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Title

Seasonal variation in patch and landscape effects on forest bird communities in a lowland fragmented landscape

Author names and affiliations

Yuki Yabuhara[1*], Yuichi Yamaura[2,3], Takumi Akasaka[4], Satoshi Yamanaka[1,5], Futoshi Nakamura[1]

1 Department of Forest Science, Graduate School of Agriculture, Hokkaido University, Kita9 Nishi9, Kitaku, Sapporo, Japan 060-8589

2 Department of Forest Vegetation, Forestry and Forest Products Research Institute, 1 Matsunosato, Tsukuba, Ibaraki 305-8687

3 Fenner School of Environment and Society, Australian National University, Canberra, ACT, 2601, Australia

4 Laboratory of Conservaion Ecology, Obihiro University of Agriculture and Veterinary Medicine, Nishi 2-sen 11, Inadacho, Obihiro, 080-8555

5 Hokkaido Research Center, Forestry and Forest Products Research Institute, Hitsujigaoka 7, Sapporo, 062-8516

* Current address: Graduate School of Technology, Industrial and Social Sciences, Tokushima University, 2-1, Minami-Josanjima, Tokushima, Tokushima 770-8506

Corresponding author

Yuki Yabuhara

plover0320@gmail.com

Phone and fax number: +81-88-656-9132

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Abstract

In fragmented temperate landscapes, species responses to patch and landscape structures are likely to vary across seasons. However, few studies have examined the dynamic effects on biodiversity across seasons. We examined the effects of patch attributes and connectivity and seasonal variation in the effects of these environmental variables on forest bird communities at woodland fragments surrounded by agricultural land across three seasons (breeding, dispersal, and wintering seasons). We surveyed birds in woodland remnants and examined the effects of patch area, woodland connectivity, woodland type, and three interaction terms between these environmental variables and season (patch area × season, connectivity × season, and woodland type × season) on forest bird communities. In the results, species richness, abundance and composition of forest bird communities were associated with patch attributes and connectivity, and some of these associations varied depending on the season. Specifically, there were significantly higher abundances of specialist birds in riparian woodlands compared to conifer woodlands during the breeding season, whereas this pattern was reversed during the winter. In addition, we found the negative effects of patch area during the dispersal and wintering seasons and the positive effect of connectivity during the dispersal season on generalist bird abundances. These results suggest that woodland patches with high conservation values differ among three seasons. The conservation planning for a fragmented landscape therefore needs to consider the role of patch attributes and

connectivity during multiple seasons rather than just the breeding season.

1. Introduction

Conversion of terrestrial land cover has caused the degradation, loss and fragmentation of natural vegetation around the world (Fischer and Lindenmayer, 2007). For example, 2.3 million square kilometers of global forests have been lost from 2000 to 2012 (Hansen et al., 2013). This has imposed huge pressures on the persistence or survival of many species (Newbold et al., 2015). Two main conservation approaches to ameliorate such effects are to increase the size and quality of individual patches (Fahrig, 2003; Hodgson et al., 2011) or to enhance the connectivity among patches (Doerr et al., 2011).

Several studies have suggested that patch attributes can strongly affect biodiversity in a fragmented landscape (Humphrey et al., 2015). Patch area increases the density of interior species and decreases that of edge species (Bender et al., 1998; Yamaura et al., 2008). Woodland type of individual patches also exerts strong influence on biodiversity by determining habitat quality and availability. For example, riparian broad-leaved woodlands often support rich biodiversity and assemblage distinct from those of non-riparian woodlands (Bennett et al., 2014; Palmer and Bennett, 2006; Sabo et al., 2005). Therefore, patches that have large habitat areas or specific vegetation structures may deserve to be preserved.

Increasing the connectivity of existing patches is often societally and economically more feasible than creating new habitat patches, particularly when large areas are rarely set aside for nature conservation (Baguette et al., 2013; Lentini et al.,

2013). Applications of habitat network approaches such as graph theory facilitate this connectivity conservation (Fletcher et al., 2016; Galpern et al., 2011; Rayfield et al., 2011). Networks of forest habitats comprising nodes (habitat patches) and links (the probability of organisms dispersing between two patches) can have a distinctive effect that is independent from patch attributes. Many studies therefore have emphasized the effectiveness of graph-based connectivity indices for biodiversity conservation (e.g. Ishiyama et al., 2014; Shanahan et al., 2011).

Although many studies have examined the effects of the patch attributes and connectivity for biodiversity and provided varying results (Hinsley et al., 1995; Martensen et al., 2008; Shanahan et al., 2011), most examined these effects in a specific period (e.g., the breeding season for birds). However, species responses to patch attributes and connectivity are likely to differ across seasons for several reasons. Firstly, the utilization of highly connected patches is associated with species life history and behavior. During the dispersal season, bird individuals actively move around, and thus connected patches receive many dispersing individuals from surrounding patches (e.g., Gutzwiller and Anderson 1992). Compared to dispersal season, some birds may be less sensitive to the connectivity during breeding season because birds behaving as central place foragers are likely to stay around the nests (Martindale, 1982). Secondly, seasonal fluctuations in resource availability may alter the species-habitat relationships. In temperate woodlands, there is great variation in invertebrate prey biomass between

broad-leaved woodlands and conifer woodlands during the breeding season, whereas they are universally scarce during the winter (Blondel et al., 1993; Huston and Wolverton, 2009). This seasonal change in prey availability among woodland types influences the distribution of insectivores (Uesugi and Murakami, 2006) and seed- or fruit-eaters (Yoshikawa et al., 2017). For these reasons, patch and connectivity effects on biodiversity should be compared across seasons. Nevertheless, studies examining these effects directly across seasons are few (Faaborg et al., 2010).

Our main objective was to clarify a variation in the effects of connectivity, patch area and woodland type on bird communities across three seasons (breeding, dispersal, and wintering season). We classified species as either forest specialists (species that primarily occur in woodland areas) or habitat generalists (species that occur in non-woodland areas as well as in woodlands) rather than using total species richness or abundance as a response variable. Because the proportion of woodlands is low in our study region and habitat specialists are more vulnerable to landscape change than generalists (Matthews et al., 2014), forest specialists would be severely exposed to the effects of forest fragmentation throughout a year. By contrast, because habitat generalists can modify their foraging behavior in response to seasonal availability of resources, the effects of patch and landscape variables on generalists would be weaker.

2. Methods

110 *2.1. Study area*

111 The study area was situated in the lowland Tokachi plain in central Hokkaido, northern
112 Japan (Fig. 1). The area covered ca. 2,400 km^2 within the watershed of the Tokachi
113 River. In this area, most part of the deciduous broad-leaved forests that originally
114 covered the land was converted to agricultural land or planted woodlands dominated by
115 both deciduous (e.g. larch *Larix kaempferi*) and evergreen (e.g. fir *Abies sachalinensis*)
116 conifer trees. The remnant broad-leaved forests mainly consist of *Quercus dentate* and
117 *Q. crispula*, and their understory is covered by dwarf bamboo (*Sasa senanensis*). The
118 riparian forests mainly consist of *Salix* spp. and *Fraxinus mandshurica* var. *japonica*.
119 The climatic conditions in this area drastically change throughout the year. The mean
120 temperatures during the bird breeding (May to July 2014), dispersal (August to October
121 2014), and wintering (December 2014 to February 2015) seasons were 16.6 °C, 15.3 °C,
122 and -4.1 °C, respectively (data provided by the Obihiro weather station, Japan
123 Meteorological Agency, 38 m a.s.l.). The mean annual temperature in 2014 was 7.6 °C
124 (ranging from -20.1 to 34.8 °C) and the total precipitation was 885.0 mm.

125 We first created a land-cover map of the study area based on the private and
126 prefectural woodland layers provided by the Department of Fisheries and Forestry of
127 the Hokkaido Government (Fig. 1). All woodland patches on the map were categorized
128 as broad-leaved or conifer woodlands. Because woodland patches managed by national
129 governments (e.g., riparian woodlands) were not included in this layer, those patches

larger than 0.05 ha were added to the map based on recent satellite images (Advanced Land Observing Satellite images from 2009 to 2010). We defined the riparian woodlands as follows: (i) broad-leaved woodland patches extending between the water courses and both sides of the levees in large rivers (e.g., main course and large tributaries of the Tokachi River) and (ii) broad-leaved woodland patches that were located within 50 m of small rivers (i.e., river width was < 50 m). The final land-cover map contained 24,158 ha of broad-leaved woodlands and nearly two-fifths of those (9,505 ha) were categorized as riparian woodlands. Conifer woodlands covered 16,923 ha and around 87 % of those were larch plantations.

2.2. Patch selection and explanatory variables

We intended to primarily examine the relative role of woodland type, patch area, and connectivity as drivers shaping bird communities. Based on the land-cover map we created, we treated the homogenous area of each woodland type, surrounded by other types of woodlands or other land-uses (mainly agricultural area; Fig. 1), as separate woodland patches. We selected several candidate patches ranging from 3 to 100 ha in area to conduct bird survey. Although our study area contained a large number of tiny woodland fragments (i.e., the number of patches less than 1 ha area was approximately 60% of the total number of patches), these were not selected for the bird survey. This is because they were usually thin (approximately 10 meters wide) and impose strong edge

150 effects, and thus seemed to be insufficient for forest bird habitat. In addition, bird
151 surveys were not conducted in several large patches (more than 100-ha area) because
152 these patches had different topographic conditions, such as sloped terrain. Note that
153 these tiny or large patches were used in calculating the connectivity indices whenever
154 they were connected with survey patches. After calculating the patch area and
155 connectivity of the candidate patches, we carefully selected the survey patches to reduce
156 the correlations of these two explanatory variables. To reduce the dependence of the
157 sampling plot, each patch was separated from the others by at least 1.6 km. Finally, we
158 used a total of 42 patches, with 14 patches situated in non-riparian broad-leaved
159 woodlands, 14 in non-riparian conifer woodlands, and 14 in riparian broad-leaved
160 woodlands (Fig. 1). These patch areas ranged from 3.0 to 85.6 ha (mean of 24.1 ha ±
161 20.1 SD).

162 We measured the connectivity of survey patches using a multi-scale graph-
163 theoretical approach. This method allowed us to address the dispersal ability of a
164 species in crossing a gap between woodland patches. Similar to the method used by
165 Martensen et al. (2008) and Shanahan et al. (2011), we measured the connectivity
166 indices as the total area of all patches that could be reached without crossing gaps wider
167 than a threshold distance (e.g., 100 m) and that were located inside a circular buffer with
168 a 5-km radius from the center of each sampling plot. These connectivity indices did not
169 include the area of the survey patch in which a sampling plot was established. We

prepared 12 types of connectivity indices combining three habitat types (i.e., all types of woodlands [Con_BRC], both non-riparian and riparian broad-leaved woodlands [Con_BR], or only non-riparian broad-leaved woodlands [Con_B]) and four threshold distances (i.e., 50, 100, 150, or 200 m). Previous studies indicate that the gap distances songbirds can cross vary depending on species and season (e.g., Creegan and Osborne, 2005; Tremblay and St. Clair, 2009). The correlations between patch area and each of the connectivity indices were considerably low ($r < 0.25$).

2.3. Bird survey

Bird communities were surveyed in each sampling plot using the line-transect method (Bibby et al., 1992) during the breeding (from May to July 2014), dispersal (from September to October 2014), and wintering (from January to February 2015) seasons. To retain the sampling effort constant irrespective of the patch size, one bird sampling plot was established in each forest survey patch. Each sampling plot covered a fixed area (2 ha), but the shape of the sampling plot varied according to the width of woodland patches. Specifically, at most of the sampling plots established in the large woodland patches, we walked along 250 m of a census route and counted all the birds that were seen or heard within 40 m on either side (i.e., 250-m × 80-m plots). Some woodland patches (e.g., narrow shelterbelts) were too narrow to establish such wide sampling plots, so 400-m × 50-m plots were used instead.

Bird censuses were conducted three times at each plot from 04:00 to 10:00 h during the breeding period, and three and two times from 06:00 to 16:00 h during the dispersal and wintering seasons, respectively. One surveyor (Y. Yabuhara) surveyed all plots on days without heavy rain, snowfall or strong winds. Each plot was visited at least once during the 3 h following sunrise in each season because bird detection rates are relatively high during this time. During the wintering season, we could not carry out multiple surveys in two plots, in which deer hunting and forest harvesting were being conducted. Therefore, a total of 42 plots were surveyed during the breeding and dispersal seasons, while 40 plots were surveyed during the wintering season.

Some bird species (e.g., ducks, hawks, and swallows) were excluded from the analysis because they were not strictly related to terrestrial vegetation cover. Candidate birds were classified as either forest specialists or habitat generalists. The classification of each bird species was determined referring to Brazil (2009) and Takagawa et al. (2011). Habitat generalists included several species foraging in an open area such as the oriental turtle dove (*Streptopelia orientalis*) and the yellow-throated bunting (*Emberiza elegans*). For a given species at a given site, we used the maximum abundance observed among the three or two visits per season rather than the average. This is because averaging values across multiple surveys are likely to underestimate the abundance of species that were not detected during one or more surveys (Bibby et al., 1992; Miller et al., 2004).

2.4. Data analysis

We estimated the effects of the three environmental variables, season, and the interaction terms on bird species richness and abundance. We used generalized linear mixed models (GLMMs) with Poisson error distributions and log link functions, considering survey plot as a random effect. In the GLMMs, the species richness or the abundance in each sampling plot was used as a response variable, and the three environmental variables (patch area, connectivity, and woodland type), season, and three interaction terms between the environmental variables and season (patch area × season, connectivity × season, and woodland type × season) were used as explanatory variables. The patch area was log transformed after adding 1. Some of the connectivity indices were also log transformed after adding 1 to lessen the effects of outliers (few plots with large values).We examined the effect of these explanatory variables on the forest specialist or generalist birds separately using model selection procedure based on an Akaike Information Criteria corrected for small sample size (AICc). We modelled all combinations of a single connectivity index, patch area, woodland type, season, and three interaction terms. That is, we ran this trial for 12 types of connectivity indices separately. Then, we selected the lowest AICc model as the best-supported model and reported all models with AICc differences less than or equal to two (Burnham and Anderson, 2002). We calculated the 95% confidence intervals (CIs) for the effect sizes

of patch area and connectivity and for estimated abundance in each woodland type in each season by using a parametric bootstrap from the best-supported model. This allowed us to decide the significance of each explanatory variable by determining whether the 95% CIs overlapped with zero (in the case of patch area and connectivity) or each other (in the case of woodland type). To investigate the effect of spatial autocorrelation, we calculated Moran's I values from the residuals of the best-supported models. These indicated no autocorrelation (|Moran's I| < 0.060, P > 0.19), and therefore, spatial autocorrelation was not considered explicitly in the model.

To analyze the bird community composition, partial redundancy analyses (RDAs) with all three explanatory variables (patch area, connectivity, and woodland type) were performed. We used the connectivity index that was included in the best-supported model for specialist abundance (i.e. ConBR_200). The preliminary analysis in detrended correspondence analysis (DCA) resulted in the short gradient length along the first axis (i.e., gradient length < 3), showing that RDA is more suitable than canonical correspondence analysis (CCA) (Leps and Smilauer, 2003). We performed an ordinary RDA including all three variables and three additional RDAs to use each of the explanatory variables with the two remaining ones as conditional variables. Then, we determined the independent effects of each variable by decomposing the total variation in the community matrix into the unique variation of each variable. Prior to the analysis, community data matrices were Hellinger-transformed, with lower weighting of rare

species (Legendre and Gallagher, 2001). A permutation test with 999 permutations was used to assess the statistical significance. In those analyses, we used function glmer, bootMer, moran.test, dca, decostand, permtest, and rda from the R package lme4, spdep, and vegan.

3. Results

In total, 60 species were observed during the bird survey (Appendix 1). Because 14 species were excluded (see section on methods), 1,089 individuals from 46 species were analyzed. We recorded 38, 30 and 22 species during the breeding, dispersal, and wintering seasons, respectively. These species were classified into forest specialists (26, 22, and 12 species in each season) or habitat generalists (12, 8, and 10 species in each season).

3.1. Factors associated with the species richness and abundance of birds

Table 1 provided all models with AICc differences less than or equal to two for species richness and abundance of specialists and generalists. The mean and 95% CIs of the effect sizes of patch area and connectivity are illustrated in Figure 2, and those of the estimated abundance of birds in each woodland type in each season are illustrated in Figure 3. For specialist species, although several models were well supported (Table 1; Figure 2a), the top-ranked model did not detect any interaction effects between the

environmental variables and season, suggesting that the negative effect of patch area and positive effect of connectivity on species richness were consistent across three seasons. By contrast, we found the interaction effects of connectivity × season and woodland type × season on specialist bird abundance. The connectivity had significant positive effects on specialist bird abundance during the dispersal and wintering seasons (Figure 2b). Specialist bird abundance was higher in riparian broad-leaved woodlands compared to conifer woodlands during the breeding season, but this pattern was reversed during the winter (Figure 3). For generalist species richness, we could not detect any effects other than season in the top-ranked model (Table 1). For generalist bird abundance, however, we found the interaction effects of patch area × season, connectivity × season, and woodland type × season. We found the negative effects of patch area during the dispersal and wintering seasons and the positive effect of connectivity during the dispersal season (Figure 2c). There were significantly higher generalist abundances in riparian and conifer woodlands compared to broad-leaved woodlands during the wintering season (Figure 3).

3.2. Bird community composition

In the analysis of bird community composition, we found that the species composition was partly changed according to the woodland types (Table 2; Figure 4). During the breeding and dispersal seasons, the three woodland types had three distinct

communities. By contrast, during the wintering season, although the effect of woodland type on community composition remained significant ($P < 0.05$), the minimum convex polygons of the three woodland types almost overlapped in the redundancy analysis plots (dashed lines in Figure 4). Connectivity had also significant effect on community composition during the breeding and dispersal seasons, while patch area did not show any effects on community composition (Table 2).

4. Discussion

Based on seasonal changes in resource availability and annual phases of the bird life cycle, birds use varied types of environments flexibly across seasons (Crampton et al., 2011; Zuckerberg et al., 2016). This study demonstrated that species richness, abundance and composition of forest bird communities were associated with patch attributes and connectivity, but also that some of these associations varied depending on the season. For example, connectivity had great influence on generalist bird abundances only during the dispersal season. Woodland type also affected bird abundance and community composition, but their effects differed among seasons.

Many studies indicated that the effects of habitat configuration becomes more important in landscapes of low habitat extent (Andrén, 1994; Fahrig, 2003). The proportion of woodland area in our study region is less than 30 %, and this may partly explain why connectivity had a greater influence than patch area on birds in this study.

Increasing connectivity has several benefits for bird communities. Connectivity increases the number of habitat patches that birds can reach and hence increases available habitat area of neighboring patches. Thus, some area-sensitive species can persist (Awade and Metzger, 2008), and this resulted in the higher species richness and compositional change (Martensen et al., 2008). In addition, dispersal flux through the links of each patch and the stepping stone function of patches would also be important (Saura and Rubio, 2010). For generalist birds, the interaction effects of connectivity × season indicated that the effect of connectivity was positive during the dispersal season only. Because birds actively move during the dispersal season, highly connected patches are more likely to receive dispersing individuals from surrounding patches (e.g., Gutzwiller and Anderson 1992).

Woodland type also explained variations in bird abundance and community composition among sites. Our results indicated that specialist bird abundances in riparian woodlands were higher than those in non-riparian woodlands during the breeding season. Many studies including ours showed that riparian woodlands maintain higher species richness and abundance, as well as distinct species composition, during the breeding season (Palmer and Bennett, 2006; Sabo et al., 2005; Soykan et al., 2012), because there are many more foraging resources and/or complex stand structures. As with many other studies, our results highlight a conservation value of riparian woodlands for raising regional biodiversity (Bennett et al., 2014; Sabo et al., 2005).

By contrast, conifer stands have the highest abundance of specialist birds during the winter. Two conifer specialist species, Coal Tit (*Periparus ater*) and Goldcrest (*Regulus regulus*), moved from high elevation area into lowland area in winter, resulting in the highest bird abundance in conifer stands (Yamaura et al., 2009). In addition, several studies have shown that microclimate (e.g., local temperature) and food availability were prominent drivers of wintering bird abundance (Carrascal et al., 2012a; Meehan et al., 2004). Although deciduous conifer plantation is dominated in our study area, some evergreen conifer stands may reduce the wind velocity and function as shelter against the harsh climatic conditions (Petit, 1989). However, the positive effects of evergreen conifer trees may not be detected in the warmer regions where snow is rare and evergreen broad-leaved trees are dominant.

Patch area had negative effects on specialist species richness throughout all seasons and generalist abundances during the dispersal and wintering season. Our study used a constant sampling size per patch rather than the area adjusted sampling size, and this may partly explain our results in which the species richness and abundance were not increased with the increasing size of habitat patches. Nevertheless, several studies have found negative relationships between bird density and patch size, especially when birds breed or rest in small habitat patches but mainly forage in the surrounding patches as well as matrix area (Estades, 2001; Haila, 1988). Indeed, we often observed birds moving into surrounding patches across the narrow gaps or foraging on the roadside

ground and cultivated fields where snowmelt started earlier than it did inside the woodland patches. Therefore, in addition to the connectivity conservation, management of small fragments and the adjacent matrix conditions may be important, especially for the ability of generalist birds to tolerate harsh climatic conditions and low prey availability in the winter (Carrascal et al., 2012b).

Our results need to be interpreted with caution. Conifer stands have the highest abundance of specialist birds in winter, but they had the least abundance during breeding season. This implies that replacing broadleaved woodlands by conifer plantation would devastate breeding bird communities. We did not consider the detectability bias and bird assemblages in continuous forests with different topographic conditions in bird surveys. Detection probability may vary among seasons because many birds tend to be more cryptic during non-breeding periods. However, unless detection probability varied widely among sites in the same season, the direction of the effects detected in the analysis would not be reversed. In addition, the study was conducted in single year and thus could not evaluate the annual variation of the effects of environmental variables. Although climatic conditions such as snow fall of the survey period were close to the long-term average, annual variation of food resources such as seed/fruit abundance might affect some bird abundances and compositions (Koenig and Knops, 2001; Naoe et al., 2011). Therefore, considering multiple years as well as detection probability and bird assemblages in continuous forests is important in future

studies. This may reinforce the conclusions, or rather lead to a better understanding of the seasonal variations of patch and landscape effects in a wide variety of contexts.

The present study suggests that both connectivity conservation and habitat management are needed, and considering them during multiple seasons could improve management applications. Riparian woodlands supported higher abundance of specialists during the breeding season, but conifer stands have the highest abundance during the wintering season. The connectivity also had positive effects on specialist species richness throughout all seasons and generalist abundances only during the dispersal season. Thus, linking habitat patches used in the breeding season (e.g. riparian woodlands) with those used in other seasons (e.g. conifer stands) through enhancing a woodland network of entire landscape is of prime importance for bird conservation in this region. In this manner, conservation planning in a fragmented landscape needs to consider the role of patch attributes and connectivity during multiple seasons rather than just during the breeding season.

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562 **Table 1**

563 Results of AICc-based model selections. All models with AICc differences less than or equal to two were reported. The connectivity

564 indices were based on three habitat types (i.e., all types of woodlands [Con_BRC], both non-riparian and riparian broad-leaved woodlands

565 [Con_BR], or only non-riparian broad-leaved woodlands [Con_B]) and four threshold distances (50, 100, 150, or 200 m).

Response variable	Explanatory variables	df	AICc	delta
(a) Specialist species				
Species richness	$\log_{10}$(Area) + $\log_{10}$(Con_BR50) + Season	6	532.1	0.00
	$\log_{10}$(Area) + $\log_{10}$(Con_BR50) + Type + Season + Type × season	12	532.5	0.38
	$\log_{10}$(Area) + $\log_{10}$(Con_BR200) + Season	6	533.0	0.90
	$\log_{10}$(Area) + $\log_{10}$(Con_BR50) + Type + Season	8	533.4	1.33
	$\log_{10}$(Con_BR200) + Season	5	533.8	1.70

Abundance	$\log_{10}$(Con_BR200) + Type + Season + $\log_{10}$(Con_ BR200) × season + Type × season	13	820.0	0.00
(b) Generalist species				
Species richness	Season	4	478.1	0.00
	ConBRC_200 + Season	5	478.4	0.29
	$\log_{10}$(ConB_50) + Season	5	479.1	1.00
	ConBRC_50 + Season	5	479.4	1.27
	$\log_{10}$(Area) + Season	5	479.5	1.34
	$\log_{10}$(ConBR_50) + Season	5	479.5	1.38
	$\log_{10}$(ConB_100) + Season	5	479.8	1.71
	$\log_{10}$(ConBR_100) + Season	5	480.1	1.99

Abundance	$\log_{10}$(Area) + $\log_{10}$(Con_B150) + Type + Season + $\log_{10}$(Area) × season + $\log_{10}$(Con_B150) × season + Type × season	16	734.7	0.00

566

Table 2

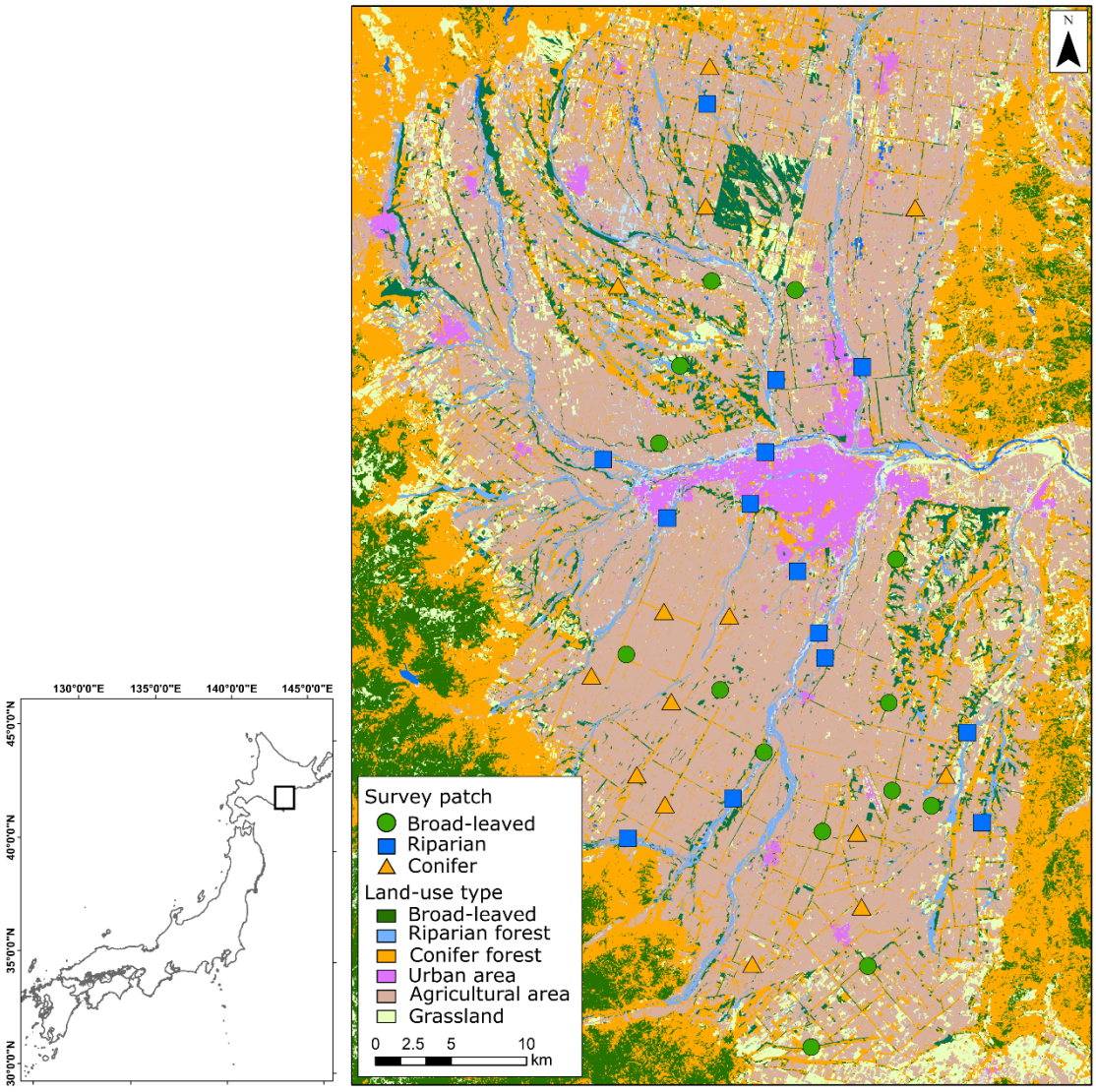
Results of redundancy analyses (RDA). Independent effects (% of variation): the proportion of variation that is explained by each measure. *F*: *F* statistics. *P*: *p* value of *F* statistics.

	Partial RDA		
	Independent effects (% of variation)	*F*	*P*
Breeding			
Area	1.8	0.81	0.732
Connectivity	3.6	1.63	**0.028**
Forest type	10.8	2.47	**0.001**
Total	18.9	2.15	**0.001**
Dispersal			
Area	2.2	1.04	0.429
Connectivity	4.0	1.86	**0.023**
Forest type	12.0	2.77	**0.001**
Total	19.7	2.28	**0.001**
Winter			
Area	1.8	0.77	0.660

Connectivity	3.3	1.40	0.140
Forest type	10.7	2.24	**0.002**
Total	16.8	1.77	**0.006**

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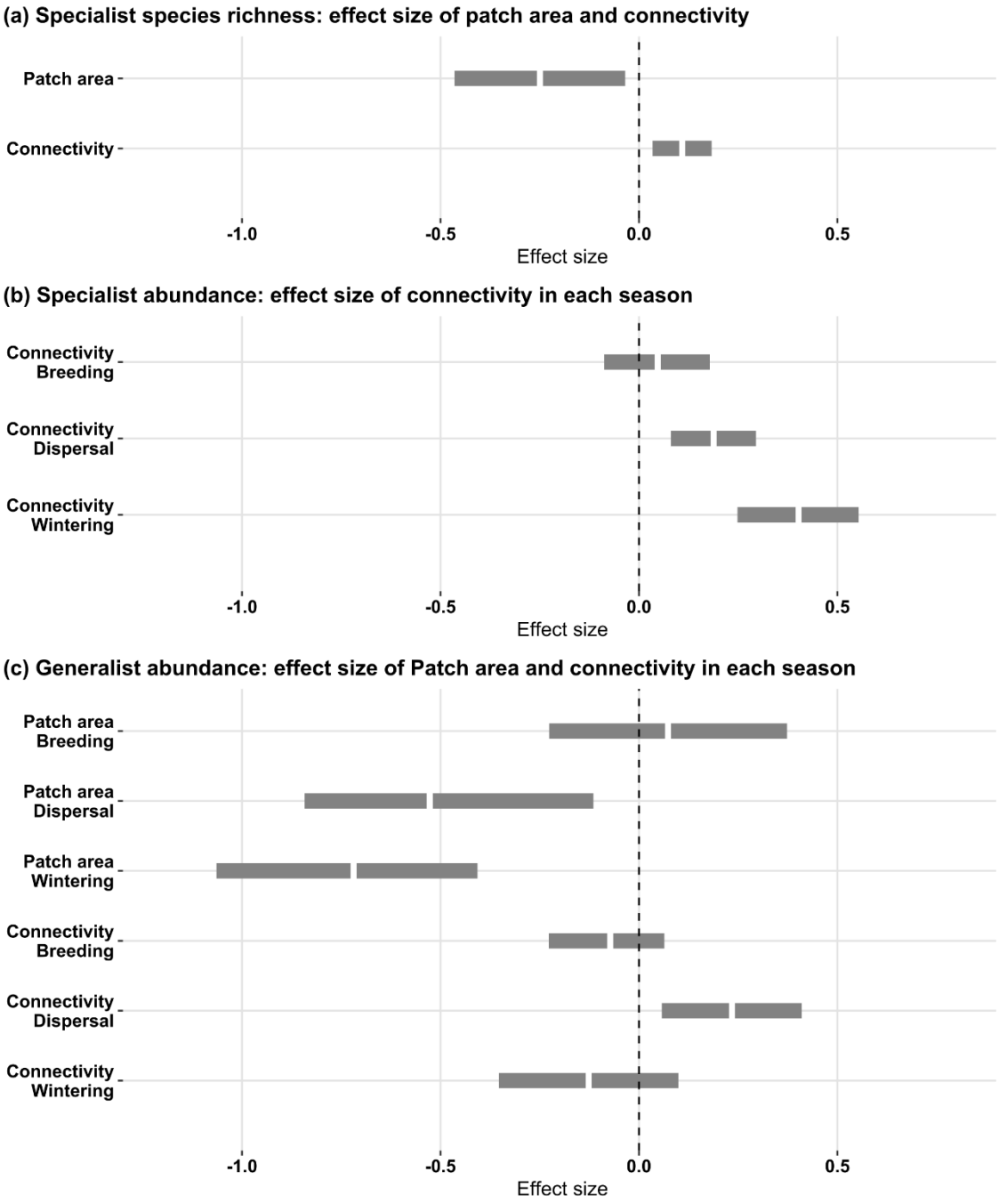
573

574 **Fig. 1.** A map of the study area showing the location of the 42 survey patches. Dots,

575 squares and triangles denote the survey patches established in broad-leaved, riparian and

576 conifer forests, respectively.

577



578

579 **Fig. 2.** The effect sizes of patch area and connectivity predicted based on the

580 coefficients of main and the interaction terms in the best-supported GLMM models. (a)

581 Effects of patch area and connectivity for species richness of specialists, (b) effect of

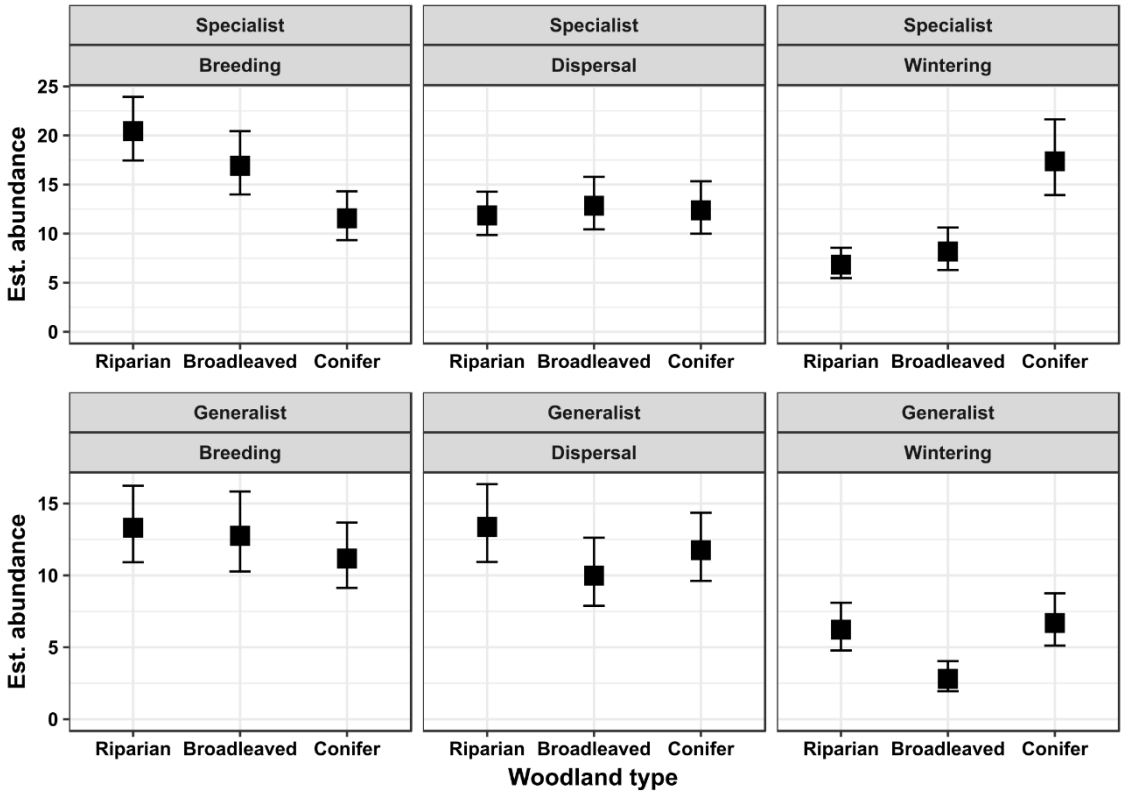
582 connectivity in each season for specialist abundances, (c) effects of patch area and

583 connectivity in each season for generalist abundances. Estimates are shown using the

584 mean values (white mark) and associated 95% CIs (horizontal bands).

585

586



587

588 **Fig. 3.** Abundance of specialist and generalist birds in three habitat types estimated by

589 GLMMs; riparian broadleaved woodlands (Riparian), non-riparian broadleaved

590 woodlands (Broadleaved), and confer woodlands (Conifer), respectively, during three

591 seasons (breeding, dispersal, and wintering season). Estimates are shown using the

592 mean values (black squares) and associated 95% CIs (vertical bars).

593

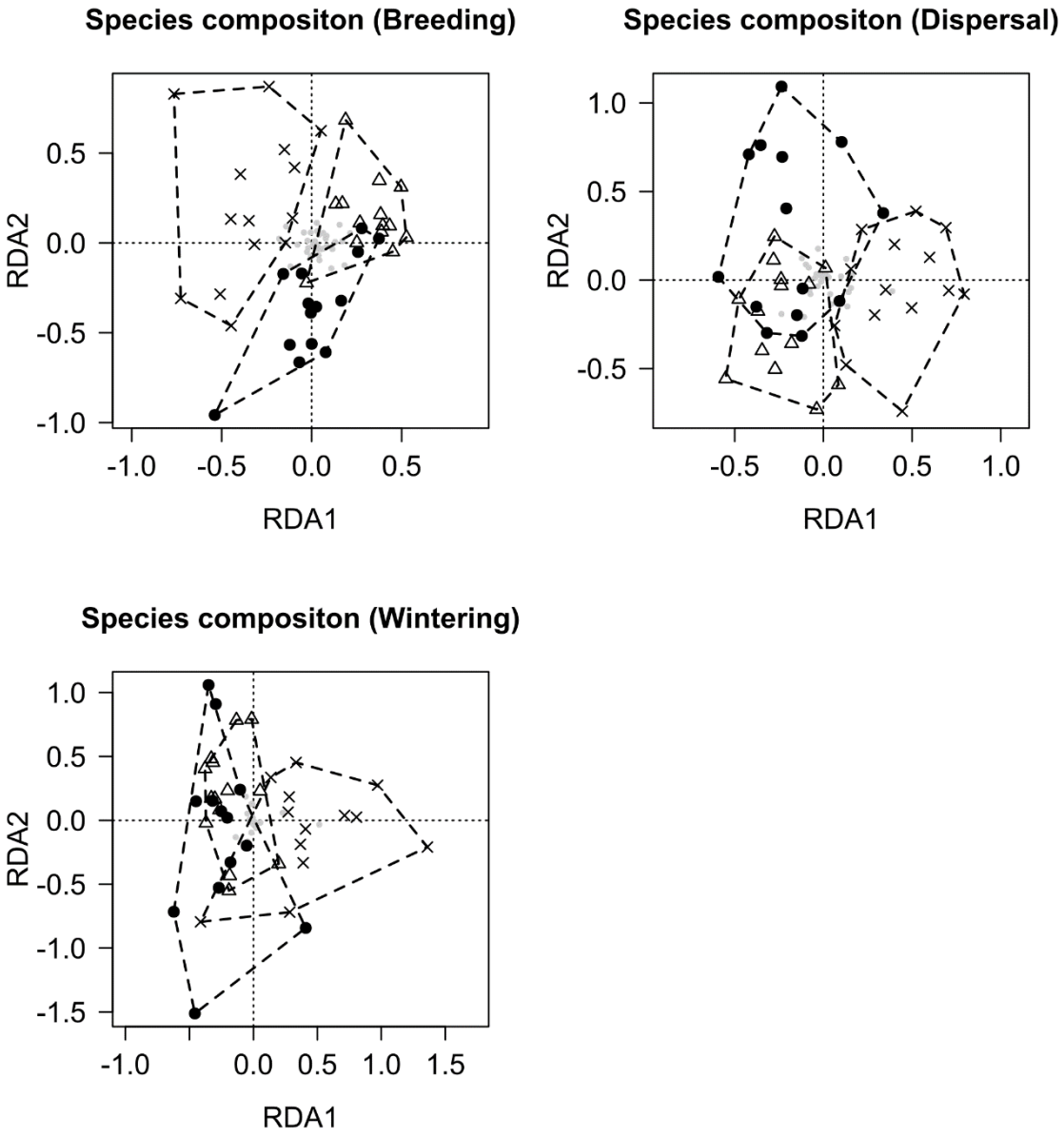


Fig. 4. Redundancy analysis plots for the species composition of all forest species during the breeding, dispersal and wintering seasons, showing the effect of forest type with minimum convex polygons (dashed lines). Closed circles, broad-leaved forest sites; cross marks, conifer forest sites; triangles, riparian forest sites.