.849
Monarchidae	*Dicaeumminullum*	2	1.2710	0.0556	0.858
Zosteropidae	*Zosteropsjaponicus*	10	1.2782	0.0430	0.699

Figure E1. The distance from the carpal joint (wrist) to the distal end of the first(innermost) secondary feather (a) and wing tip (b) were measured, respectively. Then the aspect ratio of wing was calculated as b/a. Higher wing aspect ratio refers to better flight capacity, and *vice versa*.

Appendix F Ecological traits of 27 bird species analyzed in this study

Family	Scientific name	Abbrev.	Habitat specialization	Diet	Foraging location	Nest type	Nesting location	Clutch size	Flight capacity	Mixed flocking	Body weight (g)
Ardeidae	*Gorsachiusmelanolophus*	MNHE	specialist	insectivore	ground	disk-structure	canopy	4.0	1.4878	No	472.8
Phasianidae	*Arborophilacrudigularis*	THPA	specialist	omnivore	ground	disk-structure	ground	2.5	1.2563	No	261.5
	Bambusicolathoracicus	CHPA	generalist	omnivore	ground	disk-structure	ground	5.5	1.1719	No	270.3
Columbidae	*Chalcophapsindica*	EMDO	specialist	omnivore	ground	disk-structure	canopy	2.0	1.4284	No	124.0
	Treronsieboldii	WBGP	specialist	herbivore	canopy	disk-structure	canopy	2.0	1.5371	No	169.2
Megalaimidae	*Megalaimanuchalis*	TABA	generalist	herbivore	canopy	cavity	canopy	3.5	1.2067	No	87.1
Picidae	*Dendrocoposcanicapillus*	GCPW	specialist	insectivore	canopy	cavity	canopy	6.0	1.4383	Yes	22.7
Campephagidae	*Pericrocotussolaris*	GCMI	specialist	insectivore	canopy	open-cup	canopy	3.0	1.3948	Yes	14.0
Dicruridae	*Dicrurusaeneus*	BRDR	specialist	insectivore	canopy	open-cup	canopy	3.5	1.4104	Yes	26.5
Oriolidae	*Oriolustraillii*	MAOR	specialist	insectivore	canopy	open-cup	canopy	3.5	1.3832	Yes	74.0
Corvidae	*Dendrocittaformosae*	GRTP	generalist	omnivore	canopy	disk-structure	canopy	3.5	1.1812	Yes	103.8
	Urocissacaerulea	TBMA	specialist	omnivore	canopy	disk-structure	canopy	4.5	1.2034	Yes	235.1
Paridae	*Parusvarius*	VATI	specialist	insectivore	canopy	cavity	canopy	5.0	1.2040	Yes	17.0
Pellorneidae	*Alcippebrunnea*	DUFU	specialist	insectivore	ground	open-cup	ground	3.5	1.0741	Yes	18.8
	Alcippemorrisonia	GCFU	specialist	insectivore	shrub	open-cup	shrub	2.5	1.1421	Yes	14.1
Timaliidae	*Pomatorhinuserythrogenys*	RCSC	generalist	insectivore	ground	open-cup	ground	3.0	1.0630	No	37.6
	Pomatorhinusruficollis	SBSC	generalist	insectivore	shrub	open-cup	ground	3.0	1.0618	Yes	31.7
	Stachyrisruficeps	RCBA	generalist	insectivore	shrub	open-cup	ground	4.5	1.0897	Yes	10.4
Vireonidae	*Erporniszantholeuca*	WBYU	specialist	insectivore	canopy	open-cup	shrub	3.0	1.1833	Yes	11.2
Pycnonotidae	*Hypsipetesleucocephalus*	BLBU	generalist	herbivore	canopy	open-cup	canopy	3.0	1.2934	Yes	52.8
	Pycnonotussinensis	LVBU	generalist	herbivore	canopy	open-cup	shrub	3.5	1.2013	Yes	29.2
	Spizixossemitorques	COFB	generalist	herbivore	canopy	open-cup	shrub	3.0	1.1405	No	52.8
Muscicapidae	*Myiomelaleucura*	WTRO	specialist	insectivore	ground	open-cup	ground	3.0	1.0460	No	24.5
Cettiidae	*Abroscopusalbogularis*	RFWA	specialist	insectivore	canopy	cavity	canopy	4.0	1.1373	Yes	5.8

Appendix F Continued

Family	Scientific name	Abbrev.	Habitat specialization	Diet	Foraging location	Nest type	Nesting location	Clutch size	Flight capacity	Mixed flocking	Body weight (g)
Dicaeidae	*Hypothymisazurea*	BNMO	generalist	insectivore	canopy	open-cup	shrub	3.0	1.1899	Yes	11.1
Monarchidae	*Dicaeumminullum*	PLFP	specialist	herbivore	canopy	open-cup	canopy	3.5	1.2710	No	6.2
Zosteropidae	*Zosteropsjaponicus*	JAWE	generalist	insectivore	canopy	open-cup	shrub	3.0	1.2782	Yes	9.0

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