Effects of plantation management on biodiversity: large-scale tests considering climates and seasons

（人工林の管理が生物多様性に及ぼす影響：気候と季節を考慮した広域的検証）

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Summary

Context Plantations are increasing globally. While plantations support less biodiversity compared to natural forests, existing studies showed that plantations can be important habitats by managing stand structure and composition (e.g. stand age and non-planted trees). Thus, management methods for conserving biodiversity in plantations have recently been proposed in many regions. Most of knowledges were derived from intensive surveys in a specific region, and in the breeding season for animals. However, the tree species used for plantations and biological communities differ among regions, and animals can move across seasons.

Objectives The aim of this thesis is evaluating the effects of climate, topography, and land use (e.g. landscape context and the tree species used for plantations) on biodiversity in multiple seasons and proposing plantation management for biodiversity conservation in each region.

Methods First, I examined factors determining regionality and seasonality in distribution of birds preferring early-successional or mature forests (hereafter early-successional species and forest species, respectively) by analyzing nationwide monitoring data. Second, I evaluated the effects of the planted tree species and season on biodiversity in conifer plantations by a meta-analysis. Third, I surveyed bird communities in conifer plantations across Hokkaido, northern Japan, and tried to propose plantation management based on stand age and broad-leaved tree proportion (hereafter BL tree proportion), considering regionality and seasonality.

Results Analyzing the monitoring data showed that cool regions are important breeding grounds, while warm and non-snowy regions have also important roles as wintering grounds for migratory birds, both early-successional and forest species. The meta-analysis revealed that pine family plantations in cool regions support higher biodiversity than cypress family plantations. The habitat function of plantations was higher in the wintering season than in the breeding season, although studies on vertebrates were scarce in southern Japan. Furthermore, bird surveys in pine family plantations across Hokkaido revealed as follows: 1) in the breeding season, young plantations served as habitats for early-successional species, but the duration as habitats was shorter in cooler regions; 2) species that prefer broad-leaved forests (hereafter BL forest species) increased with stand age, and increased with BL tree proportion until 25-50%, but remained almost unchanged above the thresholds values; 3) for this group in the wintering season, in regions with more severe climates, the positive effects of stand age were weaker, and the positive effects of BL tree proportion were stronger.

Conclusions Pine family plantations in cool regions of Japan can contribute to conserve biodiversity including breeding migratory birds. In these regions, reconciling both forestry and conservation of both early-successional and BL forest birds would be achieved by ensuring both young and mature plantations in each landscape and retaining BL trees within plantations. In addition, I found climate-dependent effects of stand variables in both seasons in Hokkaido. By contrast, cypress family plantations that dominate in warm regions have generally the low

habitat function. However, studies on vertebrates were scarce in southern Japan, which are important wintering grounds. Future studies should clarify the role of cypress family plantations as wintering habitats and its management effects. To conserve biodiversity across Japan with vast plantations, stand management considering climates, planted tree species, and seasonal roles in each region are needed; plantations in every region can be important roles in a breeding or wintering season.

Chapter 1 --- Introduction

1.1 Global forest changes and biodiversity decline

Natural forests have been lost, fragmented, and degraded globally (Haddad et al. 2015; Liu et al. 2019; FAO 2020). Natural forest area in 2020 decreased to 92.5% of that in 1990 (FAO 2020). 70% of the world's forests are within 1 km of a forest edge (Haddad et al. 2015). Furthermore, most natural forests have experienced to be logged, and are not primary (primary forests are about 30 % of the world's natural forests, and 1 % of temperate forests; de Gouvenain & Silander 2017; FAO 2020). These trends in natural forests have caused drastically forest biodiversity decline (Gibson et al. 2011; Haddad et al. 2015; Newbold et al. 2015; Pfeifer et al. 2017). By contrast, planted forests or plantations that are regenerated artificially are increasing, increase of 123 million ha from 1990, and now account for 7% of the world's forests (FAO 2020; hereafter plantations).

1.2 Plantations and biodiversity conservation

Many of plantations have expanded replacing to natural forests (Puyravaud et al. 2010; Hua et al. 2018). In general, conversion of natural forests to plantations have great negative effects on biodiversity, because forest composition (e.g., tree species) and structure (i.e., vertical and horizontal distribution of trees and vegetation) are less diverse in plantations than in natural forests (Franklin et al. 2000; Brockerhoff et al. 2008; Chaudhary et al. 2016). On the other hand,

in 2012, plantations produced 46.3 % of global industrial round wood for its small area (Pyan et al. 2015). Thus, it was suggested that harvesting timber mainly in plantations and reducing disturbances in natural forests can contribute biodiversity conservation, as conducted in New Zealand (Sedjo & Botkin 1997; Brockerhoff et al. 2008).

Nevertheless, biodiversity conservation in plantations can be important for multiple reasons. First, plantations are often established in productive areas where forest growth rate is high, having high potential for biodiversity conservation (Franklin 1993; Yamaura et al. 2020). Conversely, pristine natures only remain in harsh environment, i.e., cool regions or highlands (Potapov et al. 2017; Sabatini et al. 2018; Yamaura et al. 2020), and thus, it is difficult to sufficiently conserve biodiversity by only protecting these areas (Franklin 1993; Cox & Underwood 2011; Mokany et al. 2020). Only 18 % of forests distributed in protected areas (FAO 2020), and many large mammals and migratory birds do not complete their life history in one protected area (Lindenmayer & Franklin 2002; Johansson et al. 2016). Second, many landscapes are already dominated by plantations (Hartley 2002). For example, plantations as a proportion of total forest area are 36% in East Asia (e.g., 41% in Japan, 39% in China), 30% in Europe excluding Russian Federation (e.g., 95% in Czechia, 89% in UK, 68% in Portugal, and 50% in Germany, Sweden and Ukraine) (FAO 2020). Given that plantations are distributed mainly in productive areas, plantations should dominate many of warm areas and lowlands in these regions. Third, biodiversity conservation can sometimes be enhanced in plantations at little additional cost to management (Norton 1998). Therefore, in many regions across world,

the importance of conserving biodiversity in plantations was acknowledged, and specific management methods for it have recently come to be proposed (Yamaura et al. 2012a; Demarais et al. 2017; McFadden & Dirzo 2018).

1.3 Factors determining biodiversity in plantations

To reconcile forestry and biodiversity conservation in plantations at a stand scale, identifying factors determining plantation biodiversity is necessary (Brockerhoff et al. 2008; Demarais et al. 2017; Castaño-Villa et al. 2019). Previous studies suggested that the importance of plantation management, including 'what is planted', the intensity or timing of thinning and harvesting, and retaining or ameliorating the amount of non-planted native trees (Hartley 2002). For example, native, mixed plantations generally support higher bird abundance and species richness than exotic monocultures (Castaño-Villa et al. 2019). The abundance and richness of species depending forests (hereafter forest species) increase with stand age of plantations (Castaño-Villa et al. 2019; Spake et al. 2019). Furthermore, with increase in the amount of non-planted trees within plantations (e.g., broad-leaved trees within conifer plantations), the species richness and abundance of animal species depending on those trees increase (Ohsawa 2007; Yoshii et al. 2015; Lindbladh et al. 2017).

By contrast, plantations just after planting, which have open environments like grasslands, can provide important habitats for early-successional species that have recently decreased in many parts of the world (Yamaura et al. 2012b; Toyoshima et al. 2013; Ram et al.

2020; Bakx et al. 2020). Not only natural forests, but also grasslands, wetlands, and farmlands have been replaced by plantations in many regions; plantations are expected to conserve both mature forests and early-successional species (Yamaura et al. 2012a, 2012b; Iezzi et al. 2020).

1.4 Challenges—considering regional differences and multiple seasons

Most of these knowledges were derived from intensive surveys in a specific region, and in the breeding season (from spring to summer) for animals (e.g., Toyoshima et al. 2013; Lindbladh et al. 2017). Since tree species used for plantations differ among regions, planted tree species effects on biodiversity in plantations have been rarely examined in local studies (but see Mitsuda et al. 2007; Nothdurft et al. 2012), although it has been acknowledged to be a critical factor (Brockerhoff et al. 2008). Meta-analyses synthesizing various studies treated 'what is planted', but many species were grouped together, e.g., as exotic or native species (Castaño-Villa et al. 2019). However, comparisons of the biodiversity of forests planted with specific tree species are needed to inform regional planning. This is because the species that is planted can exert strong influences on resource availability (light, water, and soil nutrients; Barbier et al. 2008; Petersson et al. 2019). This has consequences for the establishment of native plant communities (Fimbel & Fimbel 1996; Petersson et al. 2019; Yamaura et al. 2019), leading to the differences in biodiversity of plantations among planted tree species ('the tree species matter'; Felton et al. 2020).

Moreover, species distributions, habitat selection, and species composition also differ

depending on regional contexts, including climatic conditions (Barbet-Massin et al. 2012; Crosby et al. 2019). Climates affect organisms both directly and/or indirectly via a wide range of processes, such as physiology, prey resources, vegetation, or disturbances (Cooper et al. 2006; Huston & Wolverton 2009; Yamaura et al. 2011; Betts et al. 2019). Reflecting these climate effects, species or community responses to land-use changes would be climate-dependent, as shown recent studies (Amano et al. 2011; Betts et al. 2019; Spake et al. 2020). Thus, at large scales, identifying environmental factors that determine regionality in biodiversity and clarifying its effects on conservation effectiveness by plantation stand management are needed.

Furthermore, climatic conditions also change seasonally, and winter specific environments (e.g., low temperature or snow cover) strongly restrict the distribution or survival of organisms from the cool-temperate to the arctic zone (Leech & Crick 2007; Somveille et al. 2015). Especially in deciduous broad-leaved forests that cover the northern half of Japan, the abundance of food resources (e.g., plants and insects) for animals increases rapidly from spring to summer, and becomes low in winter due to low temperature, snow cover, and falling leaves (Herrera 1978; Huston & Wolverton 2009). Many animal populations, especially birds with great ability to move, consequently alter their range, habitat use, behavior patterns, or food habits (Marchand 2014; Elsen et al. 2018). For example, 19 % of the world's bird species are migratory (Kirby et al. 2008). Most breeding migratory birds, which are important components of bird communities from the cool-temperate to the arctic zone, move to warmer regions in

winter (Kirby et al. 2008; Newton 2008). For bird communities, considering not only regionality, but also seasonality is therefore necessary for conservation in plantations.

1.5 Present state of plantations in Japan

In Japan, conifer monoculture plantations have replaced broad-leaved natural forests and grasslands, mainly after World War II (1950-1980), and now consequently account for 41% of forest areas (Yamaura et al. 2012a; Forestry Agency 2017a). Mature plantations are abundant, and recently, large-scale clearcutting is occurring across Japan in effort to increase domestic wood supply (Forestry Agency 2019, 2020). At the same time, introducing forest environment tax that collect 1000 JPY (~10 USD) per person annually, in total over 600 million USD across the country, from 2024 have decided; the opportunity for enhancing biodiversity and ecosystem services in plantations has been maturing (Forestry Agency 2019; Kakizawa et al. 2018).

1.6 Aim of this thesis

The aim of this thesis is twofold. One is understanding the natural and anthropogenic factors that determine the regionality in forest biodiversity and seasonality in bird diversity in Japan (Chapter 2-3). The other is proposing plantation management for bird conservation with considering regionality and seasonality (Chapter 4). In Chapter 2, to clarify factors determining seasonal large-scale distribution of forest birds and early-successional birds, which are conservation targets in plantations, I analyzed a monitoring dataset that conduct bird survey in

natural forests and grasslands across Japan in both the breeding and wintering seasons. Specifically, I examined the effects of climate, topography, and land use on bird species richness in forests and grasslands in each season. In Chapter 3, to evaluate the potential of plantations in each region and season as habitats, I collected existing studies that compare biodiversity between plantations and natural forests in Japan, and examined the effects of the planted tree species on biodiversity of a wide range of taxa and those of season on vertebrates/bird diversity in plantations by a meta-analysis. Based on findings in Chapter 2 and 3, in Chapter 4, I surveyed bird communities in plantations of Todo fir and Japanese larch across Hokkaido, northern Japan, in the breeding and wintering seasons. Considering regional differences in climates, I analyzed the effects of stand age and the broad-leaved tree proportion within plantations on broad-leaved forest species (i.e., species preferring broad-leaved forests, hereafter BL forest species) and early-successional species, in two seasons separately. Finally, I discussed the importance of conserving biodiversity in plantations and considering the regionality and seasonality.

Chapter 2

Seasonality in spatial distribution: climate and land use have contrasting effects on the species richness of breeding and wintering birds

2.1 Abstract

Many studies have examined large-scale distributions of various taxa and their drivers, emphasizing the importance of climate, topography, and land-use. Most studies have dealt with distributions over a single season or annually without considering seasonality. However, animal distributions and their drivers can differ among seasons because many animals migrate to suitable climates and areas with abundant prey resources. I aim to clarify seasonality in bird distributions across Japan and their drivers. I examined the effects of climate (annual mean temperature, snow depth), topography (elevation), and land use (extent of surrounding habitat) on bird species richness, in the breeding and wintering seasons separately, using nationwide data (254 forest and 43 grassland sites, respectively). I separately analyzed the species richness of all species, residents, short-, and long-distance migrants in forests and grasslands. In the breeding season, the annual mean temperature negatively affected all groups (except for forest and grassland residents), and the extent of surrounding habitat positively affected many groups. By contrast, in the wintering season, temperature positively affected all groups (except for forest residents), and the extent of surrounding habitat positively affected only grassland long-distance migrants. In both seasons, the species richness of forest and grassland residents was high in regions of moderate and high temperature, respectively. Moreover, snow depth negatively affected all forest groups in the wintering season. Mapping expected species richness suggested that regions with different climates served as habitats for different groups during different seasons. All regions were important bird habitats depending on the season, reflecting

the contrasting effects of temperature across seasons. In the breeding season, surrounding land-use was also an important driver. To understand the seasonal role that each region and environment plays in maintaining species/communities, a large-scale study considering both environmental seasonality and species distribution is needed.

2.2 Introduction

Exploration of large-scale biodiversity patterns and drivers thereof is a fundamental theme of ecology (Wallace 1876; Gaston 2000). Many studies have evaluated the relationships between environmental factors and the large-scale distribution patterns of various taxa (Kreft & Jetz 2007; Howard et al. 2015; Barbet-Massin et al. 2017). Both climate (e.g., temperature and precipitation) and topography (e.g., elevation) are major drivers of large-scale organism distributions; these factors determine the productivity of vegetation (Hawkins et al. 2003). Thus, the species richness of various taxa is higher in warm, wet areas with low to moderate altitude (Gaston 2000; Hawkins et al. 2003). Moreover, recent studies have suggested that land use (e.g., the extent of surrounding appropriate habitat) is also an important driver in this context (Yamaura et al. 2011; Newbold et al., 2016).

Most previous studies analyzed the distribution of organisms over a single season (particularly the breeding season) or the annual distribution based on the geographical range maps and did not consider seasonality of either environments or species distributions (Ding et al. 2006; Yamaura et al. 2011; but see Lennon et al. 2000). However, the suitability of various regions as homes for animals can differ seasonally. In cool regions (e.g., areas with deciduous broad-leaved forests), the productivity of plants and insects increases rapidly from spring to summer (Herrera 1978; Huston & Wolverton 2009). For animals using these rapidly increasing resources (termed “prey pulses”), cool regions would be more suitable than other regions at this time (Yamaura et al. 2011; Dalby et al. 2014; Fristoe 2015). By contrast, regions that are cool

in winter may be unsuitable for many animals because of their harsh climate and low productivity (Somveille et al. 2015).

To cope with such seasonality, many animals engage in seasonal migration (Bauer & Hoye 2014; Marchand 2014). For example, most breeding migratory birds, which are important components of bird communities from the cool-temperate to the arctic zone, move to warmer regions in winter (Kirby et al. 2008; Newton 2008). Furthermore, the effects of drivers may differ among seasons, and distribution studies across single seasons may overlook regions that exhibit high levels of species richness in other seasons. In winter, snow is present over vast areas from the temperate to the arctic zone, covering about half of the land mass in the Northern Hemisphere (Hori et al. 2017). In grasslands, snow may cover the vegetation completely. Even in forests, some arboreal birds forage on the ground more frequently in the wintering season than in the breeding season, probably because prey is relatively abundant on the ground in winter (Hartley 1987; Cale 1994). The availability of vegetation or prey on the ground decreases with increasing snow depth, and this affects the distribution of many animals in winter (Johnson & Sherry 2001; Leech & Crick 2007).

The effects of environmental seasonality on species distributions are important because the predicted changes in the global environment may differ among seasons. Increases in temperature due to global warming may be more apparent at higher latitudes, and in winter than in summer (IPCC 2007, 2014). Furthermore, warmer and lower altitude areas have been altered by human land-use; pristine areas only remain in harsh environments (Potapov et al. 2017;

Sabatini et al. 2018). Therefore, in this study, I explored the effects of climate (annual mean temperature and maximum snow depth), topography (elevation), and land use (extent of suitable habitat within 1.25, 5, or 10 km of a monitoring site) on bird species richness, in the breeding and wintering seasons separately, using a large monitoring dataset (254 forest and 43 grassland sites evaluated by the same method in both seasons). The sites were distributed across Japan, from the warm-temperate to the boreal zone (approximately 31–45.5°N). I analyzed the effects of environmental factors on the relative species richness of all species and of three specific groups (residents, short-distance [SD] migrants, and long-distance [LD] migrants) in each of two types of habitat (forest and grassland). Finally, to explore the seasonal role played by each region in terms of bird species richness, I separately mapped the expected species richness of each group and of all species as functions of climate, land use, and topography in the breeding and wintering seasons.

2.3 Materials and Methods

2.3.1 Bird data

Bird data were collected in a survey of terrestrial birds in Japan; this was a component of the "Monitoring Sites 1,000 Project" conducted by the Ministry of the Environment (http://www.biodic.go.jp/moni1000/findings/data/index_file_terrestrialbird.html [in Japanese]). This nationwide survey commenced in 2003; both forest and grassland sites were visited. The forest sites are principally natural forests (deciduous or evergreen broad-leaved, evergreen conifer, or mixed forests) and the grasslands include wet and dry grasslands and meadows. At each site, a survey is conducted every 1–5 years. In each survey year, trained volunteers visit each site four times in the breeding (April to July) and wintering (December to February) seasons and record all birds detected within a 50-m radius of five point-count locations, which are > 100 m apart. The surveys are conducted on both clear and cloudy days (from 0400 to 0900 h in the breeding season and from 0800 to 1100 h in the wintering season) that are not very windy. The survey period in the breeding season is earlier in southern areas where migrants first arrive (i.e., from April to May in Kyusyu, from June to July in Hokkaido), and the survey clock time is chosen, in certain regions, to avoiding the buzzing of cicadas (i.e., from 0400 h in Hokkaido and northern Honshu where cicada buzzing can be very loud, and from 0500 or 0600 h in other regions).

I used the survey results from 2009–2015 because the same survey method (i.e., point census counts) was used in each of these years. To simplify the analyses, I used only the total

species richness observed in five point-count locations for each site in the latest year as the analysis unit. To control for island size effects, I evaluated data from sites on only the four largest islands of the Japanese archipelago (i.e., Honshu, Hokkaido, Kyusyu, and Shikoku; Yamaura et al. 2011; Katayama et al. 2014; Appendix S2.1). In addition, I excluded one high-altitude site in Hokkaido (Mt. Daisetsu) because the annual mean temperature there is very low; hence, I regarded the site as an outlier. Ultimately, I used data from 254 forest and 43 grassland sites visited in both breeding and wintering seasons (Appendix S2.2). I excluded data on nocturnal birds because of mismatches in terms of diurnal survey clock times, and I also excluded data on raptors, which generally have large home ranges and may thus move among adjacent sites (Jetz et al. 2004).

Based on previous reports (Kiyosu 1965; Takagawa et al. 2011; Ueta et al. 2011; Yamaura et al. 2011), I categorized all bird species into three groups by migratory traits (LD migrants, SD migrants, and residents) and two groups by habitat preference (forest and grassland, i.e., generalists were also categorized into either group; Appendix S2.3). Next, I determined the relative species richness of all species and of each group (residents, SD migrants, and LD migrants) during each season at each site. I evaluated only species inhabiting principally forests at the forest sites and only species inhabiting principally grasslands at the grassland sites. I defined LD migrants as species migrating from outside Japan to breed or overwinter in Japan, SD migrants as species migrating within Japan to breed and overwinter in different regions, and residents as species that are relatively sedentary throughout the year (Yamaura et al. 2009).

2.3.2 Environmental factors

Environmental factors that potentially affect bird species richness include the annual mean temperature and the maximum snow depth (climatic factors; Leech & Crick 2007; Yamaura et al. 2011), elevation (a topographic factor; Davies et al. 2007), and the extent of appropriate surrounding habitat within 1.25, 5, or 10 km of the center of each site (a land-use factor; Barbet-Massin et al. 2012; Howard et al. 2015). I calculated the value of each environmental factor at the center of each site (the centroid of the five point-count locations at each site) using ArcGIS 10.2.2 software (ESRI, CA, USA).

Climate

The annual mean temperature is important in terms of breeding bird species richness in Japan (Yamaura et al. 2011). In high-rainfall regions such as Japan, temperature determines vegetation productivity and seasonality (Ichii et al. 2002; Hawkins et al. 2003; Appendix S2.4), both of which are important for bird distributions (Hurlbert & Haskell 2003; Somveille et al. 2015; Fristoe 2015). I found that the annual mean temperature was strongly correlated with the mean temperature during the breeding/wintering season, suggesting that considering these variables simultaneously in analyses would be problematic. Therefore, to compare the effects of these factors, I constructed generalized linear mixed models (GLMMs) for preliminary analyses. The results showed that, for both forests and grasslands, the annual mean temperature performed

well in both seasons (i.e., for six groups this showed the lowest Akaike information criterion [AIC], for another seven groups the ΔAIC was < 2, and for the remaining three groups the ΔAIC was < 3; Appendix S2.5). Therefore, I selected the annual mean temperature for all analyses.

In the wintering season, snow cover can negatively affect bird survival and prey availability near the ground (Leech & Crick 2007). Therefore, I selected the maximum snow depth (hereinafter: snow depth) as an additional climatic factor when analyzing data from the wintering season. I used the Mesh Climate Value 2010 (a contiguous nationwide grid of 1-km^2 squares with 30-year [1981–2010] mean monthly temperatures, snow depths, and other data provided by the Meteorological Agency of Japan; Appendix S2.6a,b; http://nlftp.mlit.go.jp/ksj/index.html [in Japanese]) to this end.

Topography

Elevation is important in terms of large-scale bird distributions (Davies et al. 2007). Therefore, I selected elevation as a topographic variable. I used the Elevation and Slope Angle Tertiary Mesh, (a contiguous nationwide grid of 1-km^2 squares with mean elevations and other data, provided by the Geospatial Information Authority of Japan; Appendix S2.6c; http://nlftp.mlit.go.jp/ksj/index.html [in Japanese]) to this end.

Land use

The extent of habitat on the landscape scale is one of the most commonly used explanatory

variables in studies on the effects of land use on the large-scale distributions of organisms (including birds; e.g., Barbet-Massin et al. 2012; Howard et al. 2015). I used the High Resolution Land-Use and Land-Cover Map (2006–2011) of the Japan Aerospace Exploration Agency (JAXA) (Appendix S2.7; http://www.eorc.jaxa.jp/ALOS/lulc/jlulc_jpn.htm [in Japanese] to this end); these are the latest land-use data. However, the accuracy of land-use categorization was low (e.g., the accuracy rate for evergreen broad-leaved forests was < 36% because of incorrect categorization of such forests as other forest types). Although the landscape effects of deciduous broad-leaved natural forests may differ from those of conifer plantations (Yamaura et al. 2011), I was forced to use the total extent of forests (i.e., evergreen broad-leaved, deciduous broad-leaved, evergreen conifer, and deciduous conifer forests) when evaluating forest sites, and the total extent of open habitats (paddy fields, grasslands, and agricultural lands) when evaluating grassland sites. To compare the effects of the extent of habitat (forests for analyses of forest groups and open habitats for analyses of grassland groups) within 1.25, 2.5, 5, 10, and 15 km of the center of each site (hereafter, surrounding habitat), I constructed GLMMs for preliminary analyses. The results showed that, for the analyses of forest groups in the breeding season, the extent of habitat within 1.25 km gave the best quality model (i.e., for all species, residents, and SD migrants this showed the lowest AIC, and for LD migrants the ΔAIC was 0.2). However, the surrounding habitat within 10 km offered the best model for analyses of forest groups in the wintering season (i.e., for SD migrants this showed the lowest AIC, and for all other groups the ΔAIC was < 2), and surrounding habitat within 5 km

performed best for analyses of grassland groups in both seasons (i.e., for all species in the breeding season and LD migrants in both seasons, this showed the lowest AIC, and for the other groups, except for SD migrants in the breeding season, the ΔAIC was < 2; Appendix S2.8). Therefore, I selected these land-use factors to analyze each habitat and season.

2.3.3 Statistical analyses

I analyzed the effects of environmental factors on the relative species richness of each group and of all species using a GLMM that considered spatial autocorrelation (a spatial GLMM, Family = Poisson, link function = log; Dormann et al. 2007). This allowed us to evaluate spatial correlation structures using a variance–covariance matrix that reflected the distances between locations, and has been used in previous studies (Lennon et al. 2011; Brambilla & Ficetola 2012). I chose the exponential distribution as the correlation function, based on the semivariograms (Appendix S2.9; Dormann et al. 2007). For each season (breeding and wintering), I separately considered the relative species richness of all species and that of three bird groups (residents, SD migrants, and LD migrants) in two habitats (forest and grassland) as response variables.

To avoid multicollinearity, I calculated variance inflation factors (VIFs) before the analyses, using models featuring linear values for each environmental factor for all species in each habitat and season. For grassland in the wintering season, I found that the VIF of the annual mean temperature was > 3; however, I considered temperature a particularly important driver

in both seasons. Therefore, I removed snow depth, which had the second largest VIF, from our analyses of grassland birds in the wintering season. Finally, in both habitats in both seasons, the VIF for every variable was < 3, suggesting that all variables were suitable (Zurr et al. 2010; Appendix S2.10). I evaluated six explanatory variables (annual mean temperature, the extent of surrounding habitat, and elevation and their squares) that might affect both breeding forest birds and breeding and wintering grassland birds, and eight explanatory variables (these three factors and snow depth, and their squares) that might influence wintering forest birds. All environmental factors were standardized prior to analyses.

The spatial GLMM did not allow calculation of the AIC because the algorithm exploits the penalized quasi-likelihood method. Thus, to select the most parsimonious model (the best spatial model), I performed backward selection based on the semi-partial R^2 of the explanatory variables (Jaeger et al. 2017). First, I created a full model featuring all explanatory variables. Then, I deleted only one insignificant variable (least semi-partial R^2), and repeated this step until only significant variables (semi-partial $R^2 > 0.02$, and lower limit 95 % confidence interval for semi-partial $R^2 > 0.001$) remained. I conducted all analyses using the *glmmPQL* function of 'MASS' v. 7.3.45 (Venables & Ripley 2002), 'nlme' v. 3.1.131 (Pinheiro et al. 2017), and the *r2beta* function of 'r2glmm' v. 0.1.2. (Jaeger 2017) running in R v. 3.3.0 (R core team 2016).

To determine whether I could use the spatial GLMMs (assuming a Poisson distribution without considering over-dispersion and survey year effects), I constructed generalized linear models (GLMs assuming a Poisson distribution), GLMMs with random site effects to account

for over-dispersion, and GLMMs with random year effects. Coefficients obtained from the GLMs and the three types of GLMMs were nearly identical, and the coefficients of the factors involved in the best spatial models never varied by more than 15%, suggesting that considering the effects of over-dispersion and survey years is unnecessary. Furthermore, when I changed the value of the semi-partial R^2 for model selection from 0.02 to 0.05 or 0.1, the main results did not change.

2.3.4 Mapping bird species richness

I mapped the expected species richness of all species and of three bird groups (all species, residents, SD migrants, and LD migrants) found in two habitats (forest and grassland). I divided the four largest islands of Japan into grid squares of 1 km in length. This was the same grid size that I used for the climate and topography data. Then I calculated the values of environmental factors (annual mean temperature, snow depth, elevation, and extent of surrounding habitat within 1.25, 5, and 10 km) at the center of each grid. Finally, I mapped the expected species richness and any differences among seasons on the grid scale, using the best (i.e., most parsimonious) spatial models derived from backward selection (Table 2.1). In this context, I assumed that the areas used for predictions were covered by homogenous forests or grasslands (i.e., forest sites were assumed to be natural forests, as were the survey sites). I used ArcGIS 10.2.2 (ESRI, CA, USA) to perform all mapping procedures.

2.4 Results

In the breeding season, the best model for all three groups (residents, SD migrants, and LD migrants) and all species in both habitats included annual mean temperature, which had highest explanatory power. For four of the six groups (LD migrants in both habitats, and forest residents and SD migrants) and all species in both habitats, the extent of surrounding habitat was also included in the model (Table 2.1). In the wintering season, the best model for all three forest groups and all forest species included annual mean temperature and snow depth (Table 2.1), and the best models for all three grassland groups and all grassland species also included temperature. Variations in species richness were substantially explained by these climatic factors alone. For all groups (except residents in both habitats), the explanatory power of the wintering season models was comparable to, or higher than, those of breeding birds (Table 2.1).

Table 2.1. The best spatial GLMMs (estimates ± standard errors [semi-partial R^2, Wald *p*-value]). SD: short distance; LD: long distance; Breeding: breeding season; Wintering: wintering season; TEMP: annual mean temperature; SNOW: maximum snow depth; ELEV: elevation; AREA: area of surrounding suitable habitat (within a radius of 1.25 km for breeding forest birds, 10 km for wintering forest birds, and 5 km for grassland birds in both seasons); Range: the average distance over which values for the response variable are correlated (note that spatial autocorrelation must be considered when these distances are greater than the minimum distance between survey sites [forest sites: 0.537 km, grassland sites: 14.648 km]); Cross marks: explanatory variables that were not used in construction of the full model to avoid multicollinearity.

Variables	All grassland species		All forest species	
	Breeding (R^2=0.377)	Wintering (R^2=0.688)	Breeding (R^2=0.173)	Wintering (R^2=0.198)
Intercept	2.15±0.08	1.52±0.16	2.82±0.02	2.56±0.03
TEMP	-0.13±0.04 (R^2=0.203, p<0.01)	0.99±0.16 (R^2=0.672, p<0.01)	-0.08±0.02 (R^2=0.068, p<0.01)	
$(TEMP)^2$	0.15±0.06 (R^2=0.142, p=0.02)	-0.35±0.16 (R^2=0.112, p=0.03)	-0.05±0.02 (R^2=0.050, p<0.01)	-0.06±0.02 (R^2=0.039, p<0.01)
SNOW	×	×	×	
$(SNOW)^2$	×	×	×	-0.06±0.01 (R^2=0.126, p<0.01)
ELEV				
$(ELEV)^2$				
AREA	0.13±0.05 (R^2=0.175, p=0.01)		0.06±0.02 (R^2=0.049, p<0.01)	
$(AREA)^2$	-0.08±0.04 (R^2=0.089, p=0.07)			
Range	3.666 km	16.091 km	0.001 km	1.046 km

Variables	Grassland residents		Forest residents	
	Breeding (R^2=0.638)	Wintering (R^2=0.424)	Breeding (R^2=0.136)	Wintering (R^2=0.082)
Intercept	0.37±0.15	-0.67±0.24	1.89±0.02	1.90±0.02
TEMP	0.78±0.14 (R^2=0.614, p<0.01)	1.10±0.22 (R^2=0.424, p<0.01)		-0.07±0.02 (R^2=0.072, p<0.01)

$(TEMP)^2$	-0.31±0.13 (R^2=0.122, p=0.02)		-0.06±0.02 (R^2=0.068, p<0.01)	
SNOW	×	×	×	
$(SNOW)^2$	×	×	×	-0.04±0.01 (R^2=0.039, p<0.01)
ELEV				
$(ELEV)^2$	0.12±0.06 (R^2=0.114, p=0.08)		0.03±0.01 (R^2=0.041, p<0.01)	
AREA			0.06±0.02 (R^2=0.026, p<0.01)	
$(AREA)^2$				
Range	0.000 km	0.001 km	0.001 km	2.546 km

Variables	Grassland SD migrants		Forest SD migrants	
	Breeding (R^2=0.191)	Wintering (R^2=0.627)	Breeding (R^2=0.129)	Wintering (R^2=0.405)
Intercept	1.44±0.09	0.93±0.19	1.72±0.03	1.59±0.04
TEMP	-0.12±0.05 (R^2=0.135, p=0.02)	0.77±0.25 (R^2=0.605, p<0.01)	-0.08±0.02 (R^2=0.053, p<0.01)	0.25±0.04 (R^2=0.178, p<0.01)
$(TEMP)^2$	0.12±0.07 (R^2=0.069, p=0.10)	-0.29±0.17 (R^2=0.109, p=0.03)	-0.04±0.02 (R^2=0.021, p=0.02)	
SNOW	×	×	×	
$(SNOW)^2$	×	×	×	-0.08±0.02 (R^2=0.134, p<0.01)
ELEV				0.12±0.04 (R^2=0.038, p<0.01)
$(ELEV)^2$				-0.07±0.03 (R^2=0.030, p=0.02)
AREA				
$(AREA)^2$			-0.04±0.01 (R^2=0.051, p<0.01)	
Range	0.017 km	9.904 km	0.000 km	1.320 km

Variables	Grassland LD migrants		Forest LD migrants	
	Breeding (R^2=0.554)	Wintering (R^2=0.493)	Breeding (R^2=0.167)	Wintering (R^2=0.194)
Intercept	0.93±0.17	-0.10±0.25	1.56±0.04	0.62±0.06
TEMP	-0.46±0.08 (R^2=0.446, p<0.01)	0.74±0.20 (R^2=0.359, p<0.01)	-0.18±0.03 (R^2=0.110, p<0.01)	0.13±0.05 (R^2=0.023, p=0.02)
$(TEMP)^2$	0.22±0.13 (R^2=0.082, p=0.10)		-0.08±0.03 (R^2=0.039, p<0.01)	-0.10±0.05 (R^2=0.023, p=0.04)
SNOW	×	×	×	-0.10±0.04 (R^2=0.073, p=0.01)
$(SNOW)^2$	×	×	×	
ELEV		0.55±0.28 (R^2=0.078, p=0.06)		
$(ELEV)^2$		-0.29±0.23 (R^2=0.084, p=0.21)		
AREA	0.38±0.10 (R^2=0.316, p<0.01)	0.37±0.13 (R^2=0.113, p<0.01)	0.07±0.03 (R^2=0.021, p=0.03)	
$(AREA)^2$	-0.19±0.08 (R^2=0.124, p=0.03)			
Range	0.148 km	12.093 km	0.000 km	0.000 km

2.4.1 Effects of annual mean temperature

During the breeding season, for SD migrants and LD migrants from both forests and grasslands, species richness was high in areas of low annual mean temperature (Fig. 2.1i, k, m, o), although the pattern shown by forest SD migrants was less pronounced than patterns shown by other groups (Fig. 2.1i). Reflecting these patterns, in cool areas, the species richness of all grassland species was high and that of all forest species also tended to be high (Fig. 2.1a, c). The species richness of forest residents was relatively higher in areas of moderate temperature (approximately 10°C), although this pattern was not obvious (Fig. 2.1e). By contrast, the species richness of grassland residents was higher in warmer areas (Fig. 2.1g).

By contrast, in the wintering season, for both forest and grassland birds in SD migrant and LD migrant groups, species richness was greater in areas of higher annual mean temperature (Fig. 2.1j, l, n, p), although the patterns of forest LD migrants were less clear than those of other groups (Fig. 2.1n). Reflecting these patterns, in warm areas, the species richness of all grassland species was high and that of all forest species also tended to be high (Fig. 2.1b, d). The positive effects of temperature on the diversity of grassland species was more notable than the effect on forest species. For forest residents, species richness tended to be low in warm areas (Fig. 2.1f). Grassland residents exhibited patterns similar to those in the breeding season; the species richness was greater in warmer areas (Fig. 2.1h).

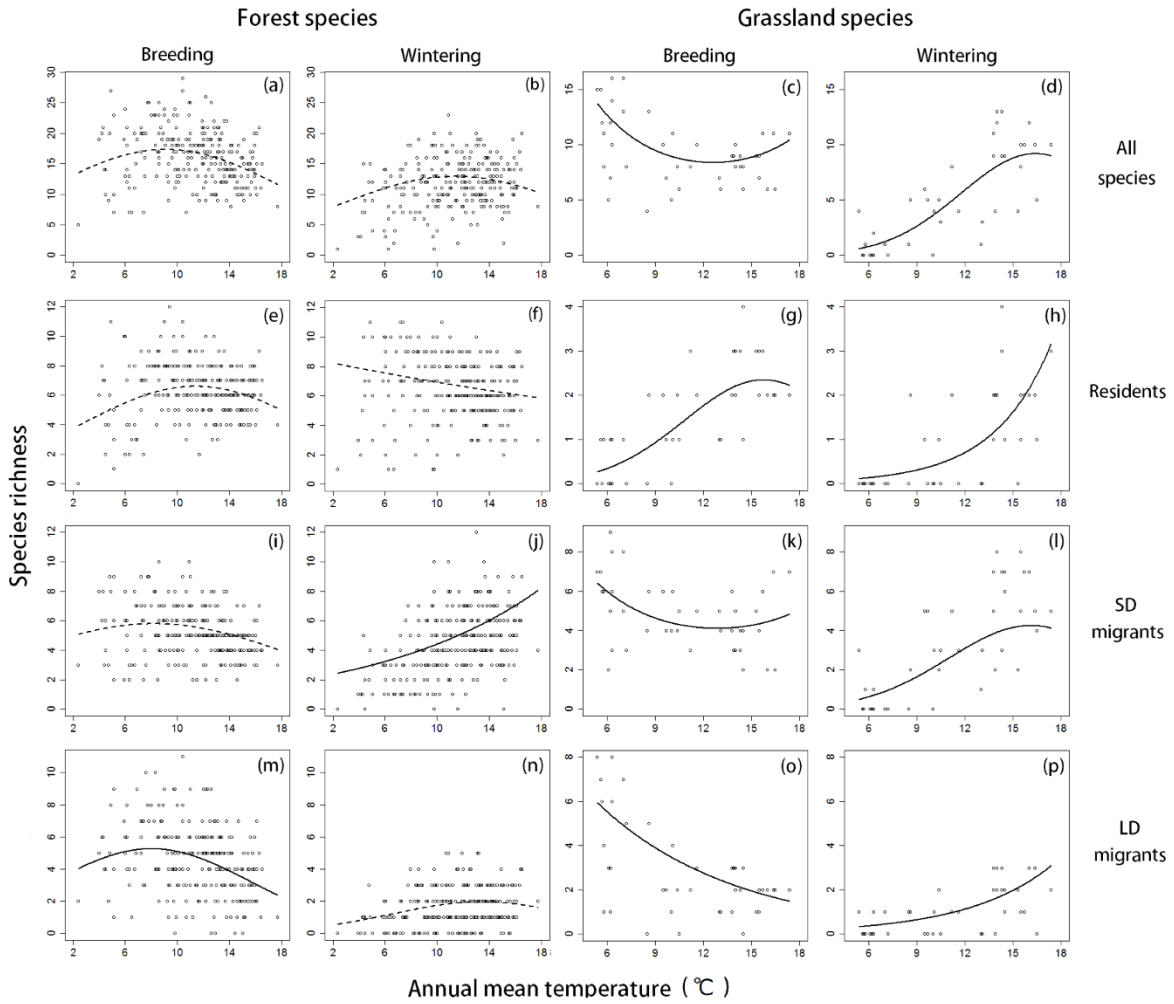


Fig. 2.1. Relationships between annual mean temperature and the species richness of forest birds [(a, e, i, m): breeding season; (b, f, j, n): wintering season] and grassland birds [(c, g, k, o): breeding season, (d, h, l, p): wintering season]. Data reflecting migratory traits are shown in each line of the Figure [(a–d): all species; (e–h): residents; (i–l): short-distance migrants; (m–p): long-distance migrants]. Dots indicate data collected at each site. Lines represent the estimates afforded by the best spatial models (solid lines indicate semi-partial R^2 of either the temperature and its squared term > 0.1, and broken lines indicate that of both the temperature and its squared term < 0.1). We used a GLMM (a multivariate analysis), and the effects of the other explanatory variables were considered and fixed to mean values in each figure. See details of the best spatial models in Table 1. Abbreviations: SD: short distance; LD: long distance; Breeding: breeding season; Wintering: wintering season.

2.4.2 Effects of snow depth

In the wintering season, in areas with deeper snow, the species richness of forest SD migrants

was lower, and that of forest residents and LD migrants also tended to be lower (Fig. 2.2b–d). In such areas, the species richness of all species was lower, reflecting the patterns of individual groups (Fig. 2.2a).

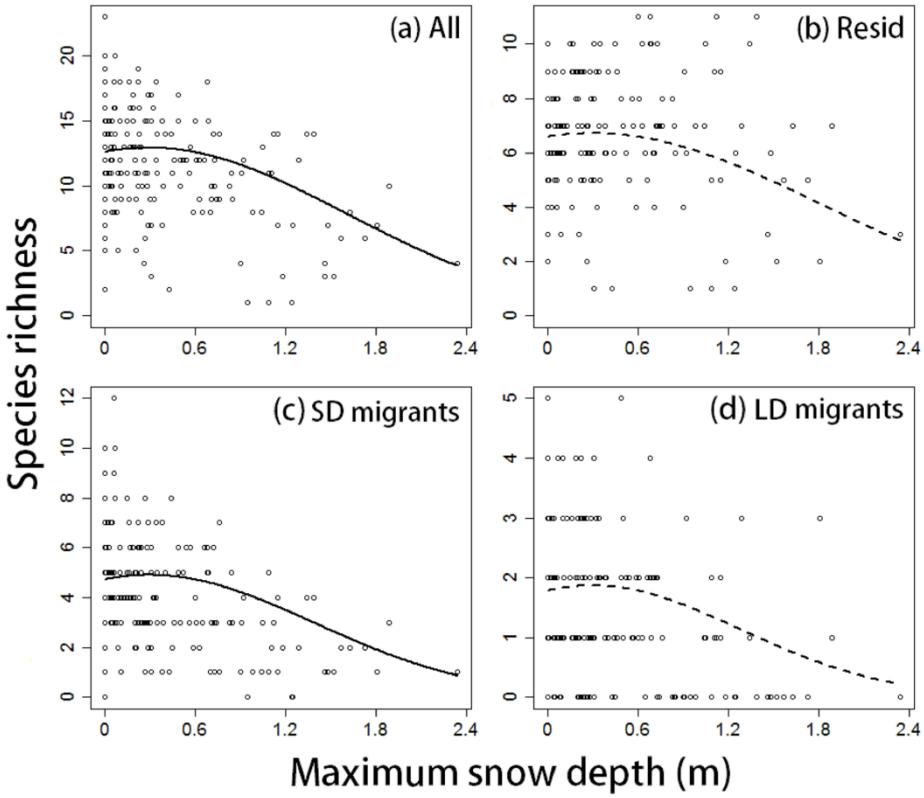


Fig. 2.2. Relationships between maximum snow depth and the species richness of wintering forest bird species [(a) all species, (b) residents, (c) short-distance migrants, (d) long-distance migrants]. Dots indicate data derived at each site; lines reflect the estimates of the best spatial models (solid lines indicate semi-partial R^2 of either the temperature and its squared term > 0.1, and broken lines indicate that of both the temperature and its squared term < 0.1). We used a GLMM (a multivariate analysis), and the effects of the other explanatory variables were considered and fixed to mean values in each figure. See details of the best spatial models in Table 1. Abbreviations: Resid: residents; SD: short distance; LD: long distance.

2.4.3 Effects of the extent of surrounding habitat

In the breeding season, for all three forest groups (residents, SD migrants, and LD migrants) and one grassland group (LD migrants), species richness tended to be high in areas with large extents of surrounding habitat, although these effects were small for all groups except grassland LD migrants (Fig. 2.3b, d–f). Reflecting these patterns, in areas with large extents of surrounding habitat, the species richness of all grassland species was high and that of all forest species also tended to be high (Fig. 2.3a, c). By contrast, during the wintering season, the species richness of only one group (grassland LD migrants) was higher in areas with larger extents of surrounding habitat (Appendix S2.11). No effects of the extent of surrounding habitat were evident in the other five groups or in all species in both habitats (Table 2.1).

2.4.4 Effects of elevation

There were no obvious effects of elevation in either season. In the breeding season, the species richness of residents in both habitats was relatively high in areas of markedly high elevation (Appendix S2.12a, c). In the wintering season, unimodal relationships between species richness and elevation were observed for forest SD and grassland LD migrants (Appendix S2.12b, d).

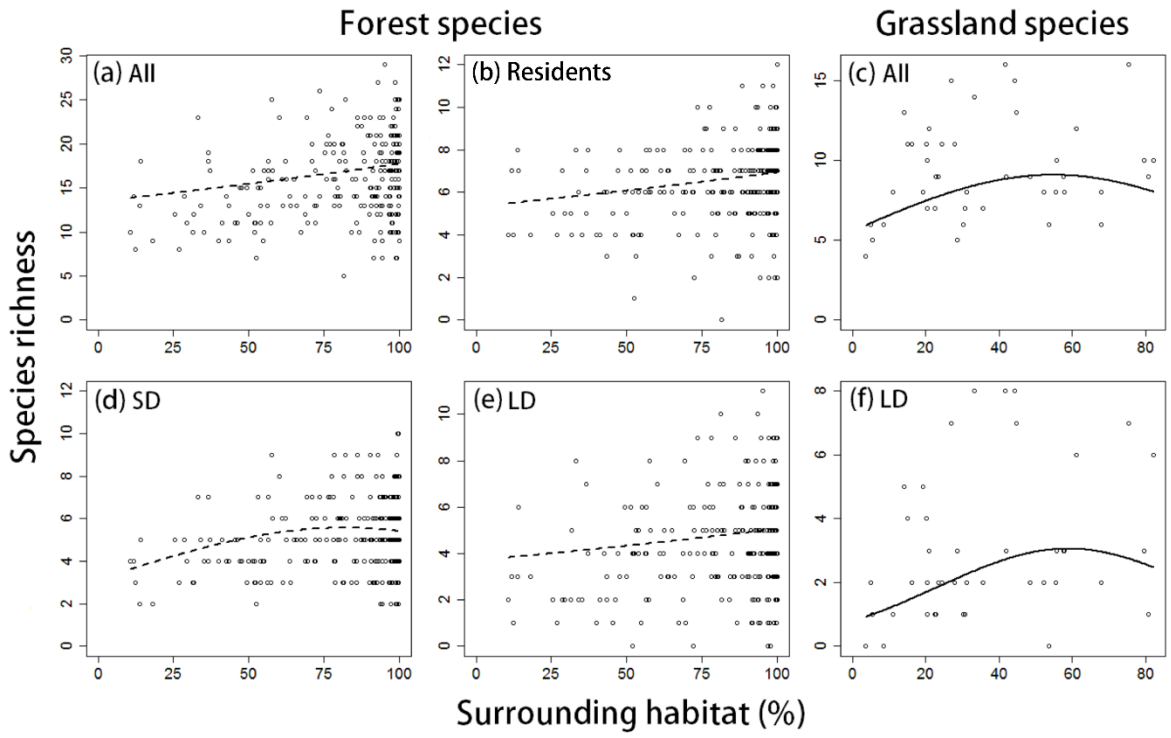


Fig. 2.3. Relationships between the extent of surrounding habitat and the species richness of breeding forest birds [(a) all species, (b) residents, (d) short-distance migrants, (e) long-distance migrants] and breeding grassland birds [(c) all species, (f) long-distance migrants]. Dots indicate data derived at each site. Lines reflect the estimates afforded by the best spatial models (solid lines indicate semi-partial R^2 of either the temperature and its squared term > 0.1, and broken lines indicate that of both the temperature and its squared term < 0.1). We used a GLMM (a multivariate analysis), and the effects of the other explanatory variables were considered and fixed to mean values in each figure. See details of the best spatial models in Table 1. Abbreviations: All: all species; SD: short-distance migrants; LD: long-distance migrants; Surrounding habitat: the extent of surrounding habitat within 1.25 km (a, b, d, e) and 5 km (c, f).

2.4.5 Mapping predicted bird species richness

Reflecting the contrasting effects of climate on the six groups (all species, SD migrants, and LD migrants of both forests and grasslands), I found that regions exhibiting high species richness differed between the breeding and wintering seasons. Specifically, in the breeding season, the species richness of the six groups was high in northern Japan, and the species

richness of the three forest groups was also high in the mountains of southern Japan (Fig. 2.4a, c; Appendices S2.13c, e; S2.14c, e; S2.15a, c, d; S2.16a, c, d). By contrast, in the wintering season, species richness was high in southern Japan, particularly in the plains near the Pacific coast (Fig. 2.4b, d; Appendices S2.13d, f; S2.14d, f; S2.15a, c, d; S2.16a, c, d).

Unlike the situation with migrants, the regions exhibiting high resident species richness of both habitats were similar in the two seasons. Therefore, the species richness of grassland residents was high in southern Japan, particularly in the plains near the Pacific coast. This was also the case for wintering migrants (Appendices S2.14a,b; S2.16b). The species richness of forest residents was high in both central Japan and inland regions of southern Japan, which have moderate annual mean temperatures; species richness was also high on the Pacific side of northern Japan during the wintering season (Appendices S2.13a,b; S2.15b).

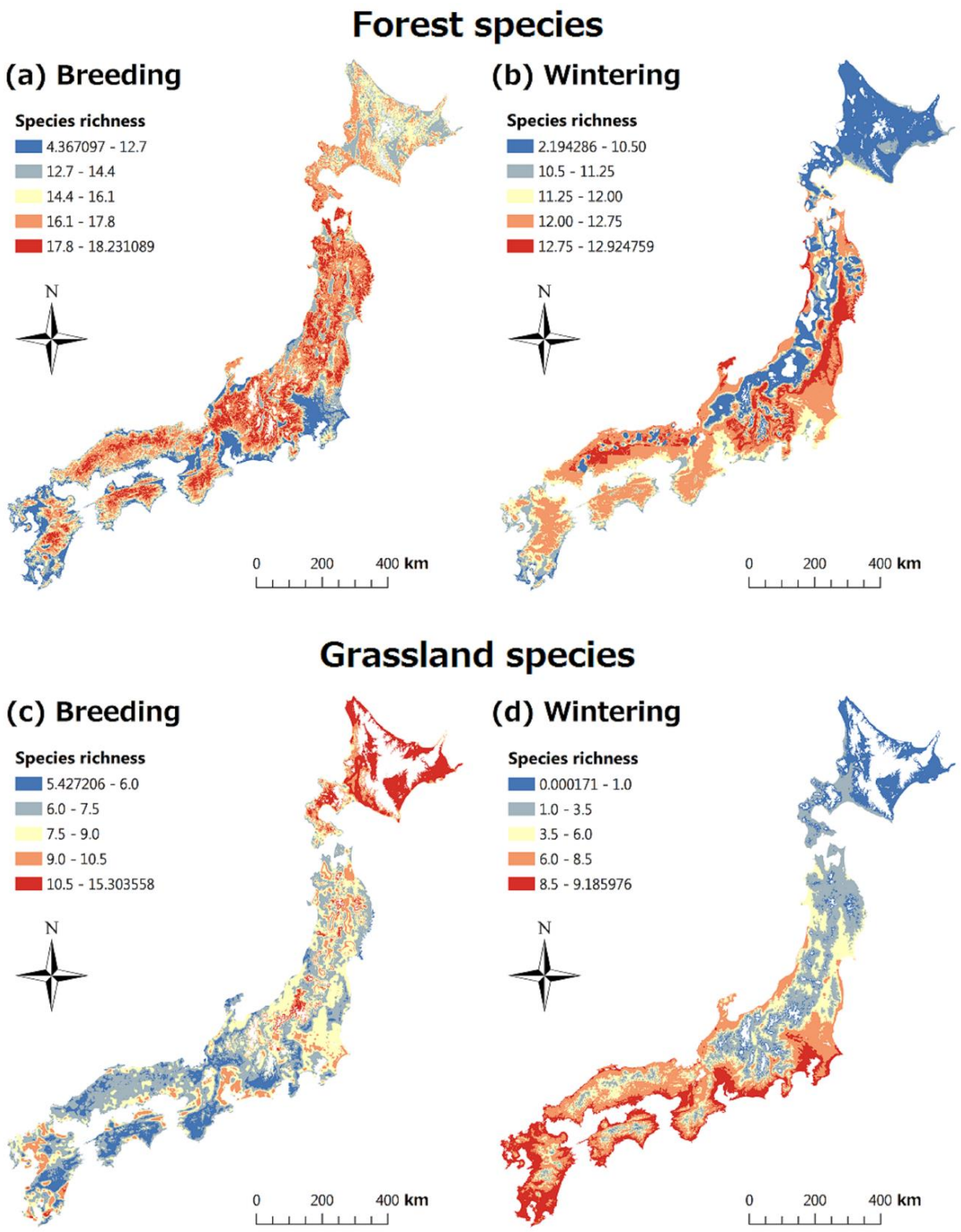


Fig. 2.4. The expected species richness of (a,b) forest birds and (c,d) grassland birds. Breeding season (a, c); wintering season (b, d). We used the best spatial models to derive these results. We excluded regions where the values of explanatory variables from the models were not within the analysis range (i.e., annual mean temperature < 2°C in forests, annual mean temperature < 5°C in grasslands, elevation > 1600 m, snow depth > 2.4 m). Coordinates: 30°59′–45°31′N; 129°33′–145°49′E.

2.5 Discussion

Previous studies on the migration of single species and the distribution of species richness on continental/global scales have shown the importance of seasonality in both bird distribution and environments (Newton 2008; Somveille et al. 2015). However, there have been few of these studies, and the seasonal effects of environmental factors on the distribution of bird communities at a national level are poorly understood. Using data from systematic field surveys across Japan, I analyzed the seasonal distribution of terrestrial birds, including migrant species. The drivers important for bird distribution differed among seasons. In the breeding season, the species richness of many groups was high in cool areas with large expanses of surrounding habitat. By contrast, during the wintering season, the species richness of all groups (except for forest residents) was high in warm areas. The extent of surrounding habitat positively affected only grassland LD migrants. Moreover, snow depth negatively affected all forest groups. These results suggest that it is important to consider seasonality in both bird distributions and environments even in Japan, a country located in the temperate to boreal zone.

2.5.1 Effects of annual mean temperature

For all species, SD migrants, and LD migrants in both forests and grasslands, the species richness during the breeding season tended to be high in cool regions (Fig. 2.1a, c, i, k, m, o). This is explained by the abundance of prey during the breeding season in cool areas, particularly in deciduous broad-leaved forests, although few empirical studies have been performed

(Appendix S2.7a; Herrera 1978; Huston & Wolverton 2009). In addition, competition may affect the patterns observed. Thus, in cool areas with few bird residents (Fig. 2.1e, g, h) and with abundant prey resources during the breeding season, breeding migrants can use prey not consumed by residents (Fristoe 2015; Somveille et al. 2015, 2018). It is also possible that high temperature reduced species richness by having negative physiological effects, such as reductions in egg viability (Cooper et al. 2006). Importantly, any negative effects of temperature would be greater in grasslands, which lack any shading from sunshine (Masatoshi Yui, personal communication).

In contrast to the case in the breeding season, the annual mean temperature tended to positively affect the species richness of all species, SD migrants, and LD migrants in both forests and grasslands in the wintering season (Fig. 2.1b, d, j, 2.l, n, p). This is because most wintering birds avoid the harsh climate and scarce prey resources characteristic of areas of low temperature (Somveille et al. 2015, 2018). The positive effects of temperature may be more pronounced in grasslands, which lack shelter from the wind, rain, and snow. In addition, distribution patterns shown by forest groups may also be explained indirectly as effects of vegetation; warm areas dominated by evergreen broad-leaved forests and conifer plantations may provide more prey resources during the wintering season than cool areas dominated by deciduous broad-leaved forests (Appendix S2.7a; Kira 1991; Yamaura et al. 2011; Huston & Wolverton 2009), in contrast to the situation in the breeding season.

Unlike the situation for migrants, the species richness of forest residents was relatively

high in both seasons in areas of moderate annual mean temperature (Fig. 2.1e,f). Such areas may yield constant amounts of prey and afford a reasonably comfortable climate throughout the year, and thus are conveniently occupied by highly sedentary residents. Although in the wintering season the species richness of forest residents was also high in cooler areas, sampling a larger number of cool areas may show the same patterns that were observed in the breeding season (i.e., unimodal relationships). In both seasons, the species richness of grassland residents was higher in warmer areas (Fig. 2.1g,h), as was also true of wintering migrants, suggesting that the costs imposed by wintering are greater than the benefits obtained during the breeding season in cool areas.

2.5.2 Effects of snow depth

Snow depth tended to negatively affect the species richness of all groups of wintering forest birds (Fig. 2.2), suggesting that snow cover restricted the distributions of various species, including arboreal species. When analyzing grassland birds, I did not use snow depth as an explanatory variable because a strong negative correlation was evident between snow depth and annual mean temperature. However, not only temperature but also snow cover could explain the poor species richness of grassland species in cooler areas (Fig. 2.1d, h, 2.1l, p). Although, in some cases, the effects of snow cover can be estimated using temperature data, snow cover would be a major driver of wintering bird distribution in studies that include areas where snowfalls were so heavy that foraging near the ground was restricted.

2.5.3 Effects of the extent of surrounding habitat

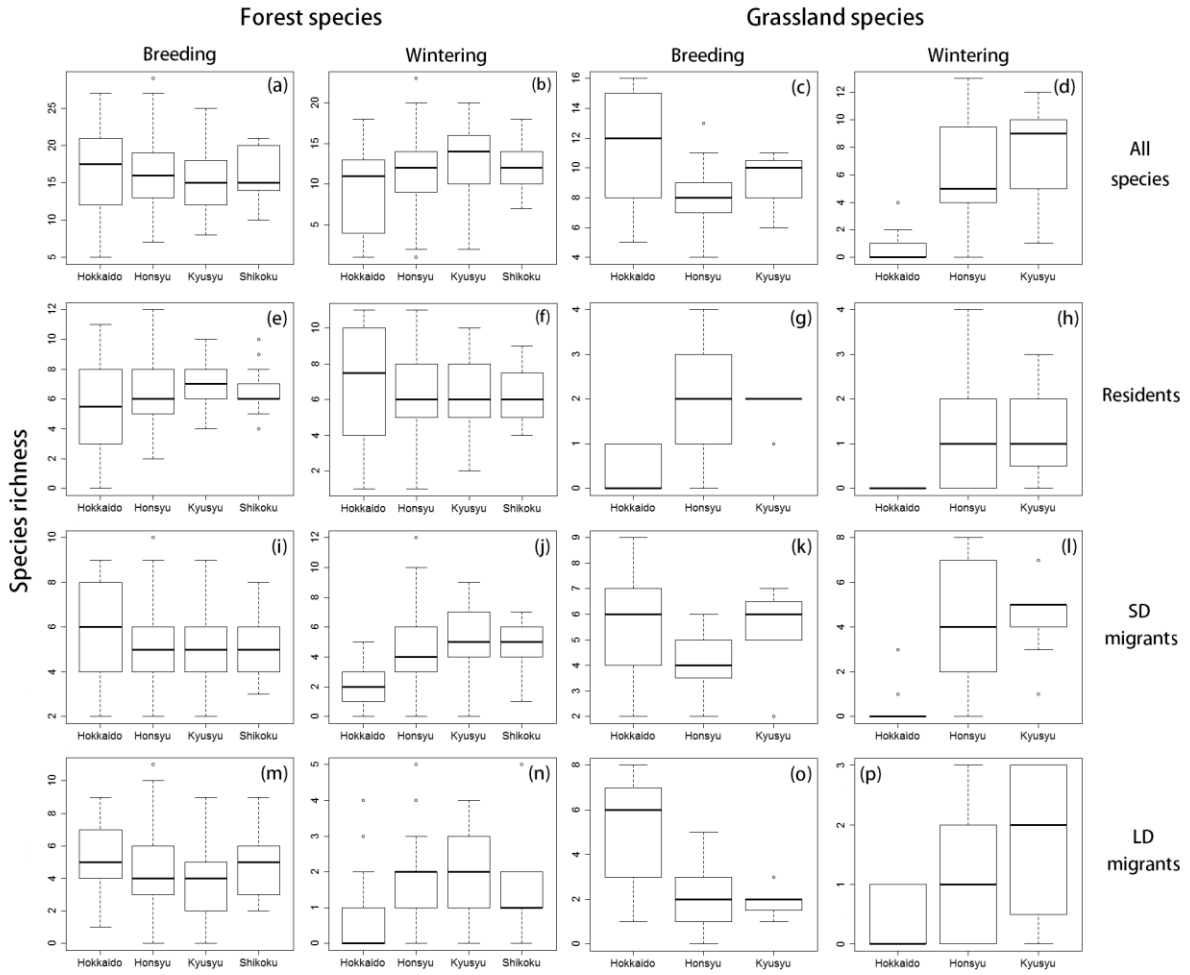
I found small but positive effects of the extent of surrounding habitat on the species richness of many groups, usually only in the breeding season (for three groups only in the breeding season [forest residents, SD migrants, and LD migrants] and one group in both seasons [grassland LD migrants]; Fig. 2.3; Table 2.1). For all species in both habitats, species richness tended to be high in areas with a large extent of surrounding habitat only in the breeding season. As surrounding habitat affords mating opportunities and the food resources required for breeding (Dunning et al. 1992; Dale 2001), the positive effects of a greater extent of surrounding habitat would be larger in the breeding than the wintering season (Yahner 2000). In some groups, the explanatory power of the breeding season model was considerably less than that of the wintering season model. Therefore, in the breeding season in particular, small-scale factors (e.g., patch area and configuration, and habitat structure) may account for unexplained variation in species richness, although the extent of surrounding habitat does correlate with some of these variables (Fahrig 2003). Alternatively, by dividing forests into natural forests and plantation forests, more apparent landscape effects may be detected (Yamaura et al. 2011).

2.5.4 Seasonality in the spatial distributions of species richness

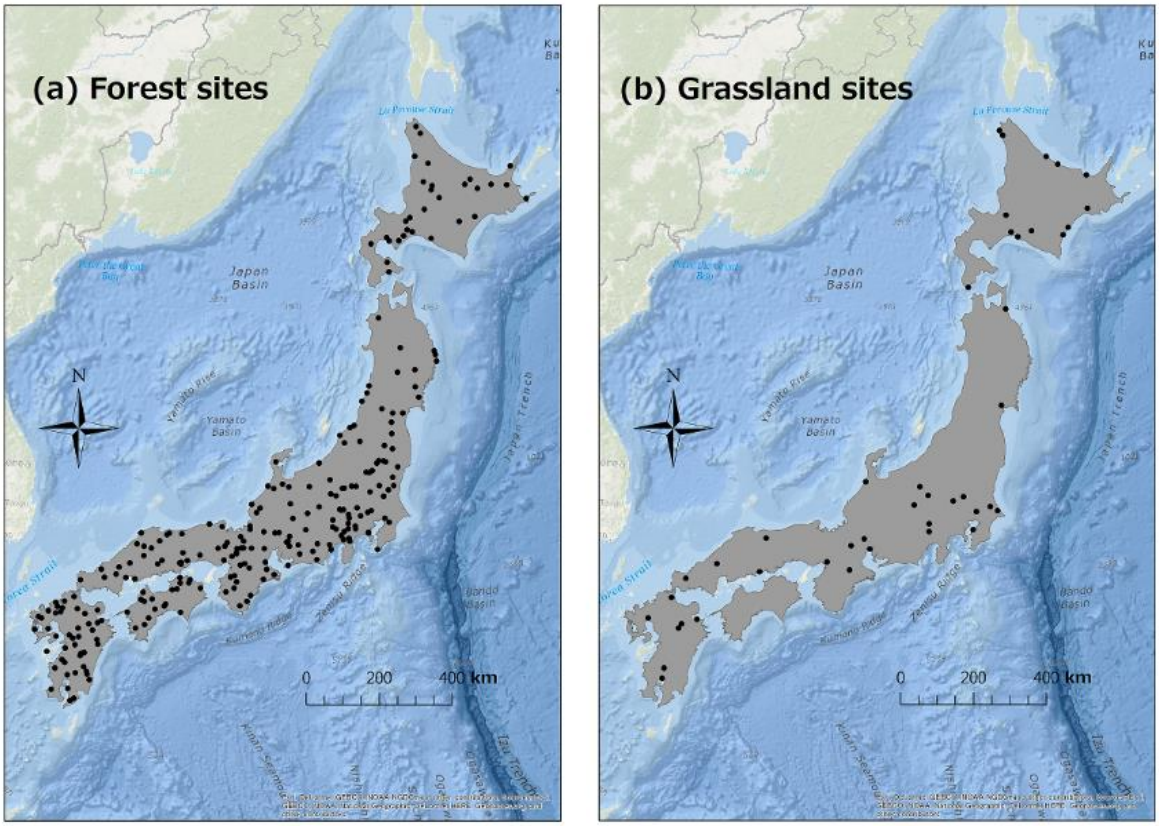
I identified only a few areas exhibiting high-level species richness throughout the year (Fig. 2.4). Rather, regions with different climates, as dictated by annual mean temperature and snow

depth, likely served as habitats for different groups in different seasons; every region surveyed played an important role as a breeding or a wintering bird habitat, contributing to the maintenance of bird diversity in Japan. Bird communities in regions that were cool in the breeding season were probably supported by migrants that overwintered in warm regions with little snow. These warm regions have few old-growth forests and wetlands that are restricted to cool or high-altitude areas, untouched by humans (Yamaura et al. 2011; Kusumoto et al. 2017). However, climate and land-use in warm areas are important and can affect breeding bird communities via migration. Conversely, these environments in cool areas would also affect wintering bird communities via migration. The explained variation in species richness was limited, especially in forests, suggesting that habitat quality was important. Future studies should examine the effects of local factors at a large scale. Identifying large-scale seasonal differences in animal distributions and investigating the associated drivers is essential to understanding the maintenance of biodiversity and ensuring its conservation.

2.6 Appendices



Appendix S2.1. Relationships between island size and species richness of forest birds [(a,b) all species, (e,f) residents, (i,j) short-distance migrants, (m,n) long-distance migrants] and grassland birds [(c,d) all species, (g,h) residents, (k,l) short-distance migrants, (o,p) long-distance migrants]. These results are from the breeding (a, c, e, g, i, k, m, o) and wintering (b, d, f, h, j, l, n, p) seasons. The size of the islands were as follows: Hokkaido: 77,984 km^2; Honsyu: 227,942 km^2; Kyusyu: 36,782 km^2; Shikoku: 18,298 km^2. Species richness did not increase on larger islands. Abbreviations: SD: short-distance, LD: long-distance, Breeding: breeding season, Wintering: wintering season.



Appendix S2.2. The survey sites. The black dots indicate (a) 254 forest sites and (b) 43 grassland sites surveyed in the breeding and wintering seasons. Coordinates: 30°59′–45°31′N; 129°33′–145°49′E.

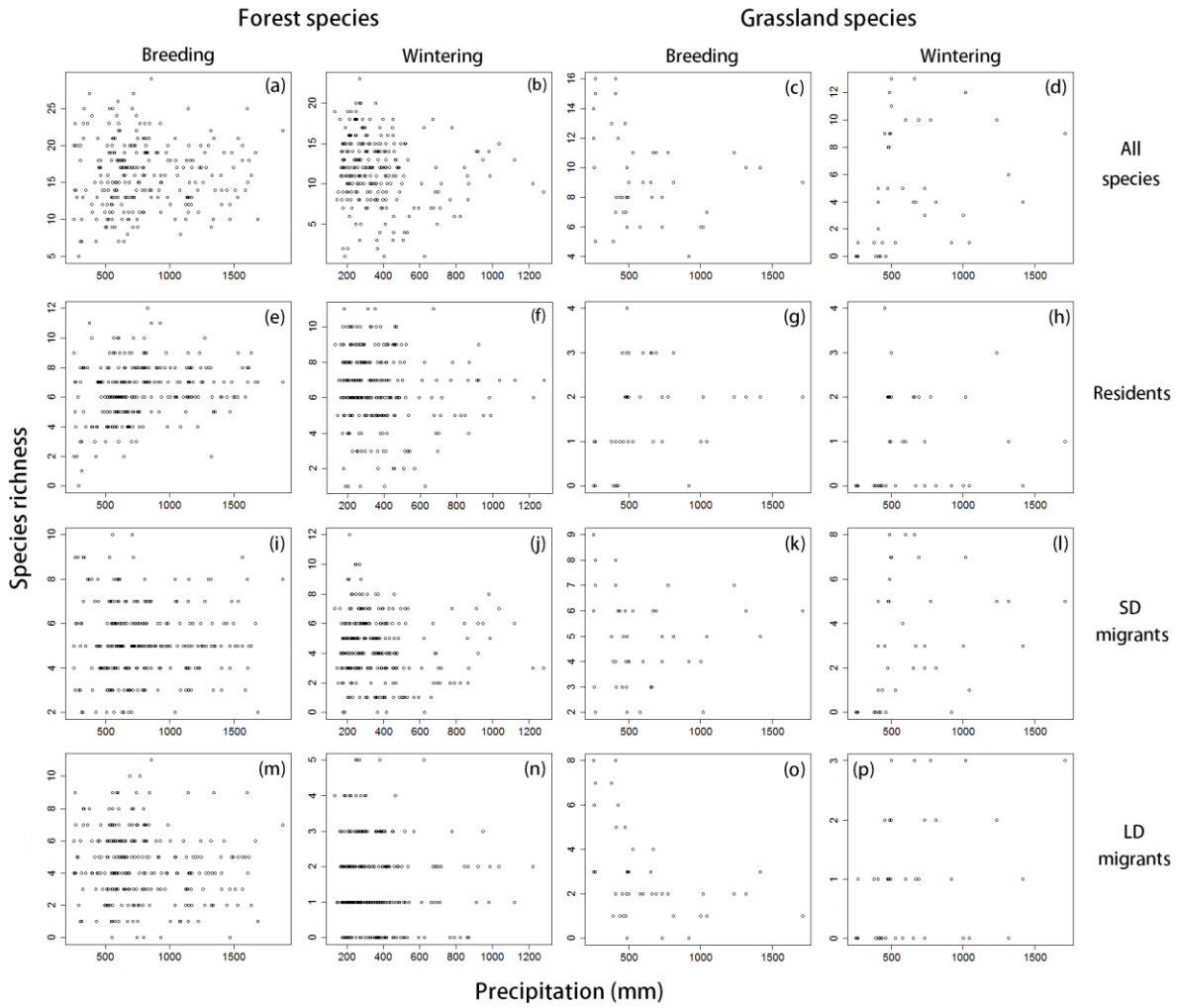
Appendix S2.3. Bird species subjected to analyses. "Season" indicates whether the species was detected in the breeding or the wintering season. For Siskin and Ashy minivet (only), we changed the migratory trait between seasons. We categorized 61 species as forest species (resident: 23, SD migrant: 17, LD migrant: 21) and 30 species as grassland species (resident: 5, SD migrant: 13, LD migrant: 12) in the breeding season, and 51 species as forest species (resident: 21, SD migrant: 17, LD migrant: 13) and 25 species as grassland species (resident: 5, SD migrant: 11, LD migrant: 9) in the wintering season. Abbreviations: Grass: grassland, SD: short-distance migrant, LD: long-distance migrant, B: breeding season, W: wintering season.

Common name	Scientific name	Habitat	Migrant trait	Season
Japanese Green Woodpecker	*Picus awokera*	Forest	Resident	B/W
Great Wpotted Woodpecker	*Dendrocopos major*	Forest	Resident	B/W
Hazel Grouse	*Tetrastes bonasia*	Forest	Resident	B
Long-tailed Tit	*Aegithalos caudatus*	Forest	Resident	B/W
White-backed Woodpecker	*Dendrocopos leucotos*	Forest	Resident	B/W
Azure-winged Magpie	*Cyanopica cyana*	Forest	Resident	B/W
Eurasian Jay	*Garrulus glandarius*	Forest	Resident	B/W
Brown Dipper	*Cinclus pallasii*	Forest	Resident	B/W
Treecreeper	*Certhia familiaris*	Forest	Resident	B/W
Black Woodpecker	*Dryocopus martius*	Forest	Resident	B/W
Lesser Spotted Woodpecker	*Dendrocopos minor*	Forest	Resident	B
Willow Tit	*Parus montanus*	Forest	Resident	B/W
Japanese Pygmy Woodpecker	*Dendrocopos kizuki*	Forest	Resident	B/W
Nuthatch	*Sitta europaea*	Forest	Resident	B/W
Great Tit	*Parus major*	Forest	Resident	B/W
Marsh Tit	*Parus palustris*	Forest	Resident	B/W
Jungle Crow	*Corvus macrorhynchos*	Forest	Resident	B/W
Carrion Crow	*Corvus corone*	Forest	Resident	B/W
Siskin	*Carduelis spinus*	Forest	Resident/LD	B/W
Varied Tit	*Parus varius*	Forest	Resident	B/W
Grey-headed Woodpecker	*Picus canus*	Forest	Resident	B/W
Greater Pied Kingfisher	*Ceryle lugubris*	Forest	Resident	B/W
Copper Pheasant	*Syrmaticus soemmerringii*	Forest	Resident	B/W

Japanese Green Pigeon	*Sphenurus sieboldii*	Forest	SD	B/W
Brown Thrush	*Turdus chrysolaus*	Forest	SD	B/W
Masked Grosbeak	*Eophona personata*	Forest	SD	B/W
Japanese Bush Warbler	*Cettia diphone*	Forest	SD	B/W
Eurasian Bullfinch	*Pyrrhula pyrrhula*	Forest	SD	B/W
Japanese Accentor	*Prunella rubida*	Forest	SD	W
Goldcrest	*Regulus regulus*	Forest	SD	B/W
Oriental Turtle Dove	*Streptopelia orientalis*	Forest	SD	B/W
Grey Wagtail	*Motacilla cinerea*	Forest	SD	B/W
Grey Bunting	*Emberiza variabilis*	Forest	SD	B/W
Hawfinch	*Coccothraustes coccothraustes*	Forest	SD	B/W
White's Thrush	*Zoothera dauma*	Forest	SD	B/W
Russet Sparrow	*Passer rutilans*	Forest	SD	B
Coal Tit	*Parus ater*	Forest	SD	B/W
Brown-eared Bulbul	*Hypsipetes amaurotis*	Forest	SD	B/W
Winter Wren	*Troglodytes troglodytes*	Forest	SD	B/W
Japanese White-eye	*Zosterops japonicus*	Forest	SD	B/W
Red-flanked Bushrobin	*Tarsiger cyanurus*	Forest	SD	B/W
Ruddy Kingfisher	*Halcyon coromanda*	Forest	LD	B
Eastern Pale-legged Leaf Warbler	*Phylloscopus borealoides*	Forest	LD	B
Blue-and-white Flycatcher	*Cyanoptila cyanomelana*	Forest	LD	B
Narcissus Flycatcher	*Ficedula narcissina*	Forest	LD	B
Grey Thrush	*Turdus cardis*	Forest	LD	B
Brown Flycatcher	*Muscicapa dauurica*	Forest	LD	B
Japanese Robin	*Erithacus akahige*	Forest	LD	B
Chestnut-cheeked Starling	*Sturnus philippensis*	Forest	LD	B
Siberian Blue Robin	*Luscinia cyane*	Forest	LD	B
Black Paradise Flycatcher	*Terpsiphone atrocaudata*	Forest	LD	B
Ashy Minivet	*Pericrocotus divaricatus*	Forest	LD/Resident	B/W
Horsfield's Hawk-cuckoo	*Cuculus fugax*	Forest	LD	B
Eastern Crowned Leaf Warbler	*Phylloscopus coronatus*	Forest	LD	B
Thick-billed Shrike	*Lanius tigrinus*	Forest	LD	B

Oriental Cuckoo	*Cuculus saturates*	Forest	LD	B
White-throated Needle-tailed Swift	*Hirundapus caudacutus*	Forest	LD	B
Little Cuckoo	*Cuculus poliocephalus*	Forest	LD	B
Siberian Thrush	*Turdus sibirica*	Forest	LD	B
Arctic Warbler	*Phylloscopus borealis*	Forest	LD	B
Fairy Pitta	*Pitta brachyuran*	Forest	LD	B
Short-tailed Bush Warbler	*Urosphena squameiceps*	Forest	LD	B
Brambling	*Fringilla montifringilla*	Forest	LD	W
Crossbill	*Loxia curvirostra*	Forest	LD	W
Pallas's Rosefinch	*Carpoducus roseus*	Forest	LD	W
Red-breasted Flycatcher	*Ficedula parva*	Forest	LD	W
Waxwing	*Bombycilla garrulus*	Forest	LD	W
Pine Grosbeak	*Pinicola enucleator*	Forest	LD	W
Pale Thrush	*Turdus pallidus*	Forest	LD	W
Dusky Thrush	*Turdus naumanni*	Forest	LD	W
Japanese Waxwing	*Bombycilla japonica*	Forest	LD	W
Eye-browed Thrush	*Turdus obscurus*	Forest	LD	W
Yellow-throated Bunting	*Emberiza elegans*	Forest	LD	W
Raven	*Corvus corax*	Forest	LD	W
Common Pheasant	*Phasianus colchicus*	Grass	Resident	B/W
Japanese Reed Bunting	*Emberiza yessoensis*	Grass	Resident	B/W
Eurasian Tree Sparrow	*Passer montanus*	Grass	Resident	B/W
Japanese Wagtail	*Motacilla grandis*	Grass	Resident	B/W
Grey Starling	*Sturnus cineraceus*	Grass	Resident	B/W
Black-faced Bunting	*Emberiza spodocephala*	Grass	SD	B/W
Wryneck	*Jynx torquilla*	Grass	SD	B
Reed Bunting	*Emberiza schoeniclus*	Grass	SD	B/W
Japanese Marsh Warbler	*Locustella pryeri*	Grass	SD	B
Oriental Greenfinch	*Carduelis sinica minor*	Grass	SD	B/W
Fan-tailed Warbler	*Cisticola juncidis*	Grass	SD	B/W
White Wagtail	*Motacilla lugens*	Grass	SD	B/W
Common Skylark	*Alauda arvensis*	Grass	SD	B/W

Olive-backed Pipit	*Anthus hodgsoni*	Grass	SD	B/W
Long-tailed Rosefinch	*Uragus sibiricus*	Grass	SD	B/W
Chestnut-eared Bunting	*Emberiza fucata*	Grass	SD	B/W
Siberian Meadow Bunting	*Emberiza cioides*	Grass	SD	B/W
Bull-headed Shrike	*Lanius bucephalus*	Grass	SD	B/W
Grey's Grasshopper Warbler	*Locustella fasciolata*	Grass	LD	B
Latham's Snipe	*Gallinago hardwickii*	Grass	LD	B
Great Reed Warbler	*Acrocephalus arundinaceus*	Grass	LD	B
Common Cuckoo	*Cuculus canorus*	Grass	LD	B
Black-browed Reed Warbler	*Acrocephalus bistrigiceps*	Grass	LD	B
Middendorff's Grasshopper Warbler	*Locustella ochotensis*	Grass	LD	B
Sand Martin	*Riparia riparia*	Grass	LD	B
House Swallow	*Hirundo rustica*	Grass	LD	B
Yellow Wagtail	*Motacilla flava*	Grass	LD	B
Siberian Rubythroat	*Luscinia calliope*	Grass	LD	B
Stonechat	*Saxicola torquata*	Grass	LD	B
Lanceolated Grasshopper Warbler	*Locustella lanceolate*	Grass	LD	B
Great Grey Shrike	*Lanius excubitor*	Grass	LD	W
Rustic Bunting	*Emberiza rustica*	Grass	LD	W
Daurian Redstart	*Phoenicurus auroreus*	Grass	LD	W
Water Pipit	*Anthus spinoletta*	Grass	LD	W
Lapland Bunting	*Calcarius lapponicus*	Grass	LD	W
European Penduline Tit	*Remiz pendulinus*	Grass	LD	W
Rosy Finch	*Leucosticte arctoa*	Grass	LD	W
Redpoll	*Carduelis flammea*	Grass	LD	W
Rook	*Corvus frugilegus*	Grass	LD	W



Appendix S2.4. Relationships between seasonal precipitation and species richness of forest birds [(a,b) all species, (e,f) residents, (i,j) short-distance migrants, (m,n) long-distance migrants] and grassland birds [(c,d) all species, (g,h) residents, (k,l) short-distance migrants, (o,p) long-distance migrants]. These results are from the breeding (a, c, e, g, i, k, m, o) and wintering (b, d, f, h, j, l, n, p) seasons. There are no clear relationships. Abbreviations: SD: short-distance, LD: long-distance, Breeding: breeding season, Wintering: wintering season.

Appendix S2.5. Comparison of the effects of annual mean temperature and mean temperature during each season (estimates ± standard errors [Wald *p*-value], and ΔAkaike information criterion [AIC]). We constructed generalized linear mixed models (GLMMs) with random site effects. In each model, we considered one explanatory variable (i.e., annual mean temperature, mean temperature during the breeding season, or mean temperature during the wintering season) and its squared term. Each row of the table shows the results of one model. Abbreviations: Breeding: breeding season; Wintering: wintering season; TEMP: mean temperature during each season.

All forest species

Season	Breeding			Wintering		
	TEMP	$(TEMP)^2$	ΔAIC	TEMP	$(TEMP)^2$	ΔAIC
Annual	-0.10±0.02 (<0.01)	-0.07±0.02 (<0.01)	0	0.06±0.02 (<0.01)	-0.07±0.02 (<0.01)	0
Sumer	-0.09±0.02 (<0.01)	-0.06±0.02 (<0.01)	6.5	0.06±0.02 (0.01)	-0.06±0.02 (<0.01)	2.3
Winter	-0.10±0.02 (<0.01)	-0.06±0.01 (<0.01)	3.6	0.07±0.02 (<0.01)	-0.05±0.02 (<0.01)	2.8

Forest residents

Season	Breeding			Wintering		
	TEMP	$(TEMP)^2$	ΔAIC	TEMP	$(TEMP)^2$	ΔAIC
Annual	-0.03±0.03 (0.35)	-0.07±0.02 (<0.01)	0	-0.06±0.03 (0.02)	-0.05±0.02 (0.03)	0
Sumer	-0.02±0.03 (0.41)	-0.06±0.02 (0.01)	3.2	-0.06±0.03 (0.02)	-0.04±0.02 (0.06)	0.7
Winter	-0.02±0.03 (0.38)	-0.06±0.02 (<0.01)	0.2	-0.06±0.03 (0.03)	-0.04±0.02 (0.05)	1.2

Forest short-distance migrants

Season	Breeding			Wintering		
	TEMP	$(TEMP)^2$	ΔAIC	TEMP	$(TEMP)^2$	ΔAIC
Annual	-0.10±0.03 (<0.01)	-0.05±0.03 (0.05)	0	0.24±0.03 (<0.01)	-0.11±0.03 (<0.01)	0.6
Sumer	-0.09±0.03 (<0.01)	-0.03±0.03 (0.20)	1.4	0.23±0.03 (<0.01)	-0.12±0.03 (<0.01)	0
Winter	-0.10±0.03 (<0.01)	-0.04±0.02 (0.06)	0.9	0.24±0.03 (<0.01)	-0.08±0.03 (<0.01)	5.7

Forest long-distance migrants

Season	Breeding			Wintering		
	TEMP	$(TEMP)^2$	ΔAIC	TEMP	$(TEMP)^2$	ΔAIC
Annual	-0.20±0.04 (<0.01)	-0.10±0.03 (<0.01)	0	0.18±0.06 (<0.01)	-0.13±0.05 (0.01)	1.0
Sumer	-0.20±0.04 (<0.01)	-0.09±0.03 (<0.01)	1.6	0.17±0.06 (<0.01)	-0.13±0.05 (0.02)	2.5
Winter	-0.20±0.04 (<0.01)	-0.09±0.02 (<0.01)	3.0	0.19±0.06 (<0.01)	-0.12±0.05 (0.02)	0

All grassland species

Season	Breeding			Wintering		
	TEMP	$(TEMP)^2$	ΔAIC	TEMP	$(TEMP)^2$	ΔAIC
Annual	-0.12±0.05 (0.02)	0.14±0.07 (0.05)	0.5	1.00±0.12 (<0.01)	-0.36±0.13 (<0.01)	2.5
Sumer	-0.11±0.05 (0.02)	0.14±0.07 (0.05)	0.4	1.02±0.13 (<0.01)	-0.37±0.13 (<0.01)	0
Winter	-0.11±0.05 (0.02)	0.14±0.07 (0.05)	0	0.98±0.12 (<0.01)	-0.29±0.13 (0.02)	5.3

Grassland residents

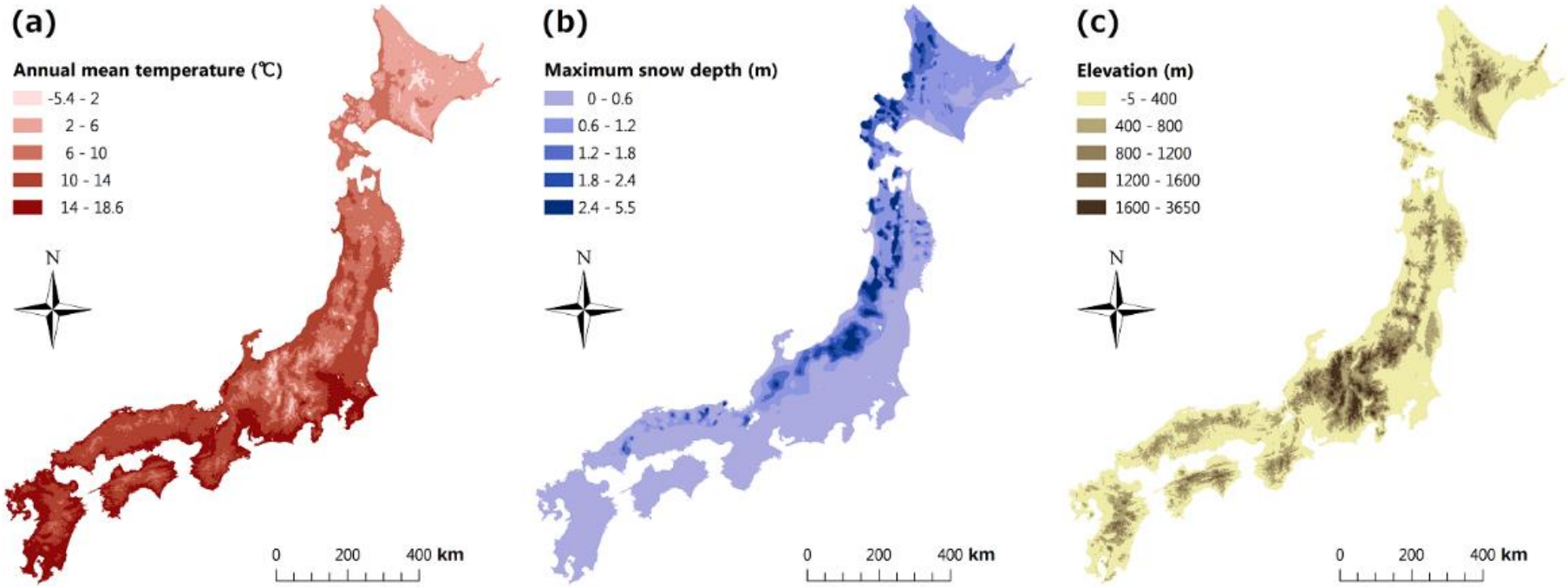
Season	Breeding			Wintering		
	TEMP	$(TEMP)^2$	ΔAIC	TEMP	$(TEMP)^2$	ΔAIC
Annual	0.67±0.17 (<0.01)	-0.28±0.19 (0.15)	2.2	1.51±0.43 (<0.01)	-0.52±0.34 (0.12)	1.8
Sumer	0.72±0.18 (<0.01)	-0.31±0.20 (0.12)	0	1.64±0.49 (<0.01)	-0.59±0.38 (0.12)	0
Winter	0.64±0.17 (<0.01)	-0.25±0.18 (0.17)	3.5	1.50±0.44 (<0.01)	-0.52±0.34 (0.12)	3.1

Grassland short-distance migrants

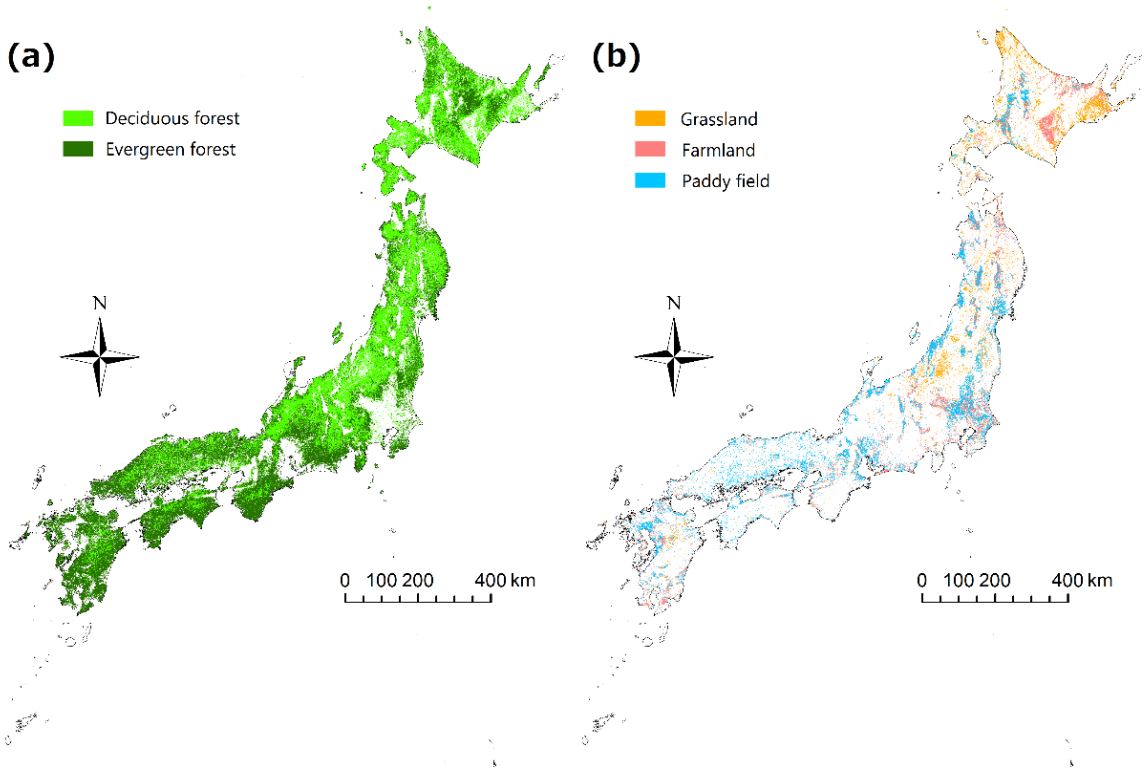
Season	Breeding			Wintering		
	TEMP	$(TEMP)^2$	ΔAIC	TEMP	$(TEMP)^2$	ΔAIC
Annual	-0.12±0.07 (0.07)	0.12±0.10 (0.23)	0.1	0.98±0.15 (<0.01)	-0.41±0.15 (<0.01)	0.9
Sumer	-0.12±0.07 (0.08)	0.10±0.10 (0.32)	0.7	1.00±0.15 (<0.01)	-0.44±0.15 (<0.01)	0
Winter	-0.11±0.07 (0.11)	0.13±0.10 (0.19)	0	0.97±0.15 (<0.01)	-0.34±0.14 (0.02)	1.4

Grassland long distance migrants

Season	Breeding			Wintering		
	TEMP	$(TEMP)^2$	ΔAIC	TEMP	$(TEMP)^2$	ΔAIC
Annual	-0.42±0.09 (<0.01)	0.24±0.14 (0.08)	2.6	0.79±0.22 (<0.01)	-0.19±0.24 (0.42)	1.0
Sumer	-0.42±0.10 (<0.01)	0.24±0.13 (0.07)	0	0.81±0.22 (<0.01)	-0.14±0.25 (0.56)	0
Winter	-0.42±0.10 (<0.01)	0.20±0.13 (0.13)	2.3	0.74±0.21 (<0.01)	-0.15±0.23 (0.51)	2.7



Appendix S2.6. (a) The annual mean temperature, (b) The maximum snow depth, and (c) The elevation at each grid (1 km^2).



Appendix S2.7. Distributions of (a) evergreen and deciduous forests and (b) grasslands, farmlands, and paddy fields.

Appendix S2.8. Comparison of the effects of the extent of surrounding habitat within each scale (estimates ± standard errors [Wald *p*-value], and ΔAIC). We constructed GLMMs with random site effects. In each model, we considered one explanatory variable (i.e., the extent of surrounding habitat within 1.25, 2.5, 5, 10, or 15 km) and its squared term. Each row of the table shows the results of one model. Abbreviations: Breeding: breeding season; Wintering: wintering season; AREA: the extent of surrounding habitat within each scale.

All forest species

Scale	Breeding			Wintering		
	AREA	$(AREA)^2$	ΔAIC	AREA	$(AREA)^2$	ΔAIC
1.25	0.07±0.03 (0.01)	-0.01±0.02 (0.44)	0	0.04±0.04 (0.23)	0.01±0.02 (0.51)	3.3
2.5	0.07±0.03 (<0.01)	-0.01±0.02 (0.59)	2.9	0.03±0.04 (0.44)	0.01±0.02 (0.55)	4.4
5	0.06±0.02 (0.02)	-0.02±0.02 (0.34)	6.3	-0.04±0.03 (0.23)	-0.02±0.02 (0.40)	3.6
10	0.05±0.02 (0.02)	-0.02±0.02 (0.30)	11.6	-0.06±0.03 (0.03)	-0.03±0.02 (0.17)	0.1
15	0.05±0.02 (<0.01)	-0.03±0.02 (0.11)	11.8	-0.05±0.02 (0.03)	-0.03±0.02 (0.18)	0

Forest residents

Scale	Breeding			Wintering		
	AREA	$(AREA)^2$	ΔAIC	AREA	$(AREA)^2$	ΔAIC
1.25	0.10±0.04 (0.02)	0.02±0.02 (0.54)	0	0.04±0.04 (0.32)	0.01±0.02 (0.71)	0.2
2.5	0.10±0.04 (0.02)	0.03±0.03 (0.34)	1.5	0.05±0.04 (0.23)	0.02±0.03 (0.51)	0
5	0.08±0.04 (0.04)	0.02±0.03 (0.52)	3.2	0.01±0.04 (0.82)	-0.00±0.03 (0.87)	1.4
10	0.06±0.03 (0.06)	0.01±0.03 (0.82)	4.4	-0.01±0.03 (0.76)	-0.02±0.03 (0.53)	1.3
15	0.06±0.03 (0.04)	-0.00±0.02 (0.98)	4.2	-0.01±0.03 (0.64)	-0.03±0.02 (0.27)	0.4

Forest short-distance migrants

Scale	Breeding			Wintering		
	AREA	$(AREA)^2$	ΔAIC	AREA	$(AREA)^2$	ΔAIC
1.25	0.03±0.05 (0.53)	-0.04±0.03 (0.18)	0	0.02±0.05 (0.71)	-0.01±0.03 (0.83)	11.4
2.5	0.05±0.04 (0.31)	-0.03±0.03 (0.35)	1.1	-0.03±0.05 (0.57)	-0.02±0.04 (0.56)	11.9
5	0.04±0.04 (0.32)	-0.03±0.03 (0.29)	1.9	-0.11±0.04 (0.01)	-0.06±0.03 (0.07)	5.9
10	0.03±0.03 (0.45)	-0.04±0.03 (0.13)	2.9	-0.14±0.04 (<0.01)	-0.06±0.03 (0.04)	0
15	0.02±0.03 (0.43)	-0.05±0.03 (0.04)	2.0	-0.11±0.03 (<0.01)	-0.04±0.03 (0.13)	2.4

Forest long-distance migrants

Scale	Breeding			Wintering		
	AREA	$(AREA)^2$	ΔAIC	AREA	$(AREA)^2$	ΔAIC
1.25	0.09±0.05 (0.09)	-0.03±0.03 (0.40)	0.2	0.06±0.08 (0.43)	0.07±0.04 (0.11)	0.5
2.5	0.07±0.05 (0.14)	-0.05±0.04 (0.21)	0	0.06±0.08 (0.45)	0.09±0.05 (0.10)	0
5	0.05±0.04 (0.23)	-0.06±0.03 (0.10)	1.6	-0.05±0.07 (0.52)	0.03±0.05 (0.62)	1
10	0.06±0.04 (0.09)	-0.03±0.03 (0.42)	7.5	-0.10±0.06 (0.13)	-0.01±0.05 (0.85)	0.4
15	0.06±0.03 (0.06)	-0.03±0.03 (0.31)	8.2	-0.09±0.05 (0.12)	0.00±0.04 (0.94)	0.4

All grassland species

Scale	Breeding			Wintering		
	AREA	$(AREA)^2$	ΔAIC	AREA	$(AREA)^2$	ΔAIC
1.25	0.06±0.05 (0.25)	-0.08±0.06 (0.18)	0.7	0.27±0.18 (0.13)	-0.15±0.19 (0.42)	2.4
2.5	0.07±0.05 (0.21)	-0.09±0.05 (0.10)	0.1	0.37±0.17 (0.03)	-0.24±0.18 (0.18)	0
5	0.11±0.06 (0.07)	-0.08±0.05 (0.15)	0	0.40±0.19 (0.04)	-0.21±0.18 (0.23)	1.1
10	0.11±0.06 (0.10)	-0.05±0.05 (0.36)	1.0	0.34±0.21 (0.10)	-0.10±0.18 (0.58)	2.5
15	0.09±0.06 (0.15)	-0.03±0.05 (0.52)	1.6	0.33±0.21 (0.12)	-0.05±0.16 (0.77)	2.4

Grassland residents

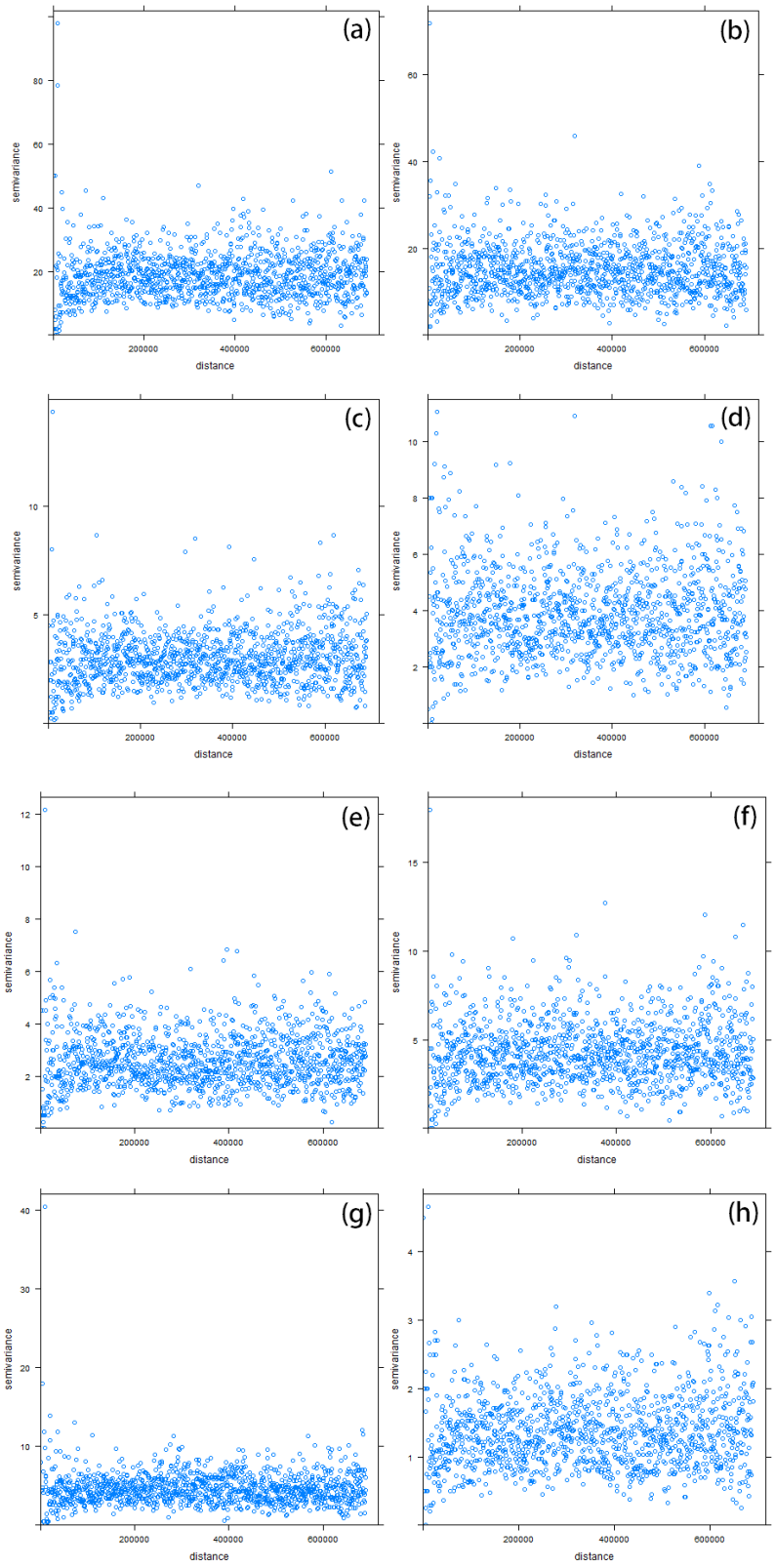
Scale	Breeding			Wintering		
	AREA	$(AREA)^2$	ΔAIC	AREA	$(AREA)^2$	ΔAIC
1.25	0.24±0.14 (0.09)	-0.16±0.15 (0.27)	0.5	0.19±0.21 (0.37)	-0.18±0.23 (0.46)	2
2.5	0.29±0.14 (0.04)	-0.08±0.13 (0.53)	0	0.37±0.23 (0.10)	-0.26±0.22 (0.25)	0
5	0.27±0.15 (0.08)	-0.09±0.13 (0.48)	1.2	0.41±0.24 (0.10)	-0.28±0.22 (0.20)	0.2
10	0.25±0.16 (0.12)	-0.09±0.13 (0.50)	1.9	0.33±0.26 (0.20)	-0.15±0.21 (0.48)	1.7
15	0.24±0.16 (0.13)	-0.05±0.11 (0.66)	1.7	0.33±0.26 (0.20)	-0.10±0.19 (0.60)	1.6

Grassland short-distance migrants

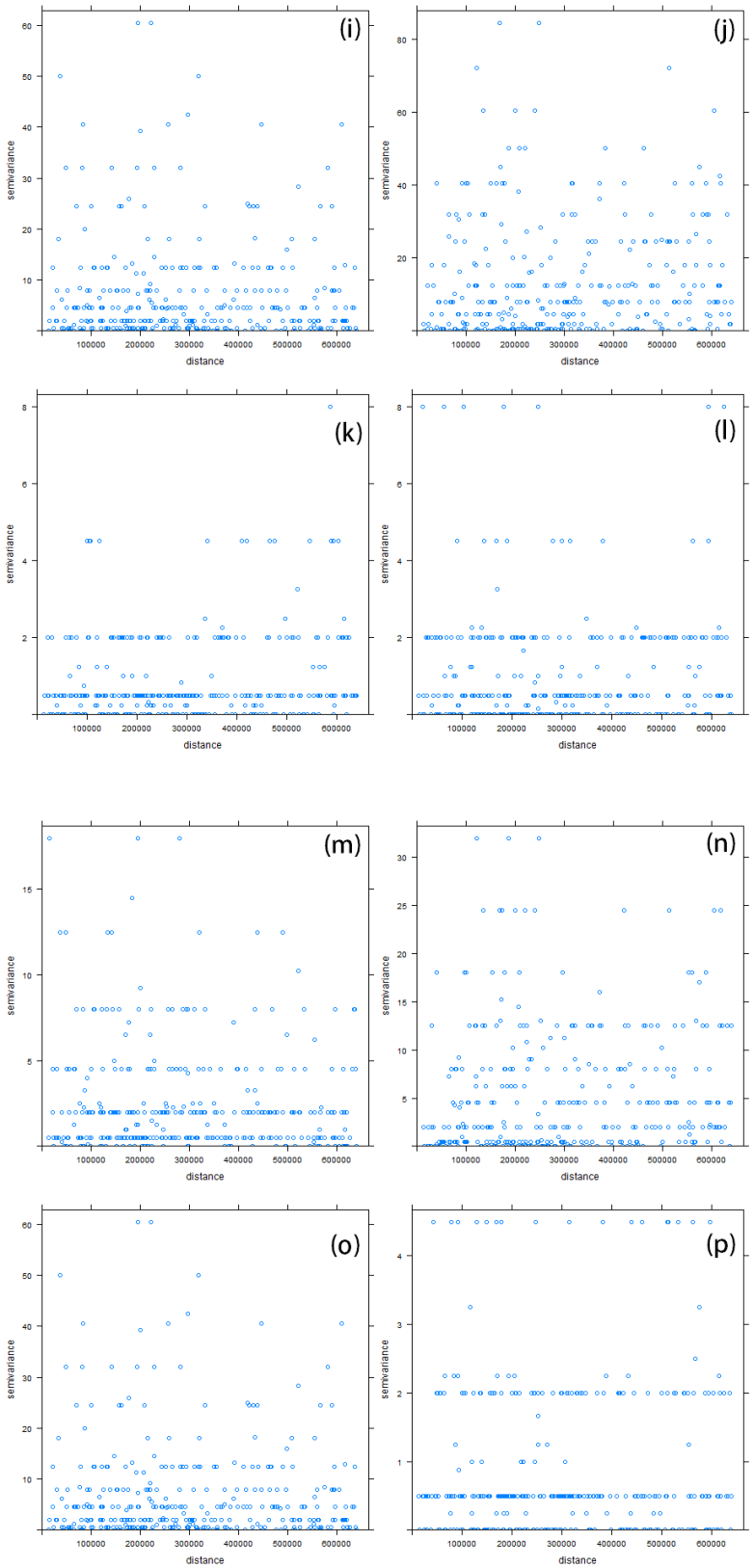
Scale	Breeding			Wintering		
	AREA	$(AREA)^2$	ΔAIC	AREA	$(AREA)^2$	ΔAIC
1.25	-0.03±0.07 (0.63)	-0.07±0.08 (0.37)	2.1	0.21±0.16 (0.20)	-0.11±0.17 (0.52)	2.1
2.5	-0.05±0.07 (0.47)	-0.11±0.08 (0.14)	0	0.29±0.16 (0.07)	-0.22±0.17 (0.19)	0
5	-0.05±0.08 (0.51)	-0.03±0.07 (0.73)	2.3	0.33±0.18 (0.07)	-0.20±0.17 (0.24)	0.8
10	-0.06±0.08 (0.48)	0.03±0.07 (0.70)	2.6	0.31±0.19 (0.11)	-0.10±0.16 (0.55)	1.5
15	-0.06±0.09 (0.47)	0.03±0.07 (0.61)	2.6	0.32±0.19 (0.10)	-0.07±0.15 (0.62)	1.1

Grassland long-distance migrants

Scale	Breeding			Wintering		
	AREA	$(AREA)^2$	ΔAIC	AREA	$(AREA)^2$	ΔAIC
1.25	0.13±0.12 (0.27)	-0.06±0.13 (0.64)	4.3	0.33±0.18 (0.08)	-0.23±0.20 (0.24)	2.8
2.5	0.16±0.12 (0.20)	-0.08±0.12 (0.49)	3.9	0.46±0.20 (0.02)	-0.22±0.18 (0.23)	0.5
5	0.32±0.14 (0.02)	-0.19±0.12 (0.11)	0	0.50±0.21 (0.02)	-0.14±0.17 (0.40)	0
10	0.34±0.15 (0.02)	-0.17±0.12 (0.13)	0.5	0.44±0.21 (0.04)	-0.07±0.15 (0.63)	0.8
15	0.30±0.15 (0.05)	-0.15±0.11 (0.17)	1.7	0.38±0.21 (0.07)	-0.03±0.13 (0.83)	1.5



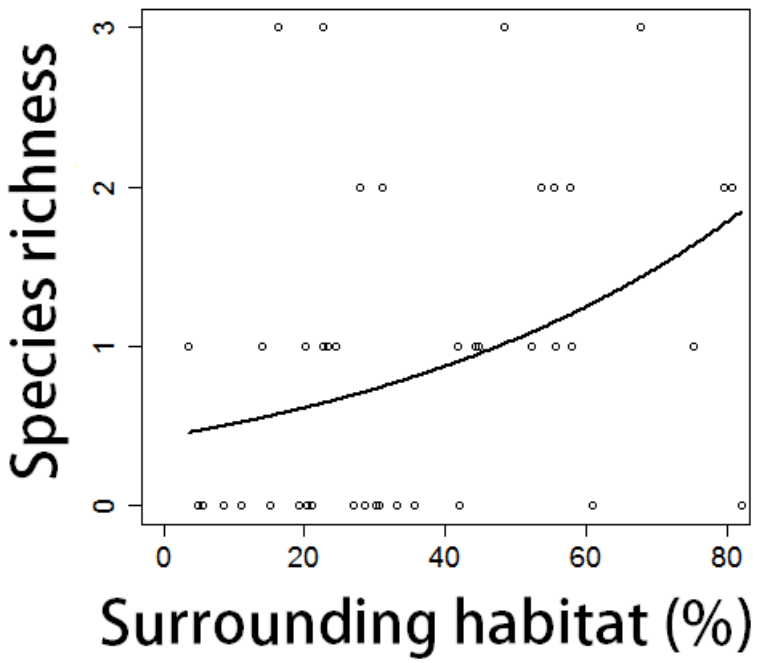
Appendix S2.9. Semi-variogram for species richness of forest birds [(a,b) all species, (c,d) residents, (e,f) short-distance migrants, (g,h) long-distance migrants] and grassland birds [(i,j) all species, (k,l) residents, (m,n) short-distance migrants, (o,p) long-distance migrants]. These results are from the breeding (a, c, e, g, i, k, m, o) and wintering (b, d, f, h, j, l, n, p) seasons.



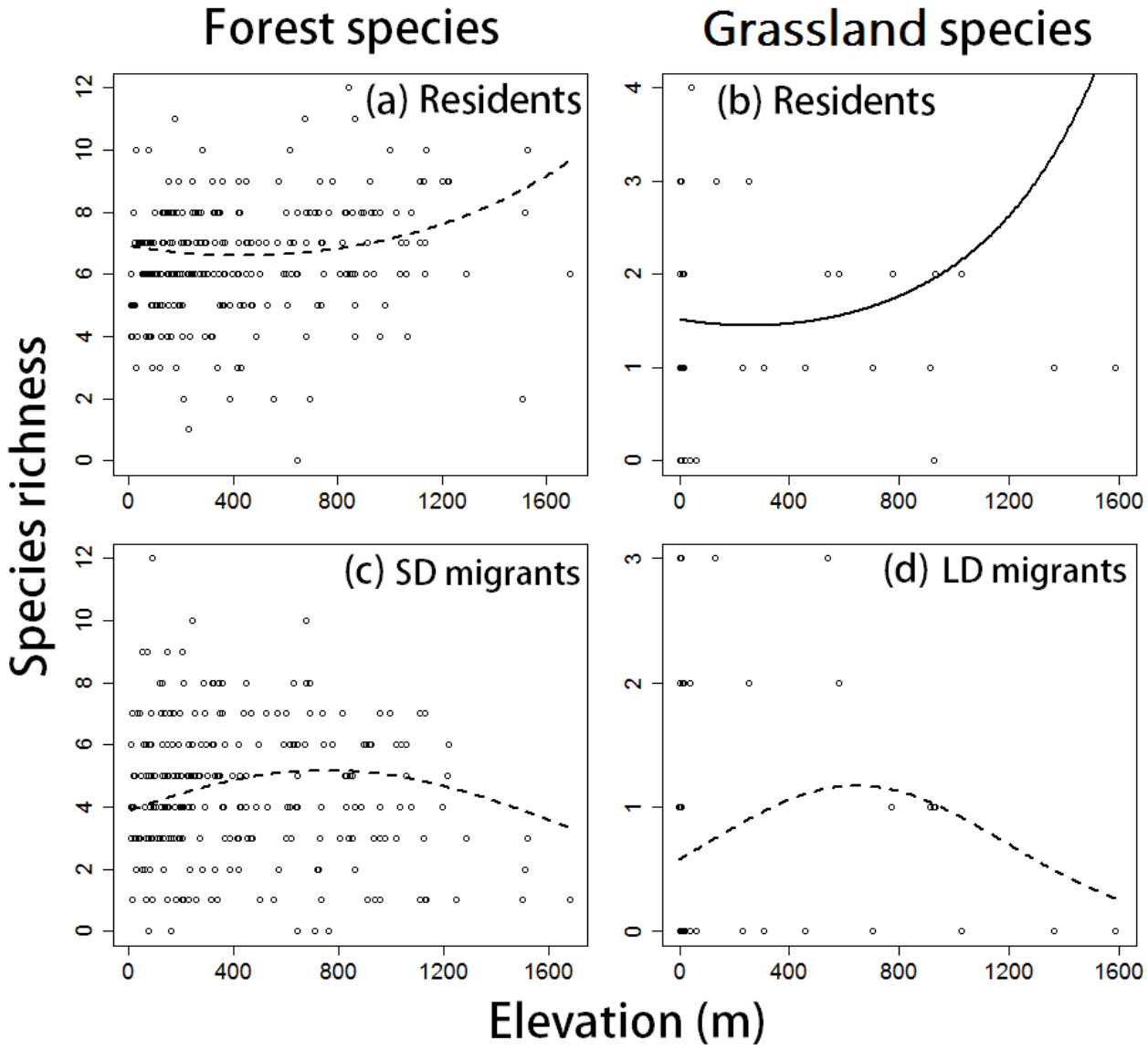
Appendix S2.9, continued.

Appendix S2.10. Variance inflation factors using linear values for each environmental factor in the analyses of all species in each habitat and season. Abbreviations: Breeding: breeding season; Wintering: wintering season; TEMP: annual mean temperature; SNOW: maximum snow depth; ELEV: elevation; AREA: area of surrounding suitable habitat (within a radius of 1.25 km for breeding forest birds, 10 km for wintering forest birds, and 5 km for grassland birds in both seasons). Cross marks: explanatory variables that were not used in construction of the full model to avoid multicollinearity.

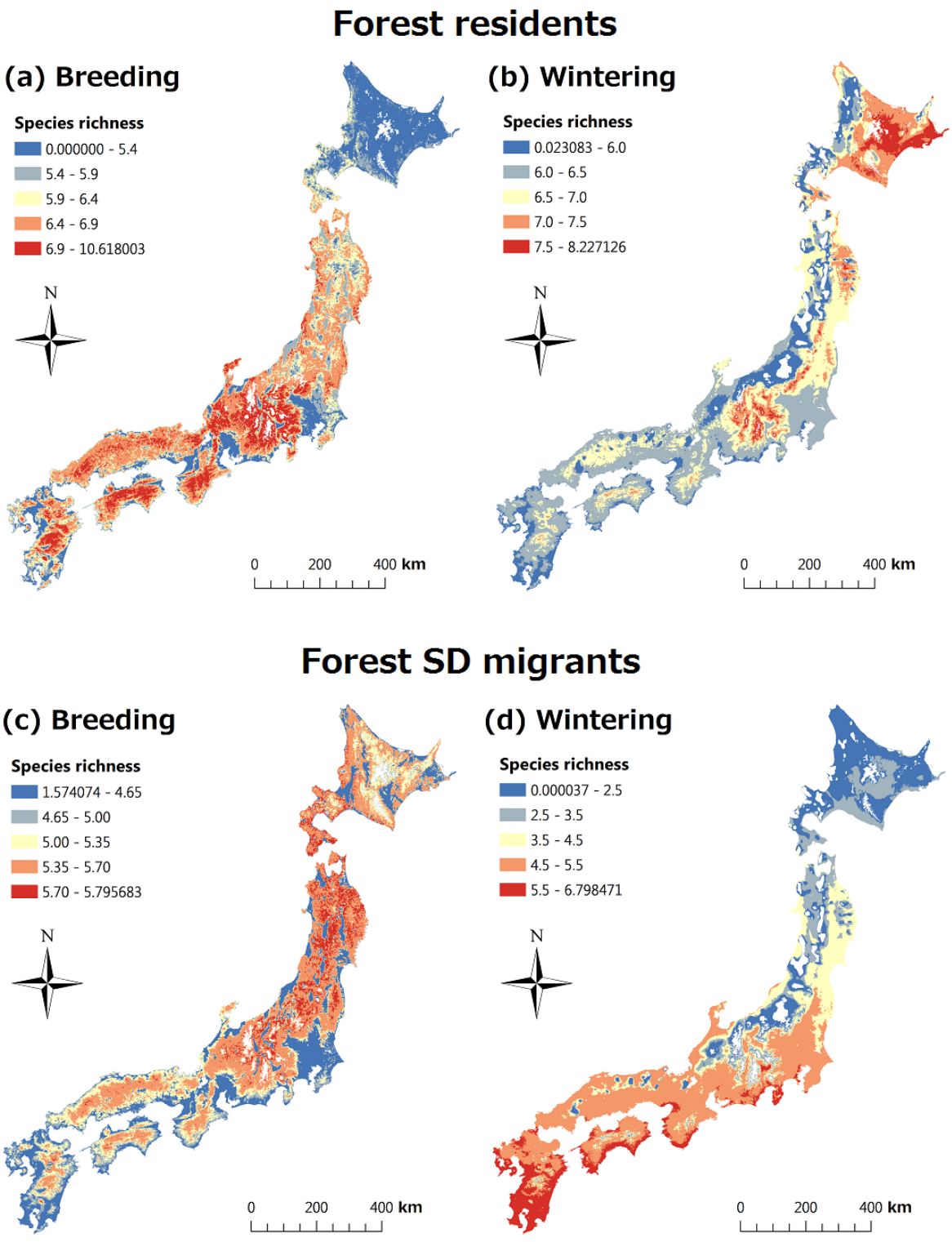
Variables	Forest		Grassland	
	Breeding	Wintering	Breeding	Wintering
TEMP	1.28	2.69	1.05	1.38
SNOW	×	1.99	×	×
ELEV	1.65	2.30	1.25	1.53
AREA	1.34	1.62	1.21	1.12



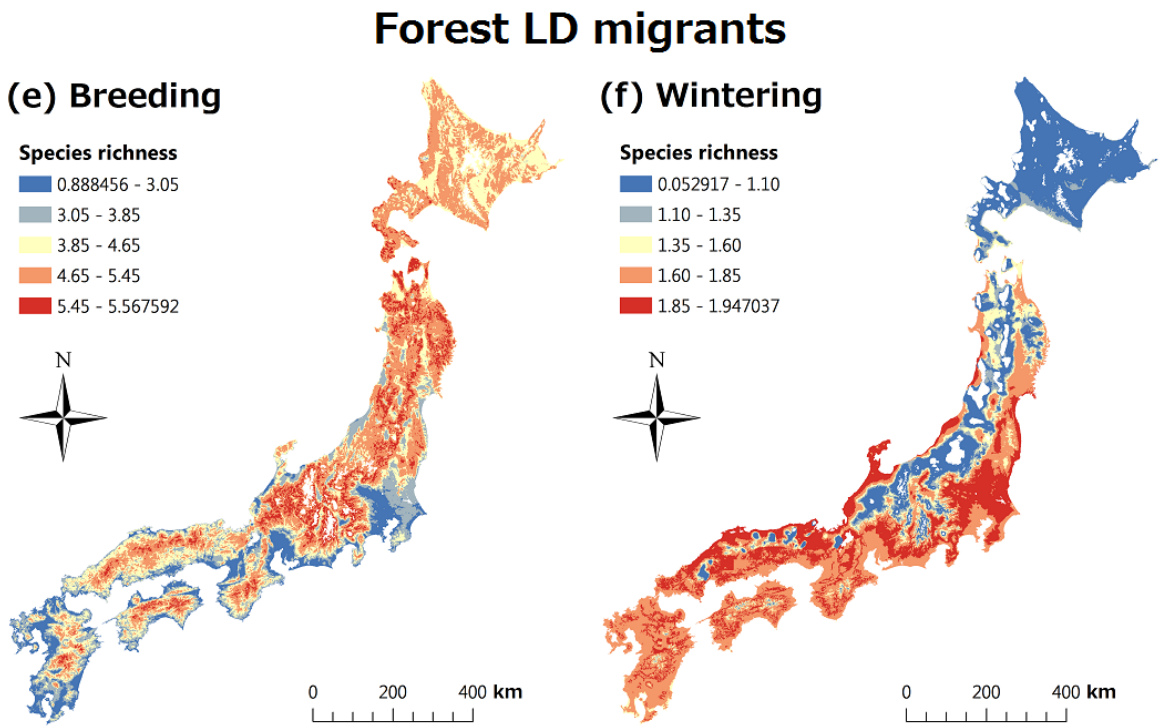
Appendix S2.11. Relationship between the extent of surrounding open habitat within 5 km and the species richness of grassland long-distance migrants, in the wintering season. Dots: Data collected at each site; solid lines: estimates afforded by the best spatial models. We used a GLMM (a multivariate analysis), and the effects of the other explanatory variables were considered and fixed to mean values in the figure. See details of the best spatial model in Table 2.1.



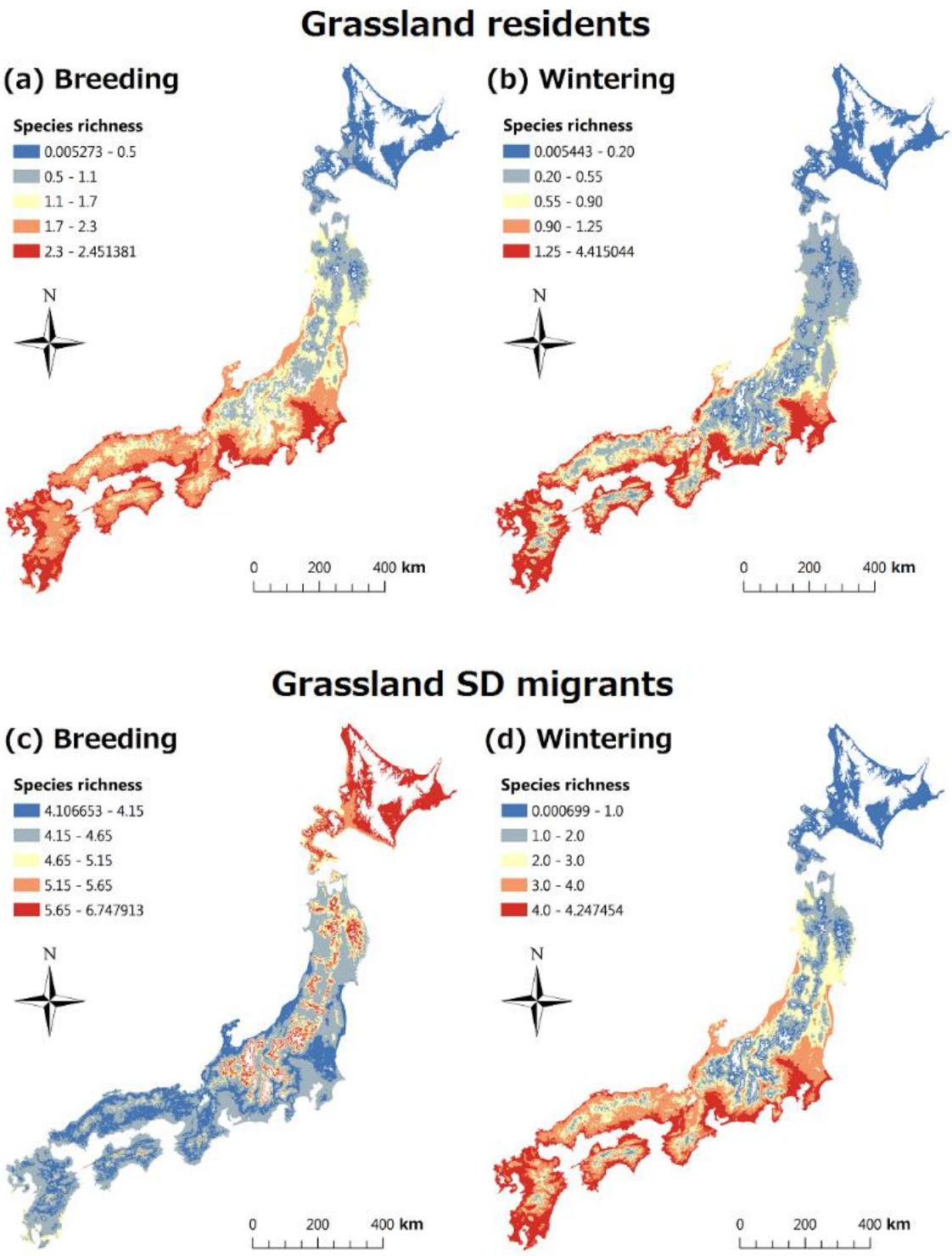
Appendix S2.12. Relationship between elevation and species richness of forest species: [(a) residents in the breeding season, (c) short distance migrants in the wintering season] and grassland species: [(b) residents in the breeding season, (d) long-distance migrants in the wintering season]. Dots: data derived at each site; lines: estimates afforded by the best spatial models (solid lines indicate semi-partial R^2 of either the temperature and its squared term > 0.1, and broken lines indicate that of both the temperature and its squared term < 0.1). We used a GLMM (a multivariate analysis), and the effects of the other explanatory variables were considered and fixed to mean values in each figure. See details of the best spatial models in Table 1. Abbreviations: LD: long distance, SD: short distance.



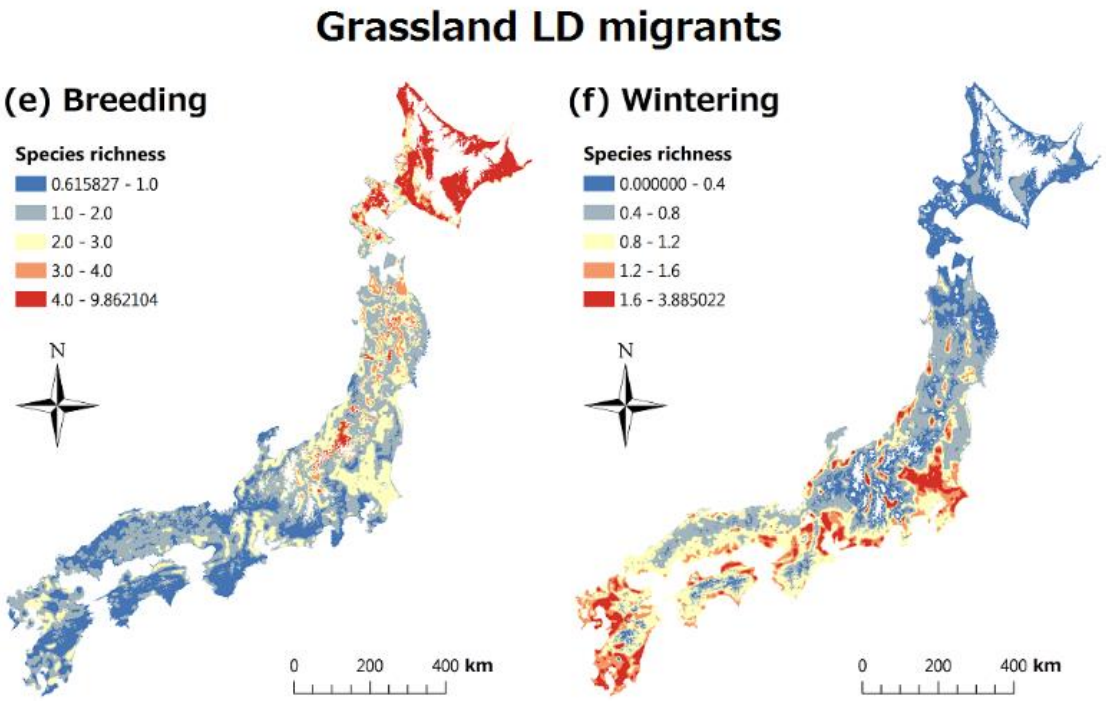
Appendix S2.13. Expected species richness of forest (a,b) residents, (c,d) short-distance migrants, and (e,f) long-distance migrants. Results are from the breeding (a, c, e) and wintering (b, d, f) seasons. We used the best spatial models to derive these results. We excluded regions where the values of explanatory variables from the models were not within the analysis range (i.e., annual mean temperature < 2°C, elevation > 1600 m, snow depth > 2.4 m). Coordinates: 30°59′–45°31′N; 129°33′–145°49′E.



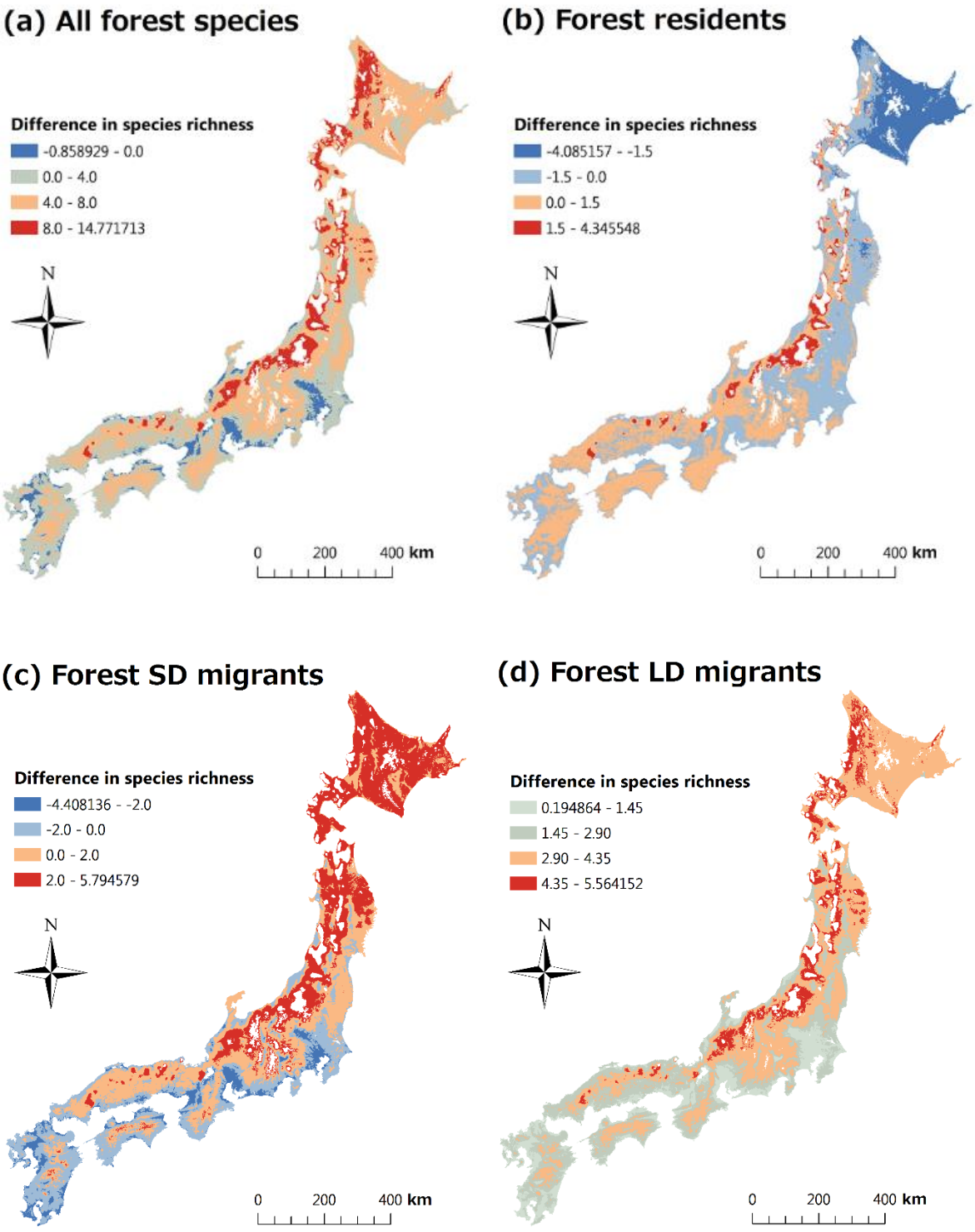
Appendix S2.13, continued.



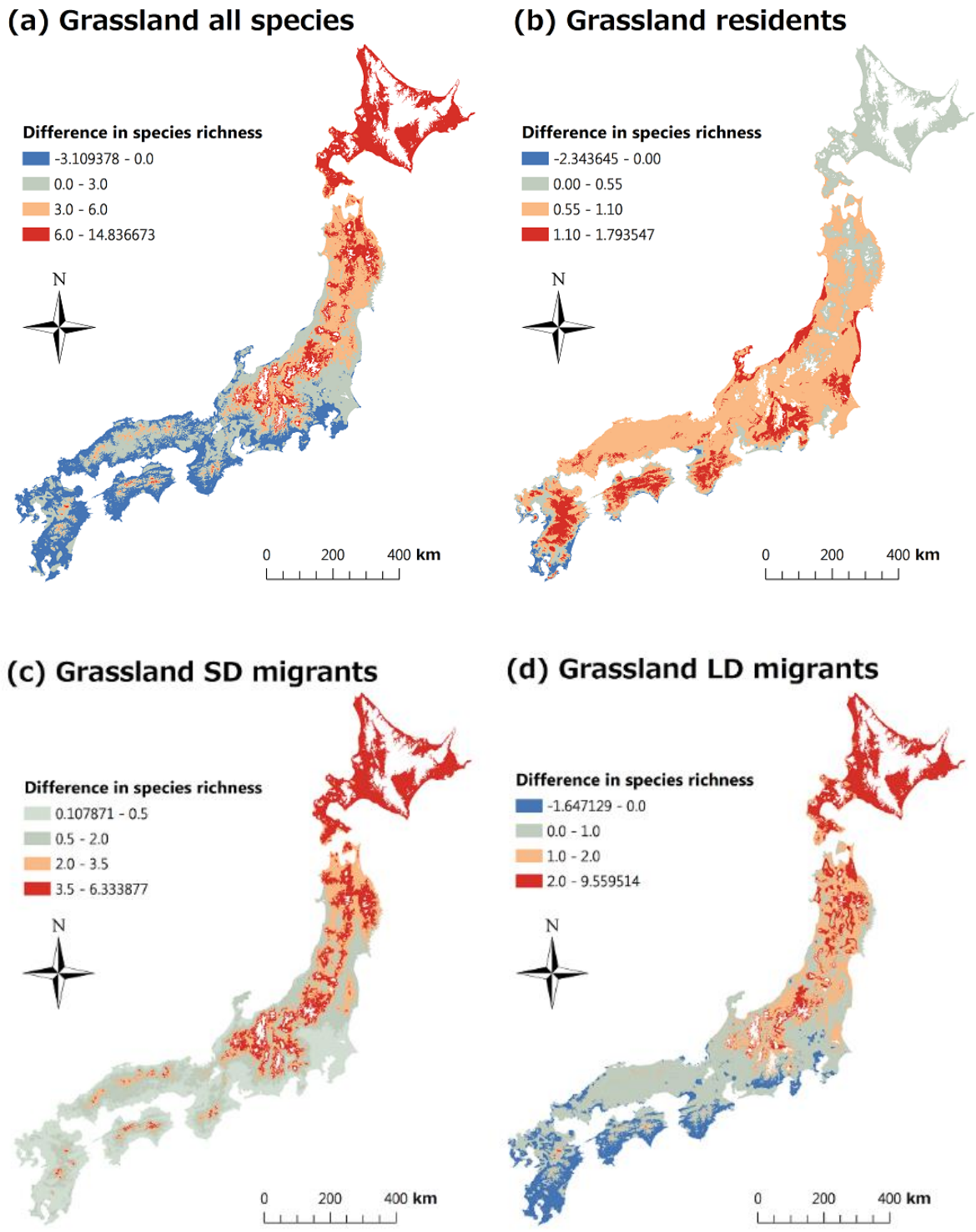
Appendix S2.14. Expected species richness of grassland (a–b) residents, (c–d) short-distance migrants, and (e–f) long-distance migrants. Results are from the breeding (a, c, e) and wintering (b, d, f) seasons. We used the best spatial models to derive these results. We excluded regions where the values of explanatory variables from the models were not within the analysis range (i.e., annual mean temperature <5 ° C, elevation > 1600 m, snow depth > 2.4 m). Coordinates: 30°59′–45°31′N; 129°33′–145°49′E.



Appendix S2.14, continued.



Appendix S2.15. Differences in expected species richness of forest birds between the breeding and wintering seasons [(a) all species, (b) residents, (c) short-distance migrants, and (d) long-distance migrants]. A positive value indicates that species richness was greater in the breeding than in the wintering season. We used the best spatial models to derive these results. We excluded regions where the values of explanatory variables from the models were not within the analysis range (i.e., annual mean temperature < 2°C, elevation > 1600 m, snow depth > 2.4 m). Coordinates: 30°59′–45°31′N; 129°33′–145°49′E.



Appendix S2.16. Difference in expected species richness of grassland birds between the breeding and wintering seasons [(a) all species, (b) residents, (c) short-distance migrants, and (d) long-distance migrants]. A positive value indicates that species richness was greater in the breeding than in the wintering season. We used the best spatial models to derive these results. We excluded regions where the values of explanatory variables from the models were not within the analysis range (i.e., annual mean temperature < 5°C, elevation > 1600 m, snow depth > 2.4 m). Coordinates: 30°59′–45°31′N; 129°33′–145°49′E.

Chapter 3

Effects of planted tree species on biodiversity of conifer plantations in Japan: a systematic review and meta-analysis

3.1 Abstract

Natural forests were increasingly replaced by plantations globally. While plantations support less biodiversity compared to natural forests, they can serve as an important habitat for forest-dependent species. Understanding the key drivers of the habitat function of plantations is necessary to reconcile both forestry and biodiversity. Planted tree species is one of the important factors determining the habitat function of plantations. Here, I systematically collected studies comparing the biodiversity between conifer plantations and natural forests, and conducted meta-analyses to quantify the effects of planted tree family/species on abundance and species richness of a wide range of taxa (all taxa, vertebrates, birds, invertebrates, terrestrial arthropods, plants, and understorey plants) in plantations in Japan. Abundance and species richness in plantations relative to natural forests differed among planted tree family/species. In plantations of pine family (mainly larch), abundance or species richness did not significantly differ from those in natural forests for many taxa, suggesting the important role as habitats. By contrast, in cypress family (mainly cedar), abundance or species richness was significantly lower than in natural forests for all analysis groups except understorey abundance. These results indicate that the habitat function of plantations and its management should be considered for each planted tree species, separately. Nevertheless, since our literature review identifies some research gaps that need to be filled, more comprehensive research efforts should be made in the future.

3.2 Introduction

Natural forests have been lost, and plantations have been expanding globally (FAO 2020). Plantations now account for 7% of the world's forests (FAO 2020), many of which have replaced natural forests (Puyravaud et al. 2010; Hua et al. 2018). Plantations are generally considered of lower biodiversity value than natural forests (Chaudhary et al. 2016), giving rise to the moniker of "green deserts" (Koh & Gardner 2010). However, several studies have shown that plantations can, in some contexts, support natural forest communities of a range of taxa (Estades & Temple 1999; Faria et al. 2007; Irwin et al. 2014; Spake et al. 2016). In landscapes already or increasingly dominated by plantations, conservation in plantations can be an effective and important means to promote biodiversity (Yamaura et al. 2012; Demarais et al. 2017; McFadden & Dirzo 2018), particularly in East Asia where one-third of the world's plantations occur (Payn et al. 2015). Identifying the factors that determine whether plantation or managed forests can sustain the biodiversity of natural forests is therefore necessary to reconcile both forestry and biodiversity (Brockerhoff et al. 2008; Demarais et al. 2017; Castaño-Villa et al. 2019).

Quantitative syntheses of studies on biodiversity in plantation or managed forests have demonstrated that their biodiversity depends on a range of factors, including plantation age (Castaño-Villa et al. 2019; Spake et al. 2019), plantation size (Castaño-Villa et al. 2019), logging intensity (Burivalova et al. 2014), thinning intensity and time since thinning (Spake et al. 2019), and landscape context (Mori et al. 2017; Castaño-Villa et al. 2019). The planted tree

species or ‘what is planted’ is likely of critical importance (Brockerhoff et al. 2008; Castaño-Villa et al. 2019). Previous syntheses of empirical research comparing the biodiversity of plantations with different tree species have made broad comparisons. For example, comparisons of plantations planted with native and exotic species, or mixed-species stands with monocultures have demonstrated that native, mixed stands generally support higher biodiversity than exotic monocultures (Castaño-Villa et al. 2019; but see Vehviläinen et al. 2008). However, comparisons of the biodiversity of forests planted with specific tree species are needed to inform regional planning. This is because the species that is planted can exert strong influences on resource availability (light, water, and soil nutrients; Barbier et al. 2008; Petersson et al. 2017). This has consequences for the establishment of native plant communities (Fimbel & Fimbel 1996; Petersson et al. 2017; Yamaura et al. 2019), leading to the differences in biodiversity across plantations (‘the tree species matter’; Felton et al. 2020).

Forest covers approximately 25 million hectares in Japan, constituting two-thirds of the total land area (FAO 2015). Plantations account for more than 40% of this area, principally as monocultures of conifer species (cypress family: Japanese cedar *Cryptomeria japonica*, Hinoki cypress *Chamaecyparis obtuse*; pine family: Japanese larch *Larix kaempferi*, Japanese red pine *Pinus densiflora*, Todo fir *Abies sachalinensis*, and Sakhalin spruce *Picea glehnii*) (Yamaura et al. 2012). All of these tree species are native to Japan (Hayashi 1960), although species have been planted beyond their naturally occurring range (Yamaura et al. 2012). Spake et al. (2019) synthesized studies measuring biodiversity responses to plantation management in

Japan, but did not consider planted tree species, so the relative biodiversity value of plantations of different tree species is unclear. I expected greater biodiversity in plantations of pine than cypress families, because the invasion by broad-leaved tree species is more prevalent in pine than cypress family plantations (Yamaura et al. 2019), leading to greater biodiversity (Yoshida et al. 2005; Ohsawa 2007; Yoshii et al. 2015; Lindbladh et al. 2017). The majority of local empirical studies surveying biodiversity of plantations have focused on only one planted tree species, because climate and topography restrict the area where each tree species is planted (Mitsuda et al. 2007; Nothdurft et al. 2012). A synthesis of planted tree species effects on plantation biodiversity is urgently needed in Japan, to inform management plans that aim to enhance biodiversity and ecosystem services in plantations, in the situation that clearcutting of mature plantations is increasing across Japan in effort to increase domestic wood supply (Forestry Agency 2018; Kakizawa et al. 2018).

Measuring biodiversity responses to forest management variables in Japan must consider seasonal variations, as biodiversity in temperate forests is season-dependent (Kawamura et al. 2019). Especially in deciduous broad-leaved forests that cover the northern half of Japan, the abundance of food resources (e.g., plants and insects) for animals increases rapidly from spring to summer, and becomes low in winter due to harsh climate and falling leaves (Herrera 1978; Huston & Wolverton 2009). Many animal populations consequently alter their range, habitat use, behavior patterns, or food habits (Marchand 2014), suggesting that the habitat function and consequent biodiversity values of plantations may vary with season.

Here I evaluate the relative biodiversity value of planted tree species in Japan. I systematically collected studies comparing biodiversity between conifer plantations and natural forest controls, and conducted meta-analyses to quantify the effects of planted tree family/species on abundance and species richness of various taxa (vertebrates, invertebrates, plants) in plantations in Japan. Specifically, I examined whether the species richness and abundance in plantations relative to natural forests differed among planted tree family or species. Furthermore, for vertebrates, I also examined whether the habitat function of plantations differed among seasons.

3.3 Materials and Methods

3.3.1 Biodiversity comparisons

I set out to measure plantation biodiversity as relative to local 'natural' forests with likely high conservation value, in order to calibrate plantation biodiversity against regional differences in species richness and abundance. I therefore sought studies that compared biodiversity between replicate plantations and natural forests, to enable the calculation of an effect size – representing the difference in biodiversity between natural and planted forests. This makes it possible to make broad biodiversity comparisons between plantation species across Japan, while accounting for regional variation in richness or abundance of natural communities, which vary greatly across Japan due to broad bioclimatic gradients (Kira 1991).

The two most commonly measured biodiversity metrics were considered: abundance

and species richness. Abundance measures per unit area included cover, biomass, or occurrence rates derived from multiple surveys in the same plots. Species richness, the number of species in a community is the most widely used biodiversity measure (Magurran 2004). I note here that authors measuring "species richness" in primary studies were actually measuring species density, the number of species per unit area (Gotelli & Colwell 2001), wherein richness is standardized against area or sampling effort across treatments. I use the term species richness to avoid confusion with abundance, which is often measured as density (per unit area).

3.3.2 Systematic review and data extraction

I performed the literature search, assessed eligibility, and extracted data following the PRISMA approach (Moher et al. 2009). To avoid language bias (Konno et al. 2020), I searched literature in both English and Japanese languages, using the Web of Science Core Collection (WoS on April 17th, 2019) and J-stage (the first time: on May 8th, 2019; the second time: on August 5th, 2019), respectively. For the WoS, I used the following search terms related to topics (TS): TS=(Japan) AND TS=(forest* OR woodland*) AND TS=("species richness" OR richness OR abundance OR density OR cover) AND TS=(plantation* OR planted OR planting). For the J-stage, due to the limited number of terms that can be used, the search was divided into searches as follows: [the first time: TS=(種数 species richness OR 個体数 abundance) AND TS=(人工林 OR 植林 plantation); the second time: TS=(密度 density OR 被度 cover) AND TS=(人工林 OR 植林 plantation)]. 4,638 articles were retrieved in total: 638 from WoS and

4,000 from J-Stage.

Potentially relevant articles were initially screened according to their titles and abstracts, after which 229 full-articles were assessed for eligibility. To be included in our meta-analysis, a study had to (1) sample biodiversity in both plantation forests (treatment group) and 'natural forests' (control group) which I defined as including secondary forests, (2) measured species richness (including family and genus richness) or abundance at least three replicate stands for both control and treatment groups (sample size), (3) report mean, standard deviation (SD) and sample size of species richness or abundance both for the control and treatment groups (or provide data from which these statistics can be derived), and (4) describe the planted tree family/species of plantations. Additional literature was identified by "snowballing": searching for references within retrieved articles. I also searched for other articles published by the first or corresponding authors of the included literature, by checking personal publication lists or the keyword search on Google Scholar using their name in English or Japanese (first 100 hits for each). These additional searches were conducted only for the studies that were deemed relevant after the initial abstract/title screen. For articles that satisfied conditions (1)-(2) but not (3) or (4), I attempted to contact authors for the required data.

A total of 115 articles satisfied the criteria for inclusion in the meta-analyses (PRISMA diagram in Appendix S3.3.1). From these studies, I extracted the following data: i) natural forest attributed (canopy tree species and stand age), and plantation attributes (planted tree family/species, and stand age), ii) surveyed taxa, iii) survey seasons, and iv) prefectures. For

abundance and/or species richness in both natural forests and plantations, I extracted mean values, SD, and sample size. When multiple articles contained the same data, the data from only one article was used for the analyses. Conversely, when an article contained multiple comparisons such as from multiple taxa, regions, states of natural forests, or states of plantations, I treated them as individual studies (see Appendix S3.3.2 for the classification of forests). For studies that surveyed biodiversity from multiple plots within plantations according to the distance from adjacent natural forests, I used only the plots most distant from natural forests, to avoid edge effects (deMaynadier and Hunter 1998).

3.3.3 Effect size estimation

I performed the meta-analyses using "metafor" v. 2.1.0 (Viechtbauer 2010) in R v. 3.6.1 (R Core Team 2019). I used the standardized mean difference, Hedges' g as the effect size metric (Borenstein et al. 2009) for examining the differences in abundance and species richness between natural forests and plantations:

$$g = (Mt - Mc)J/S$$

where *Mt* and *Mc* are the mean values of the abundance or species richness in the treatment (plantations) and control (natural forests) groups, respectively, *J* is a term that corrects bias due to small sample size, and *S* is the pooled SD of both groups. *J* and *S* are defined as follows:

$$J = 1 - 3/(4df - 1)$$

$$S = \sqrt{\{(nt - 1)St^2 + (nc - 1)Sc^2\}/(nt + nc - 2)}$$

where *df* is the degree of freedom, calculated by subtracting two from a total sample size of natural forests and plantations, *St* and *nt* are the SD and sample size of the treatment group, respectively, and *Sc* and *nc* are those of the control group. Hedges' *g*, which standardizes the mean difference by the variance of each study, allows the comparison of studies that vary in measurement units. Positive values of Hedges' *g* indicate that abundance or species richness is greater in plantations than in natural forests, while negative values correspond to lower abundance and richness. When its 95% confidence intervals did not overlap zero, I interpreted the difference between plantations and natural forests as significant. I followed Cohen's classification to interpret effect sizes, as small, moderate, and large effects from values of *g* in the region of 0.2, 0.5, and 0.8 respectively.

3.3.4 Meta-analysis

I estimated summary effect sizes characterising differences between natural and plantation forests, using weighted random-effects models, which assume that studies with different methods and materials have different true effect sizes (Borenstein et al. 2009). This was done on subgroups of the richness and abundance effect sizes as follows: for each planted tree family (pine family and cypress family) and species (Japanese cedar, Hinoki cypress, Japanese larch, Todo fir, and Japanese red pine; hereafter cedar, cypress, larch, fir, and red pine, respectively). When calculating summary effects (i.e., the averaged Hedges' *g*), weighting serves to increase the precision of overall estimates. The choice of weighting scheme can affect the overall

estimate (Spake & Doncaster 2017; Hamman et al. 2018). Preliminary analyses suggested negligible differences among summary effects using two weighting methods based on inverse variance and sample size (Appendix S3.3.1). I report results using the inverse variance method in this study.

To test whether summary effects (subgroup means) differed among planted tree family/species, I evaluated statistical differences among the subgroup means with Cochran's Q test (significant when $p<0.05$; Borenstein et al. 2009). These analyses were performed separately for abundance and species richness in each of seven taxonomic groups: i) all taxa, ii) vertebrates, iii) birds (a subset of vertebrates, excluding mammals and fishes), iv) invertebrates, v) terrestrial arthropods (a subset of invertebrates, excluding soil and aquatic animals, and mollusks), vi) plants, and vii) understorey plants (a subset of plants, excluding data only for trees above a certain height and thickness, hereafter "understorey"). For vertebrates and birds, I tested whether the effect sizes differed among seasons (spring-summer and autumn-winter). Here, I estimated summary effects for both seasons, for all effect sizes representing differences between natural forests and plantations. I did not subgroup further by planted tree families/species, due to a low sample size of studies in autumn-winter. Summary effects were only estimated for subgroups with at least three effect sizes derived from different studies.

Some subgroups contained multiple effect sizes from the same sites, and thus, pseudo-replication occurred. For example, in an article where larch plantations were compared with

primary forests and secondary natural forests, two effect sizes were obtained: larch plantations vs primary forests and larch plantations vs secondary forests. I tested for the possibility of pseudo-replication for the analyses of the effects of planted tree family/species. I estimated summary effects using one effect size randomly selected from each study. Specifically, bootstrap resampling was run 10,000 times in R, and the averaged Hedges' *g* and its 95% CI were computed for each group. Results did not change (Appendix S3.3.2). Therefore, the effects of pseudo-replication are likely to be small.

Studies that were included in our meta-analyses varied in many respects, such as study design and plot size. These differences may bias effect size and variance estimation if such factors covary with moderators of interest (Spake & Doncaster 2017). I therefore ensured that there existed no covariation of plot size with sample size, Hedge's *g*, and its variance (Appendix S3.3.3). I decided used Hedges' *g* due to its handling of zero data. Moreover, in the preliminary analyses, I examined the effects of natural forest types and those of stand age of plantations and natural forests on Hedges' *g*. For many analysis groups, there were no obvious effects (Appendix S3.2).

3.3.5 Publication bias

I tested for the possibility of publication bias, wherein the publication of results is more likely for statistically significant and expected findings (Borenstein et al. 2009). I did this for the analyses of each planted tree family (pine and cypress family) for abundance and species

richness of all taxa. First, I produced a funnel plot, in which the inverse standard error (sample size relative to variance) is plotted against the effect sizes. Asymmetry in this plot, indicative of publication bias, was tested using Egger's test (Egger et al. 1997). Using a trim-and-fill analysis with R0 estimator, I estimated the number of "unpublished comparisons" in our dataset, its effect size, and the averaged Hedges' *g* with corrected publication bias, for each planted tree family (Duval & Tweedie 2000a, 2000b; Peters et al. 2007).

3.4 Results

3.4.1 Data description

115 published articles yielded 667 individual effect sizes representing differences between planted and natural forests. Studies on plants and invertebrates were conducted widely across Japan, although few studies were from some parts of western Japan (few studies on both taxa were in the Chugoku and Kinki regions, and no studies on plants were in the Shikoku region; Table 3.1, Appendix S3.4.1a-b). By contrast, for vertebrates, most studies were conducted in eastern Japan (the Kanto, Tohoku and Hokkaido regions), and few studies were in western Japan where the proportion of plantations to natural forests is high (three studies in the Chubu and Chugoku regions on birds, one in the Shikoku region on fishes, and one in the Kyushu region on the Japanese Macaque *Macaca fuscata*; Table 3.1, Appendix S3.4.1c, 3.4.2). In terms of planted tree species, the number of studies on larch relative to its planting area was high compared to the other species of pine family, and there were fewer studies on cypress than those

on cedar (Table 3.2, Appendix S3.4.2).

Table 3.1. The number of articles focusing on each taxon in each region, the group of prefectures that are geographically close (from northeast to southwest, Hokkaido, Tohoku, Kanto, Chubu, Kinki, Chugoku, Shikoku, Kyushu, Okinawa). Values in the table indicate the number of articles per plantation area (the actual number of articles), and zero values indicate that there were no studies. Plantation area was calculated from the data released by the Forestry Agency on March 31, 2017 (Table S3).

	Number of article (/2500 km^2 plantations)							
Region	Vertebrate		Invertebrate		Plant		Others	
Hokkaido	4.74	(28)	0.68	(4)	1.02	(6)	0	(0)
Tohoku	0.79	(6)	0.53	(4)	0.79	(6)	0	(0)
Kanto	1.18	(3)	3.93	(10)	4.71	(10)	0.39	(1)
Chubu	0.27	(2)	0.95	(7)	1.76	(13)	0	(0)
Kinki	0	(0)	0.45	(2)	0.45	(2)	0	(0)
Chugoku	0.26	(1)	0	(0)	0	(0)	0	(0)
Shikoku	0.30	(1)	1.48	(5)	0	(0)	0	(0)
Kyushu	0.17	(1)	0.52	(3)	1.21	(7)	0.17	(1)
Okinawa	0	(0)	0	(0)	20.68	(1)	0	(0)

Table 3.2. The number of articles focusing on plantations of each planted tree species [Japanese cedar, Hinoki cypress, Japanese larch, Todo fir, and *Pinus* (e.g., Japanese red pine)] in each region. Hyphens indicate that there are no plantations of the planted tree species. Articles dealing with multiple planted tree species together (e.g., Japanese cedar and Hinoki cypress) were not used for aggregation. See details in Table 1.

	Number of article (/2500 km^2 plantations)									
Region	Cedar		Cypress		Larch		Fir		*Pinus*	
Hokkaido	0	(0)	0	(0)	17.60	(28)	4.19	(13)	128.93	(1)
Tohoku	1.81	(9)	6.43	(1)	3.68	(3)	0	(0)	1.43	(2)
Kanto	7.28	(10)	3.11	(2)	8.75	(2)	-	-	5.67	(1)
Chubu	1.68	(5)	1.34	(3)	11.89	(15)	0	(0)	3.37	(2)
Kinki	1.43	(3)	0.50	(1)	0	(0)	-	-	0	(0)
Chugoku	0.78	(1)	0	(0)	0	(0)	-	-	3.38	(2)
Shikoku	1.85	(3)	1.28	(2)	0	(0)	-	-	0	(0)
Kyushu	2.13	(7)	0.50	(1)	0	(0)	-	-	6.70	(1)
Okinawa	0	(0)	-	-	-	-	-	-	36.10	(1)

3.4.2 Effects of planted tree family

In cypress family plantations, both abundance and species richness were significantly lower than natural forests for all biological groups except understorey abundance (*g* took values between −0.75 for bird abundance and −0.22 for invertebrate abundance; Fig. 3.1). By contrast, in pine family plantations, the value was significantly lower than that in natural forests only for species richness of all taxa (*g*=−0.28, upper *CI*=−0.002; Fig. 3.1h) and abundance of vertebrates and birds (vertebrates: *g*=−0.14, upper *CI*=−0.02, birds: *g*=−0.18, upper *CI*=−0.05; Fig. 3.1b-c), and rather, tended to be higher for abundance of invertebrates and terrestrial arthropods (invertebrates: *g*=0.17, lower *CI*=−0.10; terrestrial arthropods: *g*=0.26, lower *CI*=−0.02; Fig. 3.1d-e). Effect sizes that were generally negative for both biodiversity metrics tended to be more strongly negative for abundance and richness in cypress than pine family plantations (Fig. 3.1, Appendix S3.4.3). Differences between subgroup mean effect sizes for pine and cypress families were significant for seven of 14 biological groups (abundance: all taxa, vertebrates, birds, invertebrates, and terrestrial arthropods; species richness: all taxa and terrestrial arthropods; Fig. 3.1a-e, h, k-l, Appendix S3.4.3). For all subgroups except abundance and species richness of birds in cypress family plantations, I found significant between-study heterogeneity of effect sizes (Appendix S3.4.3). Confidence intervals for abundance and species richness of understorey in pine family plantations were extremely wide (abundance: Q_{20}=76.94, p<0.0001, species richness: Q_{21}=172.55, p<0.0001; Fig. 3.1g, n, Appendix S3.4.3).

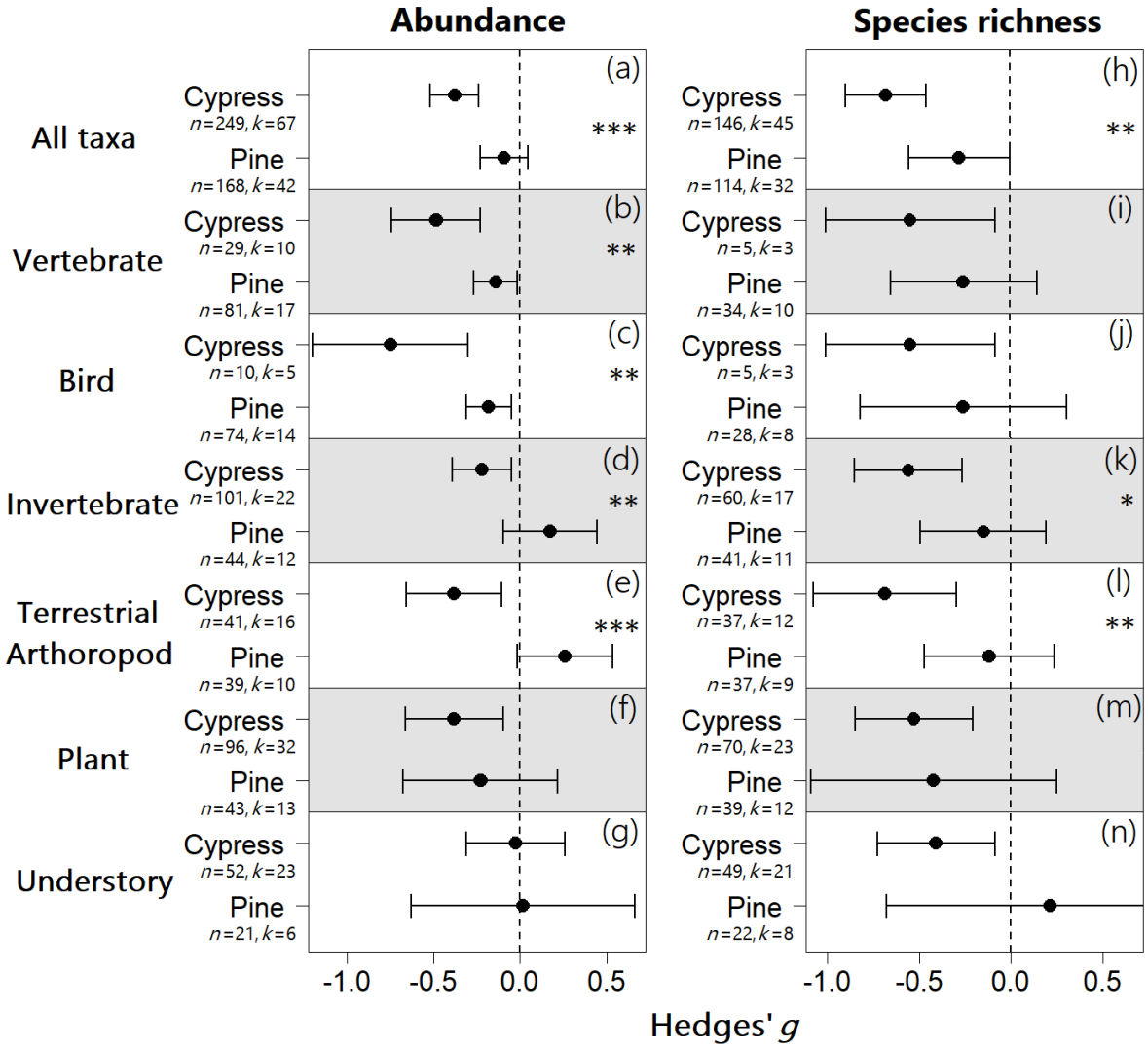


Fig. 3.1. Effects of planted tree family (cypress and pine family) on the averaged Hedges' *g* for abundance (a-g) and species richness (h-n) of each analysis group. Hedges' *g* indicates the difference in abundance or species richness between plantations and natural forests, and negative values mean that abundance or species richness is lower in plantations than in natural forests. Filled dots and solid bars indicate the estimated means and its 95% confidence intervals, respectively [for understorey species richness in pine family plantations (n), the upper 95% *CI* (=1.11) is not shown]. Cochran's Q test was conducted for each analysis to examine the difference in estimates between planted tree families, and the significance was indicated by asterisk on the right side of each block (***: $p<0.01$, **: $p<0.05$, *: $p<0.1$). *n* and *k* left outside the frame represent the number of comparisons and that of independent comparisons, respectively.

3.4.3 Effects of planted tree species

For all biological groups with available data, with the exception of plant and understorey abundance, cedar plantations were the most strongly negative, indicating lower abundance and species richness in cedar plantations than natural forests (Fig. 3.2a-b, d-e, Fig. S3.5a, d-g in Appendix S3.3.2, Appendix S3.4.3). Studies on larch plantations generally showed only weakly negative effect sizes (Fig. 3.2, Fig. S3.5, Appendix S3.4.3), and rather positive for abundance of invertebrates and terrestrial arthropods (invertebrates: g=0.21, lower CI=−0.08; terrestrial arthropods: g=0.20, lower CI=−0.10), and understorey species richness (g=1.24, lower CI=−0.56) (Fig. 3.2d-e, Fig. S3.5g in AppendixS3.3.2, Appendix S3.4.3). These suggest larch plantations supported similar biodiversity levels to natural forests, and are superior to cedar plantations. Data were limited for comparing biodiversity of other tree species. For all taxa and birds, abundance in red pine plantations and species richness in fir plantations were comparable to those in natural forests (Fig. 3.2a, c, Fig. S3.5a, c in Appendix S3.3.2). For plants including understorey, abundance in fir plantations was significantly lower than that in natural forests, by contrast, abundance and species richness in cypress plantations did not significantly differ from those of natural forests (Fig. 3.2f-g, Fig. S3.5f-g in Appendix S3.3.2).

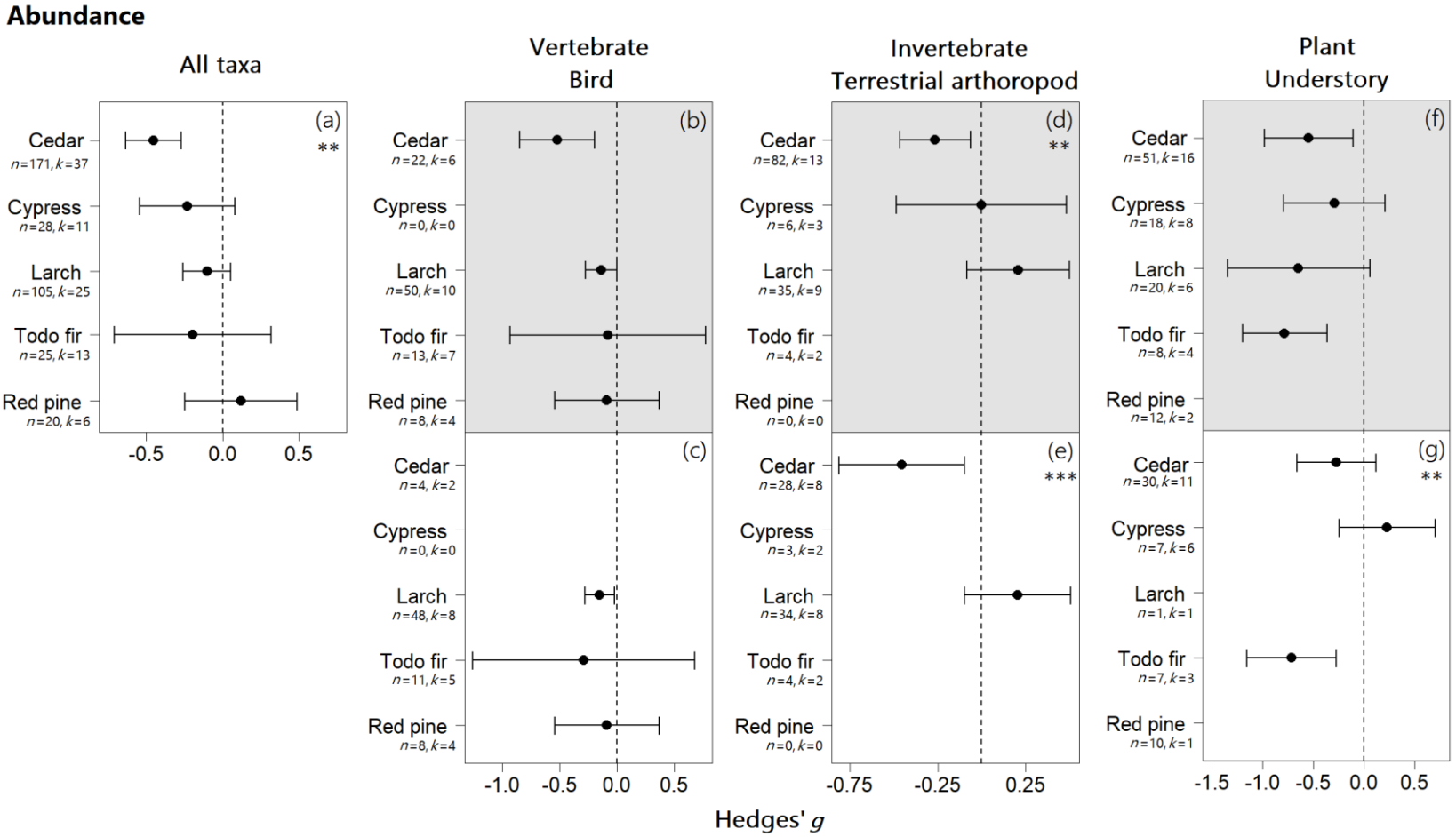


Fig. 3.2. Effects of planted tree species (Japanese cedar, Hinoki cypress, Japanese larch, Todo fir, and Japanese Red pine) on the averaged Hedges' *g* for abundance of each analysis group [all taxa (a), vertebrates (b), birds (c), invertebrates (d), terrestrial arthropods (e), plants (f), and understorey (g)]. Filled dots and solid bars indicate the estimated means and its 95% confidence intervals, respectively. Cochran's Q test was conducted for each analysis to examine the difference in estimates among planted tree species, and the significance was indicated by asterisk on the right side of each block (***: $p<0.01$, **: $p<0.05$). *n* and *k* left outside the frame represent the number of comparisons and that of independent comparisons, respectively.

3.4.4 Effects of seasons

Effect sizes representing biodiversity differences among plantations and natural forests varied according to season (Fig. 3.3, Appendix S3.4.3). For bird and vertebrate abundance and bird richness, effect sizes were more strongly negative when surveying in spring-summer than in autumn-winter (Fig. 3.3). This demonstrates that the animal abundance and richness in plantations were lower than those of natural forests in the spring-summer (Fig. 3.3). By contrast, in autumn-winter, abundance and species richness in plantations were comparable to, or significantly higher than those in natural forests (vertebrate abundance: g=0.11, lower CI=0.03; Fig. 3.3).

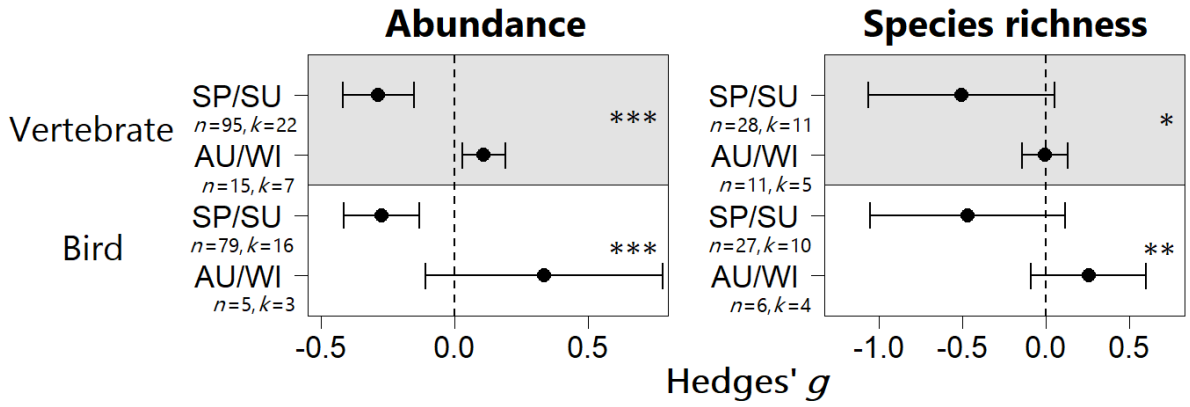


Fig. 3.3. Effects of survey seasons (SP/SU: spring-summer, AU/WI: autumn-winter) on the averaged Hedges' g for abundance and species richness of vertebrates and birds. Filled dots and solid bars indicate the estimated means and its 95% confidence intervals, respectively. Cochran's Q test was conducted for each analysis to examine the difference in estimates between seasons, and the significance was indicated by asterisk on the right side of each block (***: p<0.01, **: p<0.05, *: p<0.1). n and k left outside the frame represent the number of comparisons and that of independent comparisons, respectively. We dealt with only the differences between natural forests and plantations, not with those among planted tree species, due to the scarcity of studies in autumn-winter.

3.4.5 Publication bias

For studies on abundance of all taxa, the presence of publication bias for cypress family plantations was indicated by Egger's test (cypress family: t=−3.19, $d.f.$=247, p<0.01; pine family: t=−1.77, $d.f.$=166, p=0.08), however, trim and fill analysis estimated the existence of zero unpublished studies (i.e., correcting the publication bias was not necessary). For the effect size of species richness of all taxa, the presence of publication bias for both cypress and pine family plantations was suspected by Egger's test (cypress family: t=−4.34, $d.f.$=144, p<0.01; pine family: t=−2.01, $d.f.$=112, p=0.05). The trim-and-fill analysis estimated that there were 11 unpublished comparisons with higher effect sizes for cypress family plantations, although correcting the publication bias was not necessary for pine family plantations (Fig. S3.9 in Appendix S3.4.4). After adding false data of unpublished comparisons, species richness in cypress family plantations still remain to be significantly lower than that in natural forests, and the value of averaged Hedges' g for cypress family plantations was lower than that for pine family ones, however, the difference among planted tree family became not significant (Fig. S3.10 in Appendix S3.4.4).

3.5 Discussion

To our knowledge, this is the first meta-analysis to examine whether the biodiversity value of plantations, relative to natural forests, varies according to planted tree family/species. While

abundance and richness were consistently lower in plantations than in natural forests for a range of taxonomic taxa, the difference was less strongly negative for pine family plantations (mainly larch) than cypress family plantations (mainly cedar) (Fig. 3.1-3.2, Fig. S3.5 in Appendix S3.3.2). These results are important for biodiversity conservation in plantation landscapes because it demonstrates that forests collectively treated as "plantations", will differ in their ability to support biodiversity according to planted tree species.

3.5.1 Effects of planted tree family or species

I found that plantations of pine family (mainly larch) had a less negative effect on biodiversity, relative to natural forests, than plantations of cypress family (mainly cedar). There are several potential explanations for this finding. First, the relative abundance of canopy broad-leaved tree species is also generally higher within pine family plantations of pine family, including fir and Sakhalin spruce *Picea glehnii* that have darker forest floor (Yamaura et al. 2019). This is likely due to the generally lower stocking density of pine plantations, permitting the establishment of broad-leaved species (Yamaura et al. 2019). Secondly, larch and red pine plantations, in addition fir or spruce plantations with mixed broad-leaved trees, have sparser canopies and allow more light to reach the forest floor, supporting more abundant understorey than those of cypress family plantations (the relative light intensity: cedar/cypress/fir (2~8%) < larch < red pine/birch (one of the dominant broad leaved tree species in northern Japan: 5~20%; Maebashi Forestry Office 1997; Yamaura et al. 2008; Takahata et al. 2017; Forestry Agency 2019). Third, red pine

and larch trees support more insect larvae (e.g. moths and butterflies) than cedar trees (up to 4.5 times more), comparable to that supported by deciduous broad-leaved trees (Yui & Ishii 1994). Therefore, pine family plantations with abundant broad-leaved trees and understorey provide various and abundant food and habitat resources for invertebrates including terrestrial arthropods (e.g., dead woods, flowers, and leaves; Ohsawa 2004; Taki et al. 2010). In turn, these forests would provide important prey resources for birds and other vertebrates, as well as suitable structures for nesting or shelter from predators (e.g., cavity trees and dense bush) (Yui & Ishii 1994; Newton 1998; Kikuchi et al. 2013; Simonetti et al. 2013).

Contrary to previous studies suggesting that pine family plantations support more abundance of understorey or canopy tree species than cypress family ones, I did not detect an effect of planted tree family on abundance and species richness for plants (Fig. 3.1f-g, m-n). Abundance and species richness of understorey in cypress plantations tended to be similar to natural forests (Fig. 3.2g, Fig. S3.5g in Appendix S3.3.2). I note here that five of six comparisons for this analysis came from a single article, but were considered independent because surveys were conducted in five distinct regions (see Methods). In this article, the plantations surveyed in each region exceeded typical rotation ages (oldest stand age in each region: 67-287). Older cypress family plantations would also likely support richer understorey because of both artificial and natural (self) thinning (Igarashi & Kiyono 2008). Our set-up yielded wide confidence intervals for understorey effect sizes for pine family plantations, suggesting that habitat function of plantations for supporting plant communities can vary

strongly, in relation to subtaxon or management practice (e.g., stand age and thinning). However, the number of studies on plants may be not enough to measure the effects of planted tree family/species. More studies on plants in plantations are therefore needed to clarify the effective situation for conserving plant communities in plantations of each planted tree species.

3.5.2 Effects of season

For vertebrates (mainly birds), the function of plantations to support natural forest biodiversity differed among seasons. In spring-summer, both abundance and species richness were lower in plantations than natural forests. In autumn-winter however, plantation richness and abundance levels were comparable to natural forests. From spring to summer, breeding vertebrates rely on prey and suitable structures for nesting or hiding (e.g., cavities and shrubs) that are more abundant in natural forests (Yui & Ishii 1991; Kikuchi et al. 2013). By contrast, in autumn to winter, the amount of prey resources is drastically reduced and the difference between plantations and natural forests would diminish. Therefore, plantations in this season may be comparable habitats to natural forests. Moreover, plantations with high densities of trees, especially those with evergreen conifer species, may provide superior shelter against harsh climate and predators in winter conditions than natural deciduous broad-leaved forests (Petit 1989; Minamino et al. 2007; Minamino & Akashi 2008). Furthermore, conifer plantations in lowlands are preferred as wintering habitats by some migratory bird species breeding conifer forests in highlands or cool regions (Yamaura et al. 2009; Yabuhara et al. 2019). For vertebrate

conservation and management, we should consider the possibility that abundant conifer plantations existing across Japan play important roles as wintering habitats.

3.5.3 Limitations and future research directions

For species richness of all taxa, differences in effect sizes between pine and cypress families became non-significant after accounting for publication bias using trim-and-fill methodology (Appendix S3.4.4). This suggests that our analyses overestimated the magnitude of negative effect size. Even in cypress family plantations, there are cases with abundant broad-leaved trees (treated as unsuccessful plantations), and such stands would support rich biota (Masaki et al. 2004). Thus, when the function of plantations as habitats are evaluated to be high, it is important to publish the results as valuable knowledge, even in small sample situations. Not only the amount of broad-leaved trees, but also stand age would be important for many taxa (Appendix S2.1; Spake et al. 2019). Managing these stand variables is needed to utilize the potential of plantations as habitats for both cypress and pine family.

Studies on pine family plantations were predominantly on larch, especially for taxa other than birds, and there were fewer studies on plantations of cypress than those of cedar (Table 3.2; Fig. 3.2). Thus, I could examine the habitat function of plantations of less-studied tree species (i.e., Todo fir, Japanese red pine, and Hinoki cypress) for only some taxonomic groups. Furthermore, few studies on vertebrates were conducted in western Japan, where the proportion of plantations to forests is high and cypress family is mainly used (Table 3.1,

Appendix S3.4.2). Results of this meta-analysis indicated that the function as habitats compared with natural forests was generally low in cypress family plantations, and the function of plantations for vertebrates increased in autumn-winter. However, the roles of plantations of each planted tree family/species in each season remain unknown, especially those of cypress family plantations in western Japan where many forest birds including migratory species overwinter (Kawamura et al. 2019). Therefore, to understand the role of plantations as habitats in each season, studies are required on cypress family plantations in western Japan, especially in the wintering season.

3.5.4 Implications for conservation and forest management

Pine family plantations such as larch have important roles as biodiversity resources in Japan. This means that it is possible to manage these plantations as alternative habitats to natural forests. It provides an important implication for conservation in an era when plantations are expanding worldwide; timber production and biodiversity conservation can be achieved simultaneously depending on the planted tree species (‘matrix management’; Lindenmayer & Franklin 2002). By contrast, cypress family plantations, which account for 68% of plantations in Japan (Appendix S3.4.2), had generally low functions to conserve biodiversity. Whereas, results among comparisons varied, and many of them exhibited positive effect sizes: abundance or species richness was higher in plantations than in natural forests (for abundance: 101 of 249 comparisons; for species richness: 45 of 146 comparisons). It suggests that we have room for

improving the function of cypress family plantations. Indeed, thinning cypress family plantations can promote the recruitment of broad-leaved trees (Utsugi et al. 2006), and the amount of broad-leaved trees increases when stand age of cypress family plantations exceeds 100 years (Igarashi & Kiyono 2008; Yamaura et al. 2019). It has been suggested that retaining mixed broad-leaved trees when thinning or harvesting is important to enhance plantation biodiversity, and management for transforming some conifer plantations to mixed forests has been proposed and addressed for many parts of Japan (Forestry Agency 2018; Yamaura et al. 2019). Especially within cypress family plantations, it would be important to retain and raise broad-leaved trees, even if they are small trees.

3.6 Appendices

Appendix S3.1. Details of literature search and study selection process

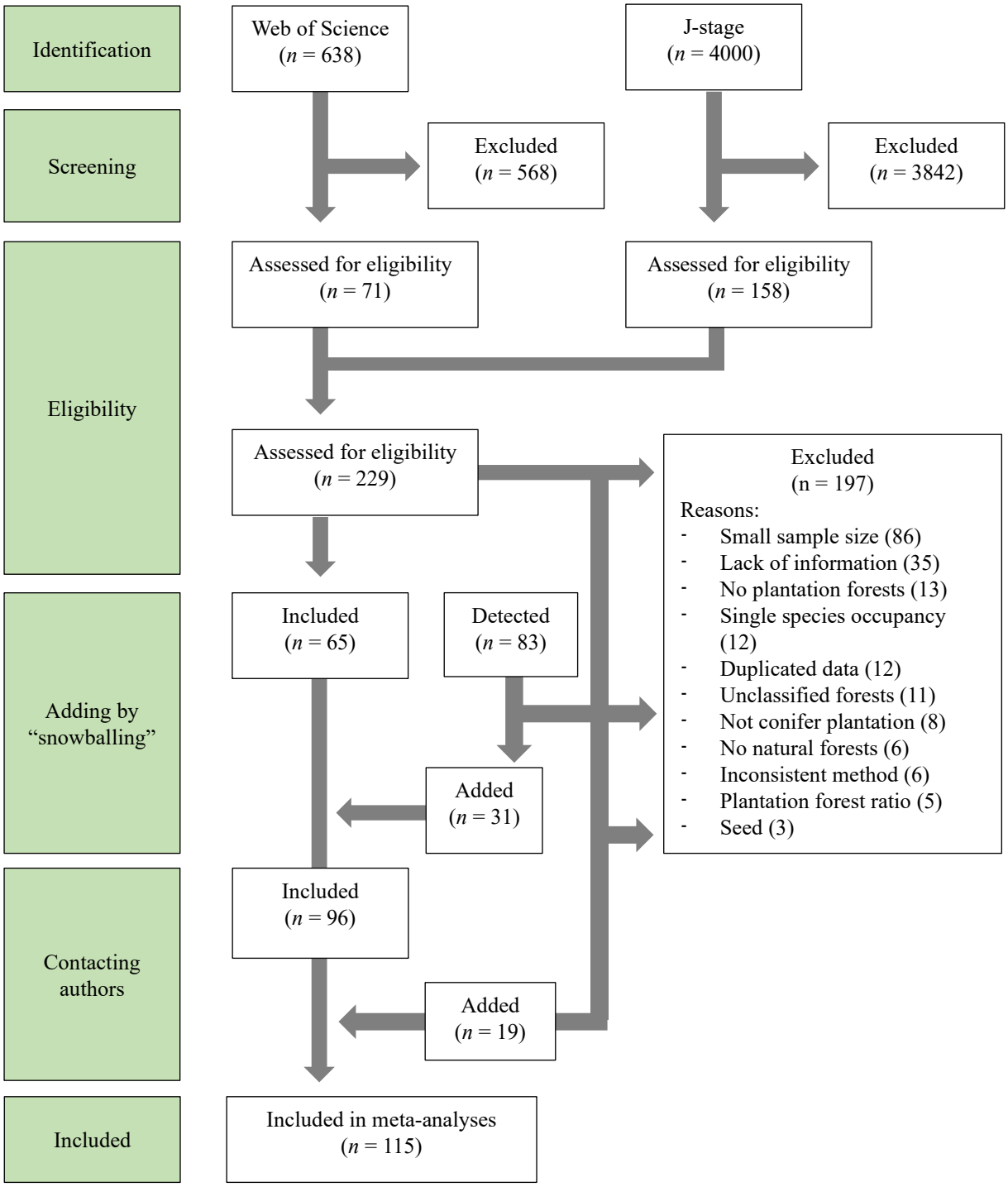


Fig. S3.1. Flow diagram of literature search and study selection process. *n* indicates the number of articles.

Appendix S3.2. Effect size variation with factors other than the planted tree species

Appendix S3.2.1. Effect size variation with stand age

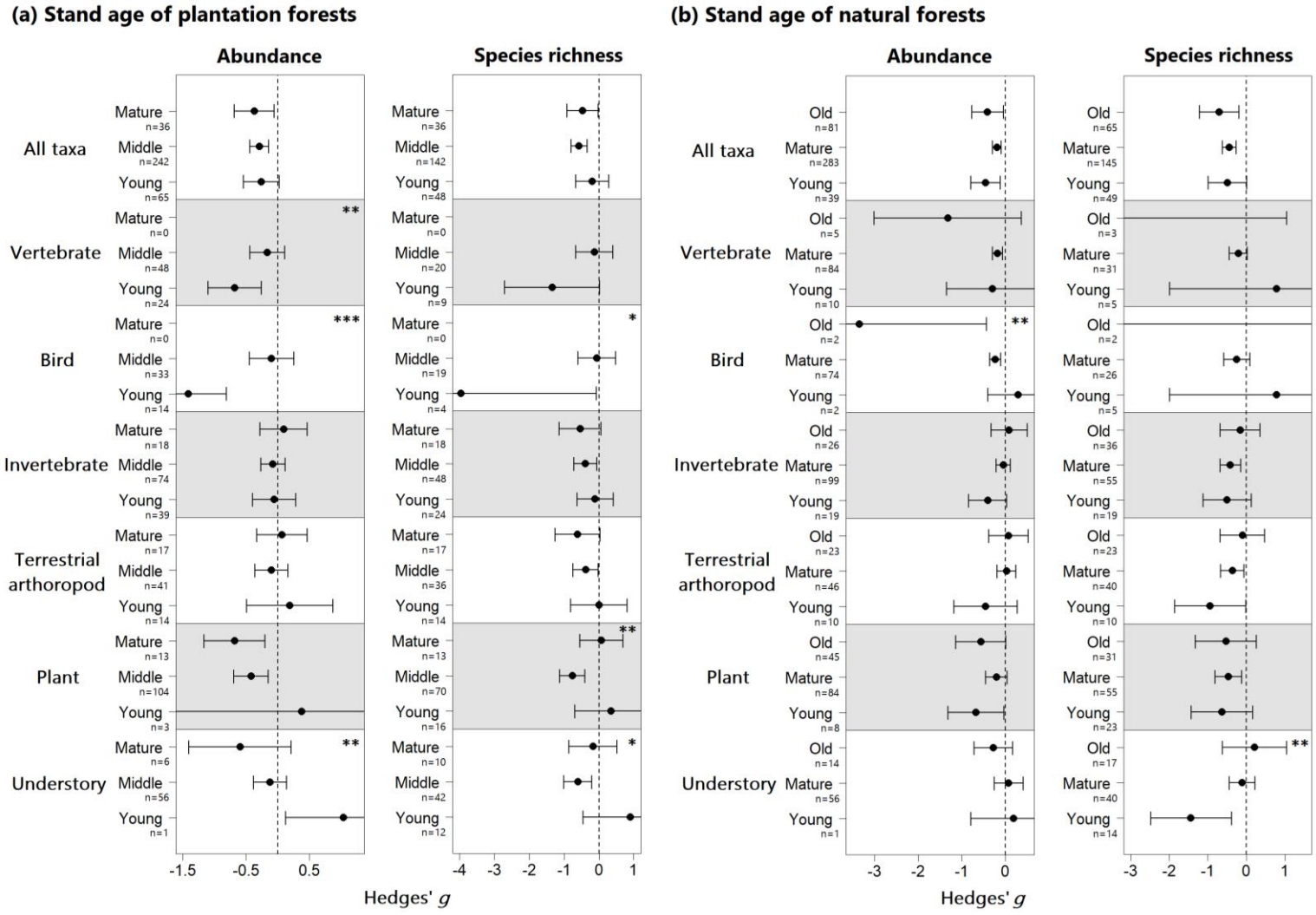


Fig. S3.2. Effects of (a) stand age of plantations [mature (50 years<), middle (20-50 years), young (<20 years)] and (b) stand age of natural forests [old (100 years<), mature (40-100 years), young (<40 years)] on the averaged Hedges' *g* for abundance and species richness of each taxonomic group. Filled dots and solid bars indicate the estimated means and its 95% confidence intervals. Cochran's Q test was conducted for each analysis to examine the difference in estimates among stand age groups, and the significance was indicated by asterisk on the right side of each block (***: $p<0.01$, **: $p<0.05$, *: $p<0.1$). *n* left outside the frame represents the number of comparisons. In the analyses for stand age of natural forests, the averaged Hedges' *g* was extremely low for species richness of vertebrates (mean: −4.37, 95%*CI*: −9.78 to 1.04) and birds (mean: −14.62, 95%*CI*: −14.62 to 2.17), and thus, these value are not shown.

Results & Discussion

The difference in the averaged Hedges' *g* among stand age groups of plantations was significant for plant species richness and abundance of vertebrates, birds, and undersoty (a). The difference in the averaged Hedges' *g* among stand age groups of natural forests was significant for bird abundance and understory species richness (b). For bird abundance, the effect size was higher in mature plantations than in young ones, and lower when compared to older natural forests. Moreover, for bird speices richness, and abundance and species richness of vertebrates, the analyses showed similar patterns.

By contrast, for plant species richness and understory abundance, the effect size was highest in young plantations, and the patterns for plant abundance and understory species richness were similar to these (a). The effect size for understory species richness was lower when compared to younger natural forests (b). Combining the results of the analyses for stand age of both planted and natural forests, the stand age had positive effects on birds and negative effects on understory plants. These results were consistent with previous studies (Spake et al. 2019).

Spake R, Yanou S, Yamaura Y, Kawamura K, Kitayama K, Doncaster CP (2019) Meta-analysis of management effects on biodiversity in plantation and secondary forests of Japan. Conserv Sci Pract 1:e14.

Appendix S3.2.2. Effect size variation with natural forest types

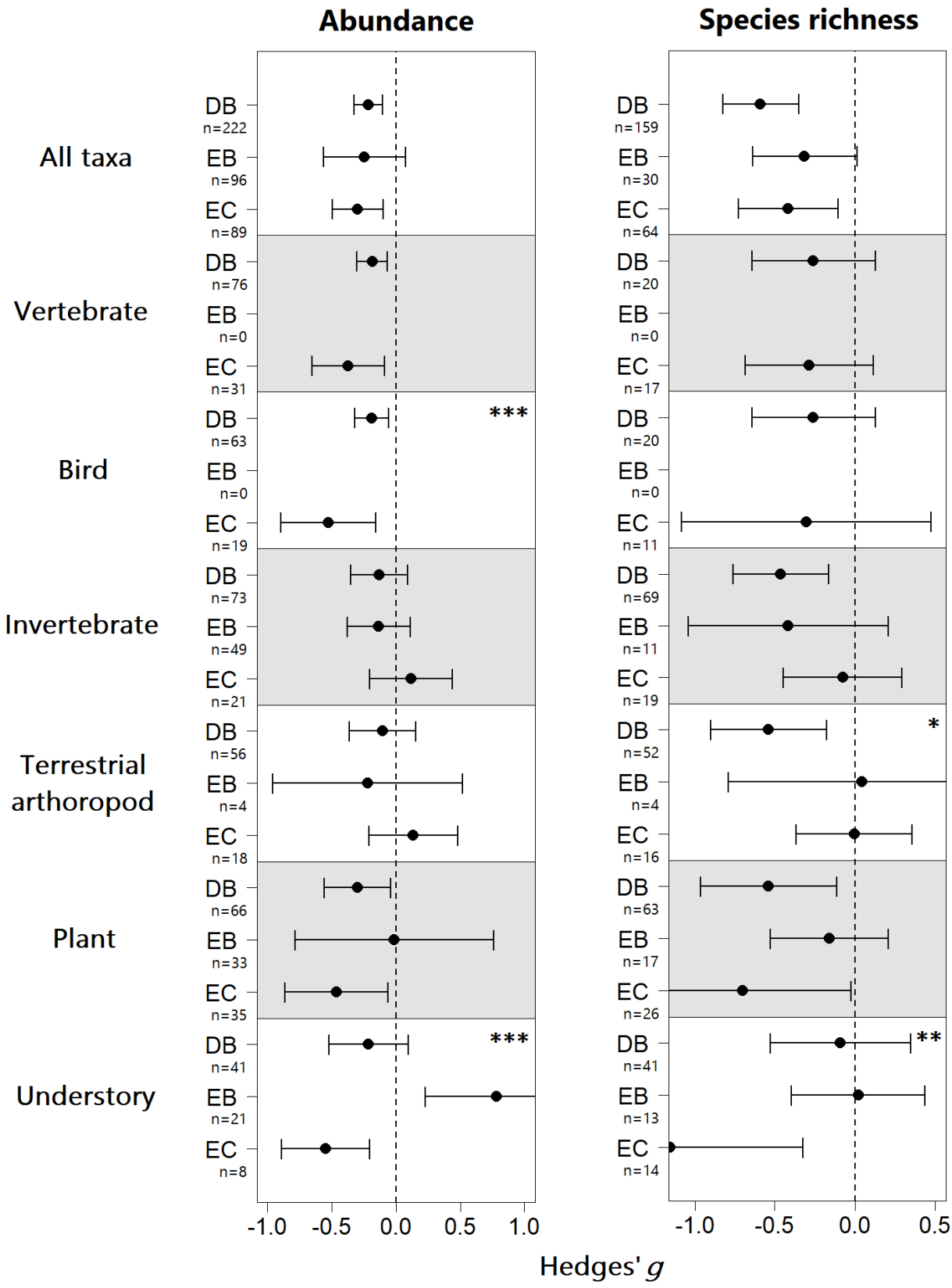


Fig. S3.3. Effects of natural forest types (DB: deciduous broad-leaved forests, EB: forests including evergreen broad-leaved trees, EC: forests including evergreen conifer trees) on the

averaged Hedges' *g* for abundance and species richness of each taxonomic group. Many of EB and EC were mixed forests with deciduous broad-leaved trees. See details in Fig. S3.2.

Results & Discussion

For understory species richness, abundance of understory, and that of birds, the effect size was lower when compared to EC than DB. It indicated that many species of these groups preferred forests including evergreen conifer trees as habitats. Natural forests including evergreen conifer trees distribute in cool regions and highlands (Kira 1991), and most of these have not been used intensively (Totman 1989; Yamaura et al. 2011; Yamaura et al. 2020). In fact, Yamaura et al. (2008) pointed out that hemlock and fir forests were important habitats for bird communities in montane zone of Nagano Prefecture.

By contrast, for species richness of terrestrial arthoropods, the effect size tended to be lower when compard with DB than EC. It is likely because many insect species depend on deciduous broad-leaved trees (Makino et al. 2007). As with the cases of stand age (Appendix 3.2.1), the effects of natural forest types may differ depending on focused taxa.

Kira T (1991) Forest ecosystems of east and southeast Asia in a global perspective. Ecol Res 6:185-200.

Totman CD (1989) The green archipelago: forestry in pre-industrial Japan. University of California Press, California.

Yamaura Y, Amano T, Kusumoto Y, Nagata H, Okabe K (2011) Climate and topography drives macroscale biodiversity through land-use change in a human-dominated world. Oikos 120:427-451.

Yamaura Y, Lindenmayer D, Yamada Y et al (2020) A spatially explicit empirical model of structural development processes in natural forests based on climate and topography. Conserv Biol 34:194-206.

Yamaura Y, Katoh K, Takahashi T (2008) Effects of stand, landscape, and spatial variables on bird communities in larch plantations and deciduous forests in central Japan. Can J For Res 38:1223-1243.

Makino S, Goto H, Hasegawa M, Okabe K, Tanaka H, Inoue T, Okochi I. (2007) Degradation of longicorn beetle (Coleoptera, Cerambycidae, Disteniidae) fauna caused by conversion from broad-leaved to man-made conifer stands of Cryptomeria japonica (Taxodiaceae) in central Japan. In: Nakashizuka T. (ed.) Sustainability and Diversity of Forest Ecosystems. Springer, Tokyo, pp. 372-381.

Appendix S3.3. Further methodological details for meta-analysis

Appendix S3.3.1. Weighting methods

Table S3.1. Comparisons of results derived from different weighting methods based on inverse variance and sample size.

Metric	Taxa_Planted tree family	*n*	*k*	Weighting method					
				Inverse variance			Sample size		
				95CI.l	Mean	95CI.u	95CI.l	Mean	95CI.u
Abundance	All taxa_Cypress	249	67	-0.52	-0.38	-0.24	-0.60	-0.40	-0.21
	All taxa_Pine	168	42	-0.23	-0.09	0.05	-0.32	-0.13	0.06
	Vertebrate_Cypress	29	10	-0.74	-0.49	-0.23	-0.81	-0.53	-0.26
	Vertebrate_Pine	81	17	-0.27	-0.14	-0.02	-0.46	-0.23	0.00
	Invertebrate_Cypress	101	22	-0.39	-0.22	-0.05	-0.48	-0.15	0.17
	Invertebrate_Pine	44	12	-0.10	0.17	0.44	-0.11	0.19	0.49
	Plant_Cypress	96	32	-0.66	-0.38	-0.10	-0.80	-0.47	-0.13
	Plant_Pine	43	13	-0.68	-0.23	0.22	-0.81	-0.26	0.29
Species richness	All taxa_Cypress	146	45	-0.90	-0.68	-0.46	-1.34	-1.00	-0.66
	All taxa_Pine	114	32	-0.56	-0.28	0.00	-0.71	-0.31	0.09
	Vertebrate_Cypress	5	3	-1.01	-0.55	-0.08	-1.07	-0.57	-0.07
	Vertebrate_Pine	34	10	-0.65	-0.26	0.14	-1.27	-0.47	0.33
	Invertebrate_Cypress	60	17	-0.86	-0.56	-0.26	-1.09	-0.74	-0.38
	Invertebrate_Pine	41	11	-0.49	-0.15	0.19	-0.13	-0.54	0.28
	Plant_Cypress	70	23	-0.85	-0.53	-0.21	-1.10	-0.68	-0.27
	Plant_Pine	39	12	-1.10	-0.42	0.25	-1.20	-0.35	0.50

Appendix S3.3.2. Pseudo-replication

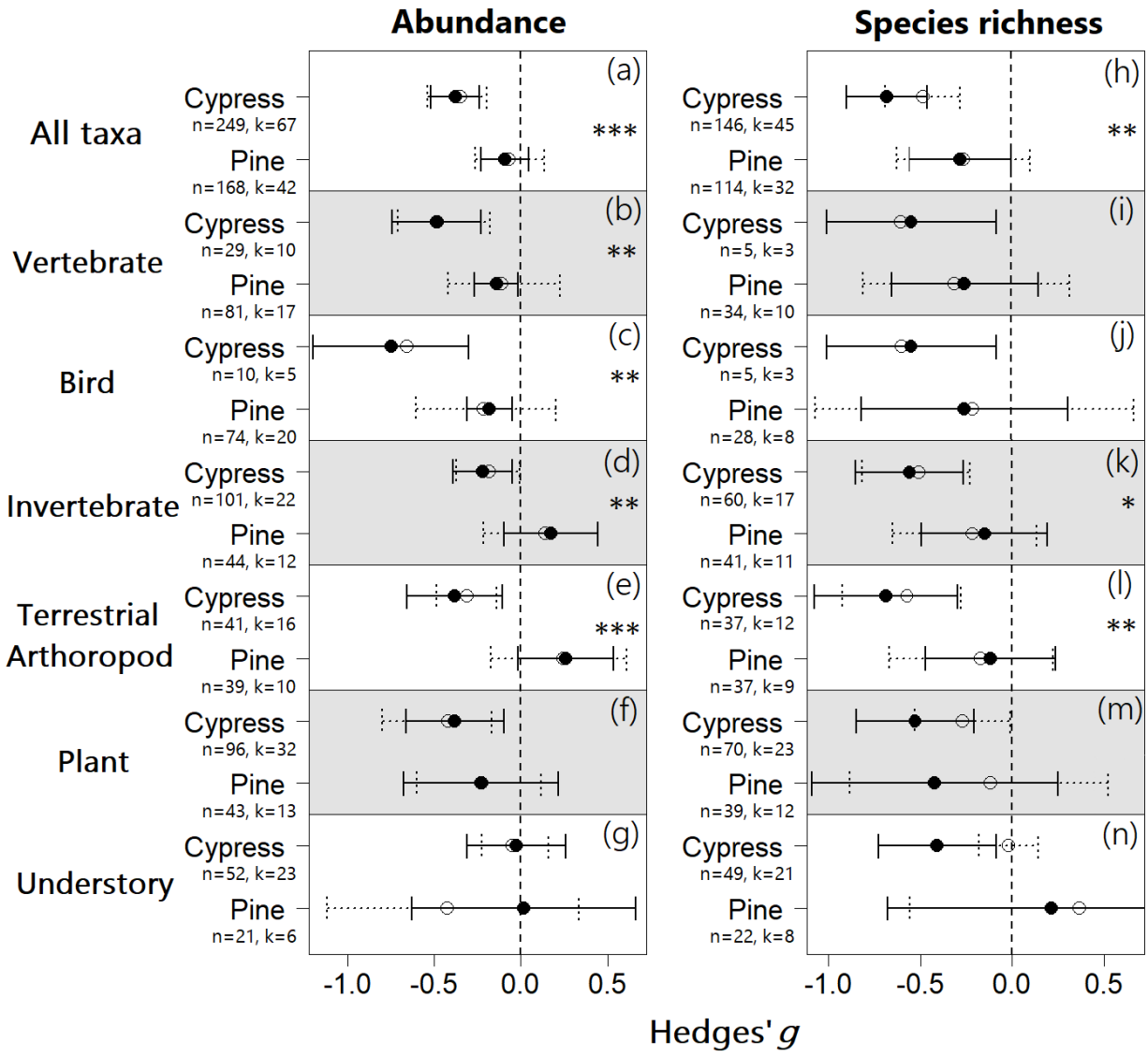


Fig. S3.4. Effects of pseudo-replication on the analyses of planted tree family for abundance (a-g) and species richness (h-n) of each taxonomic group. Filled dots and solid bars indicate the estimated means and its 95% confidence intervals, respectively. Open dots and dotted bars indicate the estimated means and its 95% CIs derived from bootstrap resamplings by a percentile method (range within which the estimated mean values of 9,500 out of 10000 trials), respectively. Cochran's Q test was conducted for each original analysis to examine the difference in estimates between planted tree families, and the significance was indicated by asterisk on the right side of each block (***: p<0.01, **: p<0.05, *: p<0.1). n and k left outside the frame represent the number of comparisons and that of independent comparisons, respectively.

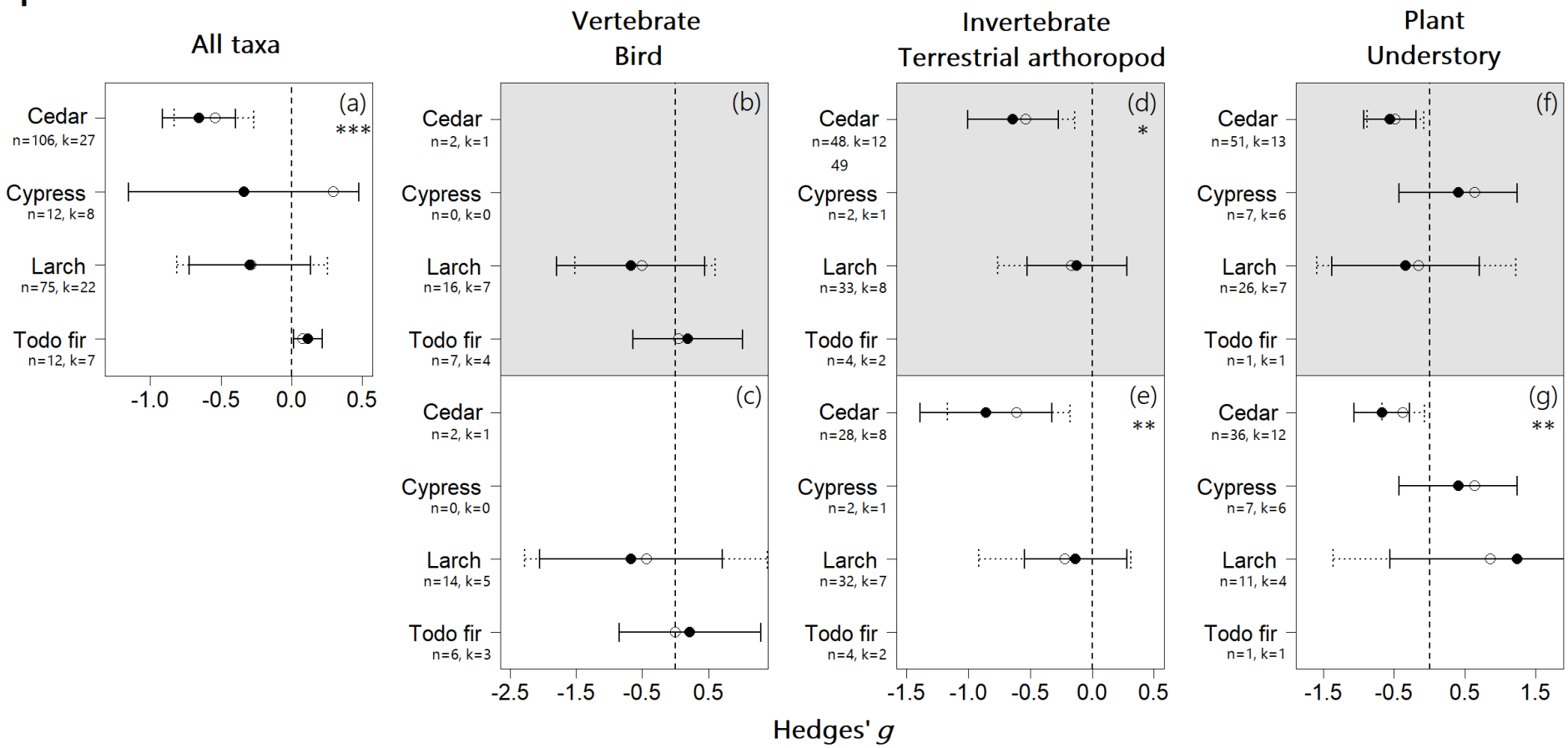


Fig. S3.5. Effects of planted tree species (Japanese cedar, Hinoki cypress, Japanese larch, and Todo fir) on the averaged Hedges' *g* for species richness of each taxonomic group [all taxa (a), vertebrates (b), birds (c), invertebrates (d), terrestrial arthoropods (e), plants (f), and understory (g)], and effects of pseudo-replication on these estimates. See details in Fig. S3.4. When there were few combinations of comparisons in bootstrap resampling, we did not calculate the 95%CI.

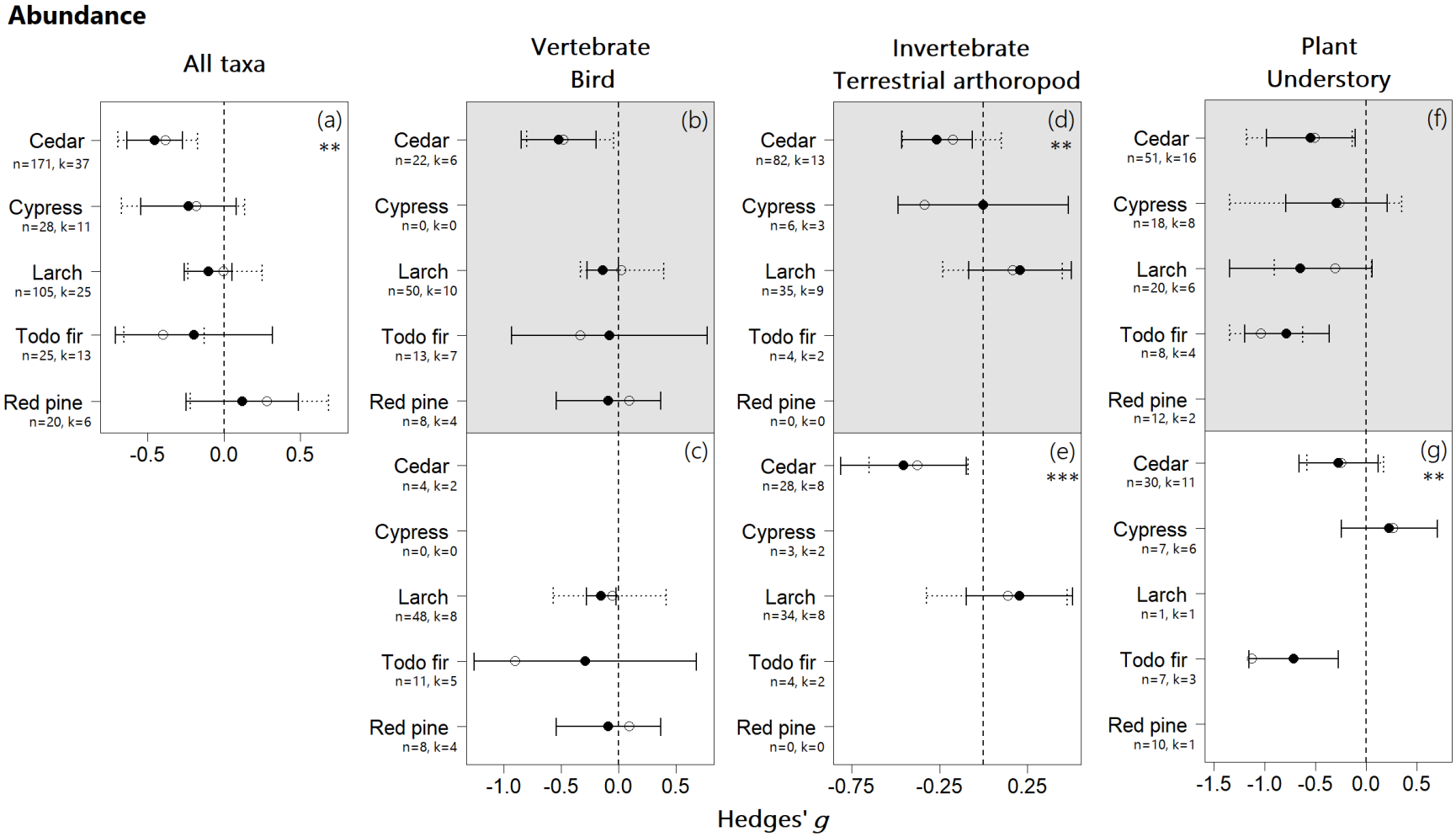


Fig. S3.6. Effects of pseudo-replication on the analyses of planted tree species for abundance of each taxonomic group [all taxa (a), vertebrates (b), birds (c), invertebrates (d), terrestrial arthoropods (e), plants (f), and understory (g)]. See details in Fig. S3.4. When there were few combinations of comparisons in bootstrap resampling, we did not calculate the 95%CI.

Appendix S3.3.3. Bias derived from differences in plot size

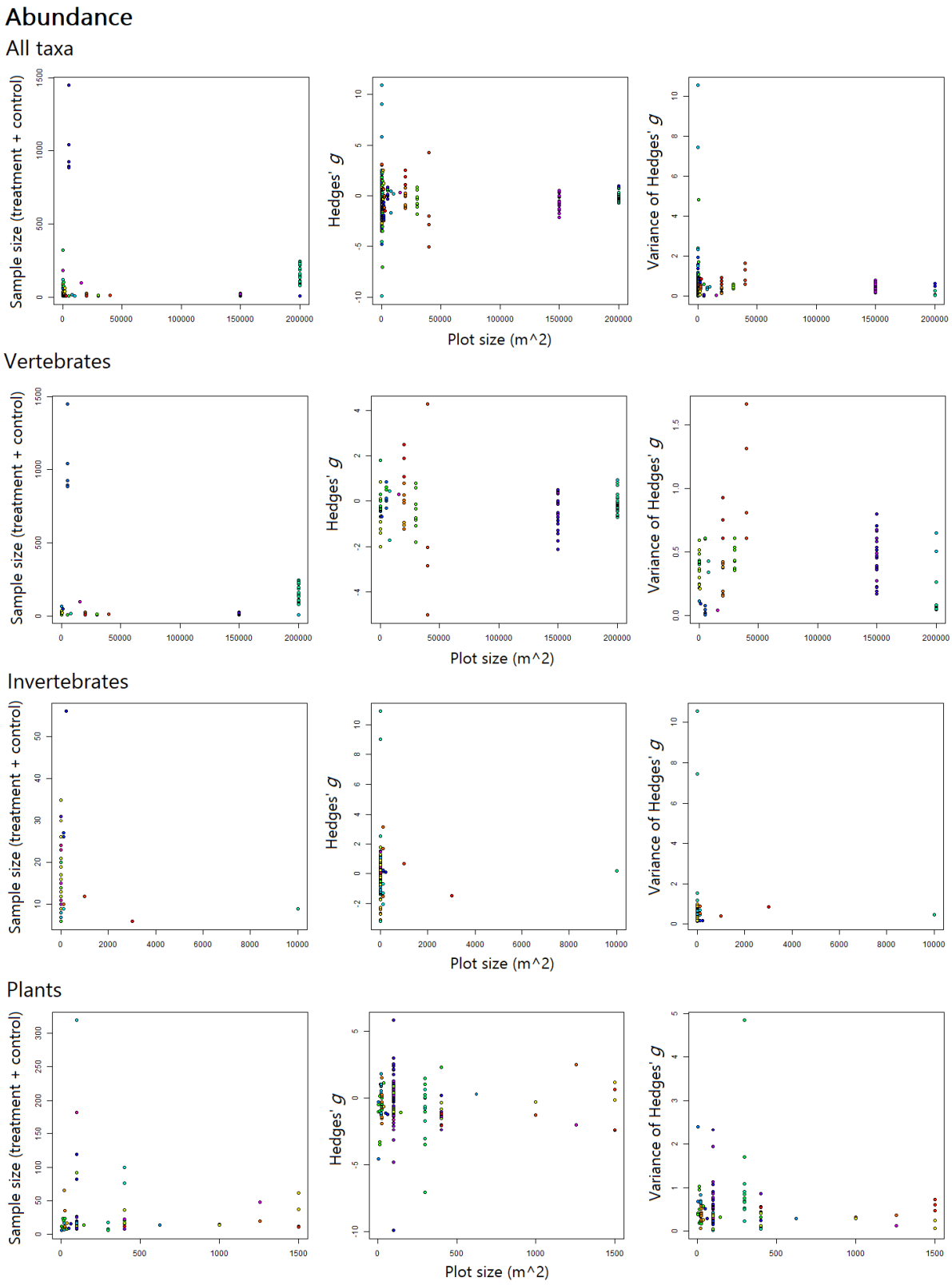


Fig. S3.7. Covariation of plot size with sample size, Hedges' *g* and its vaiance. Dots indicate values of each study, and its colors are consistent in three adjacent figures.

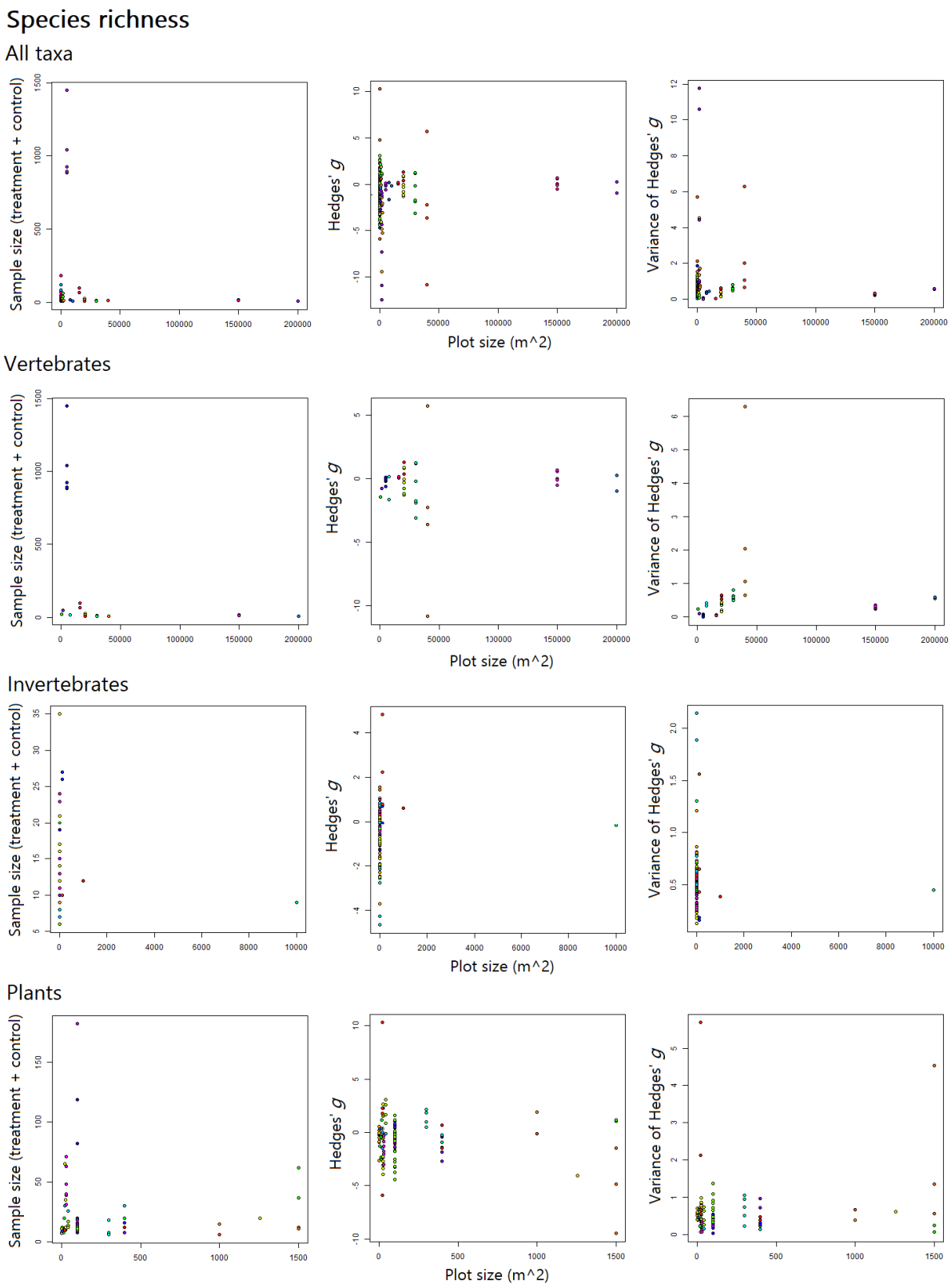


Fig. S3.7., continued

Appendix S3.4. Details of results

Appendix S3.4.1. Spatial distribution of articles included in the meta-analysis

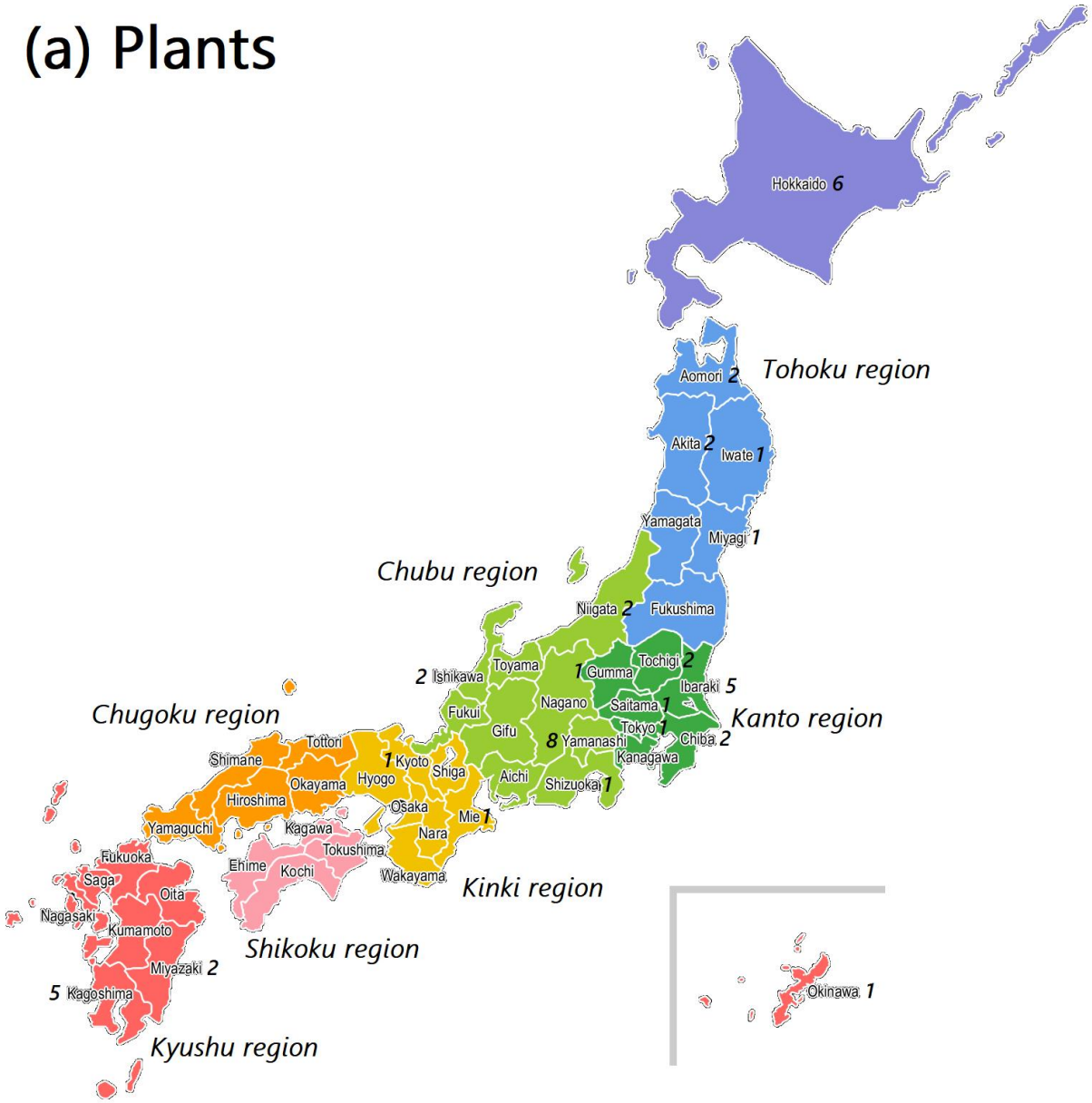


Fig. S3.8. Distribution of articles comparing biodiversity between plantations and natural forests for (a) plants, (b) invertebrates, and (c) vertebrates. The values adjacent each prefecture name indicate the number of the articles.

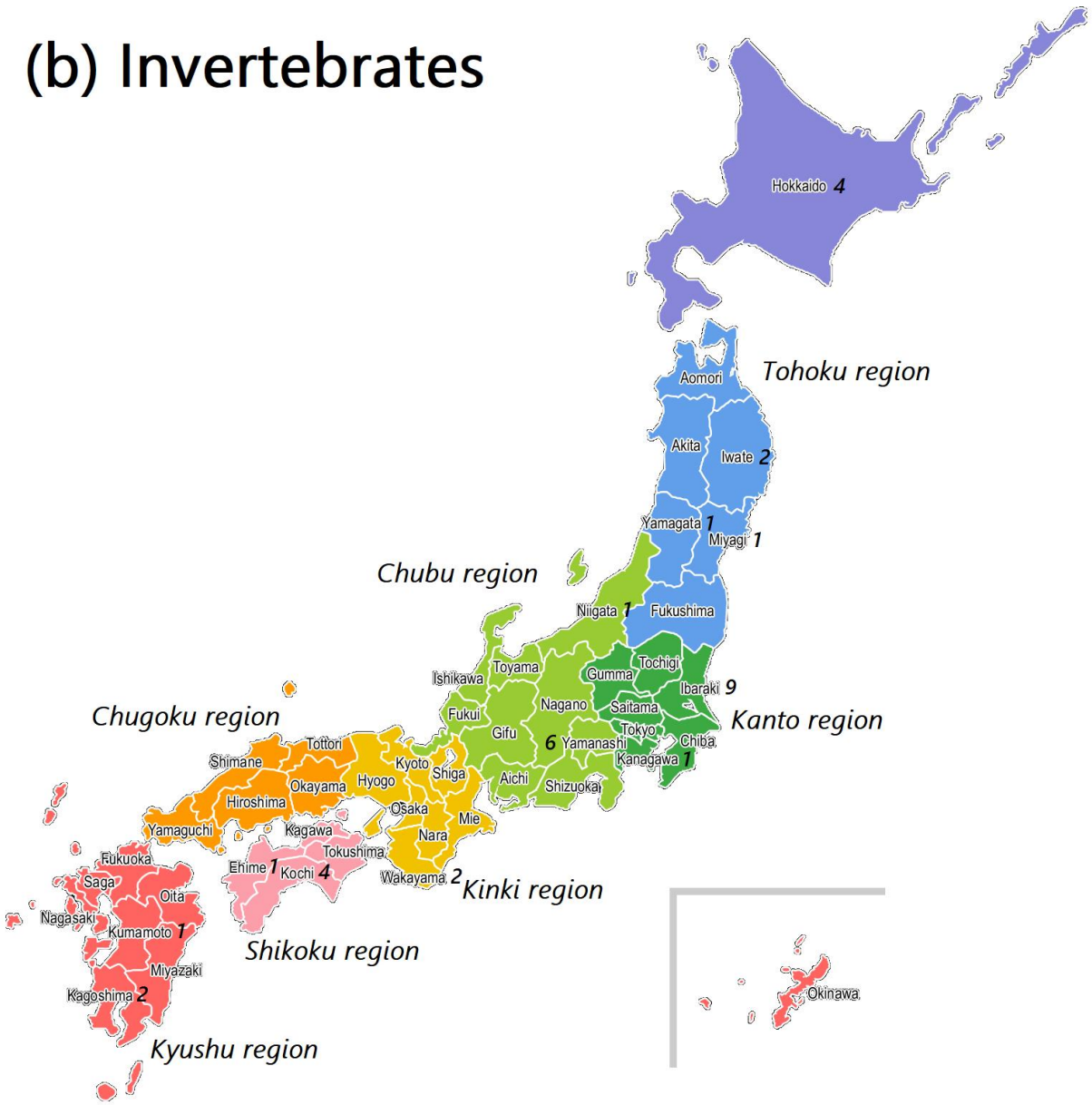


Fig. S3.8., continued

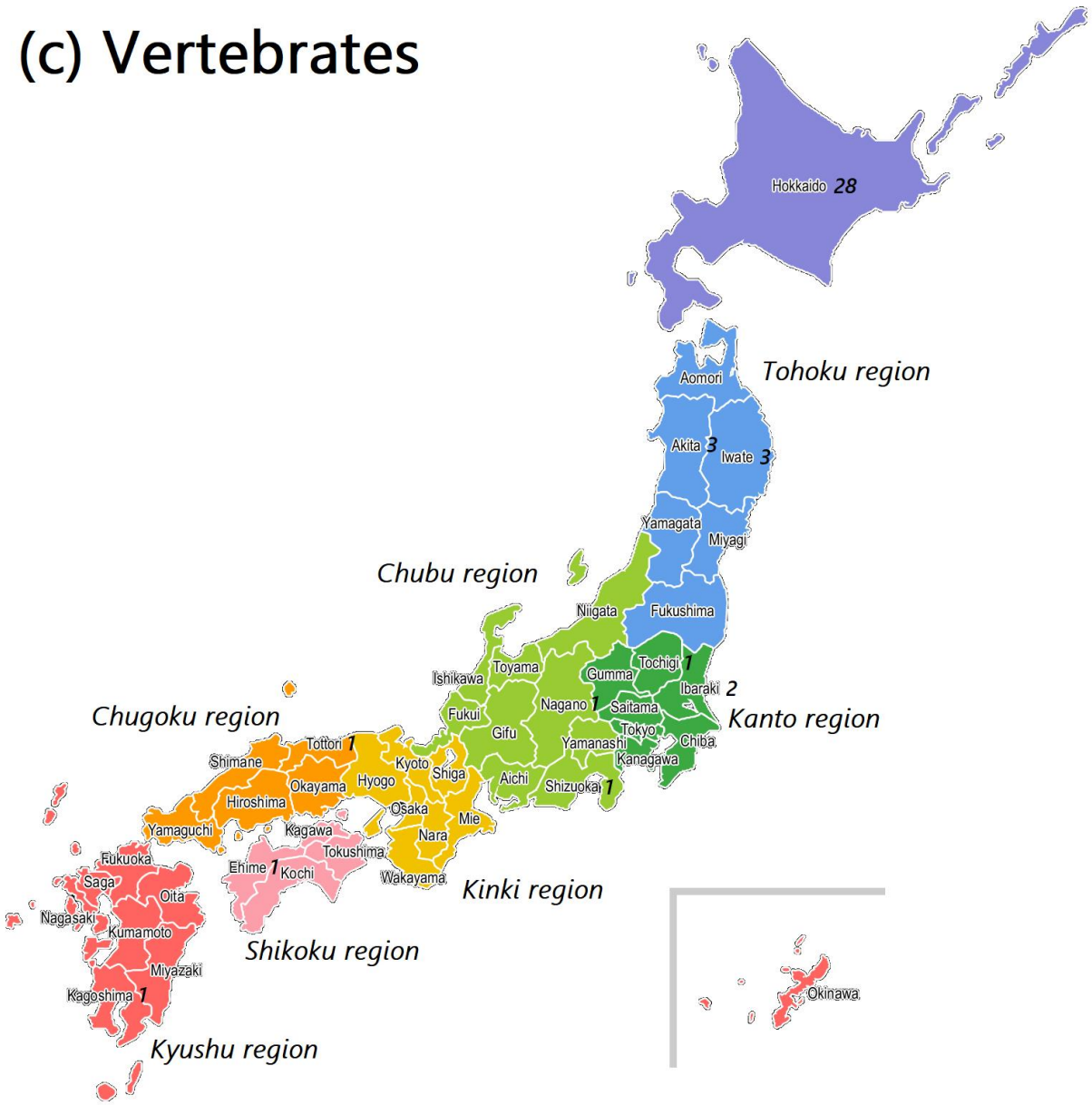


Fig. S3.8., continued

Appendix S3.4.2. Details of forest condition and the number of articles in each region

Table S3.2. Details in forest conditions and studies on biodiversity in plantations in each region and prefecture. Abbreviations; VERT: vertebrate, INVERT: invertebrate, CE: Japanese cedar, CY: Hinoki cypress, LA: Japanese larch, TO: Todo fir, PI: *Pinus*. Proportion of plantations in each region was calculated by plantation area/forest area. Proportion of each planted tree species in each region was calculated by each species plantation area/overall plantation area.

Region Prefecture	Number of articles				Number of articles					Forest (ha)	Plantation (ha)	Prop. of plantations (%)	Prop. of each planted tree species (%)				
	VERT	INVERT	Plant	Others	CE	CY	LA	TO	PI				CE	CY	LA	TO	PI
Hokkaido	**28**	**4**	**6**	**0**	**0**	**0**	**28**	**13**	**1**	**5,538,447**	**1,475,342**	**27**	**2**	**0**	**27**	**53**	**0**
Tohoku	**6**	**4**	**6**	**0**	**9**	**1**	**3**	**0**	**2**	**4,703,690**	**1,892,521**	**40**	**66**	**2**	**11**	**0**	**18**
Aomori			2		1					632,805	269,438	43	74	0	8	0	16
Iwate	3	2	1		2		3		2	1,171,446	488,680	42	41	1	25	0	32
Akita	3		2		4					839,247	409,506	49	90	0	3	0	4
Miyagi		1	1		1	1				417,086	198,235	48	67	4	5	0	21
Yamagata		1			1					669,272	185,636	28	87	0	6	0	6
Fukushima										973,834	341,026	35	54	8	8	0	25
Kanto	**3**	**10**	**12**	**1**	**10**	**2**	**2**	**0**	**1**	**1,409,605**	**636,303**	**45**	**54**	**25**	**9**	**0**	**7**
Ibaraki	2	9	5	1	8	1	1			186,781	111,106	59	56	28	0	0	14
Tochigi	1		2				1			349,006	155,946	45	50	34	7	0	4
Gunma			1		1					423,141	176,947	42	44	13	24	0	10
Chiba			2		1	1				157,276	61,416	39	77	14	0	0	5
Saitama			1						1	119,779	59,235	49	61	32	4	0	2
Tokyo			1							78,927	35,158	45	64	26	3	0	1
Kanagawa		1								94,695	36,495	39	53	40	0	0	3
Chubu	**2**	**7**	**13**	**0**	**5**	**3**	**15**	**0**	**2**	**5,010,865**	**1,846,136**	**37**	**40**	**30**	**17**	**0**	**8**
Niigata		1	2		3				1	855,159	161,993	19	89	0	1	0	6
Toyama										284,994	54,513	19	93	1	3	0	2
Ishikawa			2		2					286,046	101,645	36	71	5	0	0	9
Fukui										312,025	124,399	40	85	6	0	0	7
Yamanashi		6	8				14			347,781	153,541	44	17	29	28	0	18
Nagano	1					1	1			1,068,636	444,655	42	14	19	54	0	11
Gifu										861,978	384,574	45	32	54	6	0	4

Shizuoka	1		1			2			1	497,123	280,435	56	40	51	2	0	3
Aichi										497,123	140,381	28	37	48	0	0	14
Kinki	**0**	**2**	**2**	**0**	**3**	**1**	**0**	**0**	**0**	**2,179,675**	**1,105,303**	**51**	**48**	**45**	**0**	**0**	**5**
Mie			1							372,230	229,969	62	44	48	0	0	8
Shiga										202,890	84,910	42	55	41	0	0	3
Kyoto			1		1	1				342,300	131,591	38	48	43	0	0	7
Osaka										57,220	28,140	49	27	45	0	0	19
Hyogo										560,006	238,170	43	49	41	0	0	8
Nara										283,701	172,203	61	56	41	0	0	1
Wakayama		2			2					361,328	220,320	61	42	54	0	0	2
Chugoku	**1**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**2**	**2,315,040**	**946,955**	**41**	**34**	**47**	**0**	**0**	**16**
Tottori	1				1				1	258,988	140,234	54	51	27	0	0	18
Shimane										524,495	205,350	39	41	34	0	0	23
Okayama										483,378	205,431	42	22	67	0	0	8
Hiroshima									1	611,222	200,926	33	27	56	0	0	13
Yamaguchi										436,957	195,014	45	35	47	0	0	16
Shikoku	**1**	**5**	**0**	**0**	**3**	**2**	**0**	**0**	**0**	**1,398,425**	**845,387**	**60**	**48**	**46**	**0**	**0**	**3**
Tokushima										314,829	189,685	60	73	20	0	0	4
Kagawa										87,514	23,181	26	8	62	0	0	21
Ehime	1	1								401,050	244,597	61	46	50	0	0	2
Kochi		4			3	2				595,032	387,924	65	40	56	0	0	2
Kyushu	**1**	**3**	**7**	**1**	**7**	**1**	**0**	**0**	**1**	**2,664,690**	**1,443,807**	**54**	**57**	**34**	**0**	**0**	**3**
Fukuoka						1				222,394	140,234	63	51	43	0	0	2
Saga										110,403	73,828	67	56	40	0	0	1
Nagasaki										242,595	104,591	43	29	67	0	0	1
Kumamoto		1								462,965	280,267	61	55	39	0	0	2
Oita										452,791	233,485	52	63	29	0	0	2
Miyazaki			2	1	2					585,559	332,801	57	68	19	0	0	4
Kagoshima	1	2	5		5				1	587,983	278,601	47	55	34	0	0	3
Okinawa	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**1**	**106,730**	**12,089**	**11**	**2**	**0**	**0**	**0**	**57**
Japan	**42**	**35**	**47**	**2**	**38**	**10**	**48**	**13**	**10**	**25,327,167**	**10,203,843**	**40**	**43**	**25**	**10**	**8**	**8**

Appendix S3.4.3. Details of results of meta-analysis

Table S3.3. Estimates of each meta-analysis (subgroup analysis).

Analysis	Metric	Taxa	Subgroup	*n*	*k*	95CI.l	Mean	95CI.u	Heterogeneity	Between-subgroup difference
Planted tree family	Abundance	All taxa	Cypress	249	67	**-0.52**	**-0.38**	**-0.24**	*Q248*=1077.32, ***p*<0.0001**	*Q1*=8.09, ***p*=0.004**
			Pine	168	42	-0.23	-0.09	0.05	*Q167*=543.43, ***p*<0.0001**	
		Vertebrate	Cypress	29	10	**-0.74**	**-0.49**	**-0.23**	*Q29*=41.56, ***p*=0.048**	*Q1*=5.69, ***p*=0.02**
			Pine	81	17	**-0.27**	**-0.14**	**-0.02**	*Q80*=249.59, ***p*<0.0001**	
		Bird	Cypress	10	5	**-1.20**	**-0.75**	**-0.30**	*Q9*=15.20, *p*=0.09	*Q1*=5.70, ***p*=0.02**
			Pine	74	20	**-0.31**	**-0.18**	**-0.05**	*Q73*=207.51, ***p*<0.0001**	
		Invertebrate	Cypress	101	22	**-0.39**	**-0.22**	**-0.05**	*Q100*=174.22, ***p*<0.0001**	*Q1*=5.85, ***p*=0.02**
			Pine	44	12	-0.10	0.17	0.44	*Q43*=103.12, ***p*<0.0001**	
		Terrestrial arthropod	Cypress	41	16	**-0.66**	**-0.38**	**-0.11**	*Q40*=72.64, ***p*=0.001**	*Q1*=10.30, ***p*=0.001**
			Pine	39	10	-0.02	0.26	0.54	*Q38*=89.85, ***p*<0.0001**	
		Plant	Cypress	96	32	**-0.66**	**-0.38**	**-0.10**	*Q95*=811.41, ***p*<0.0001**	*Q1*=0.31, *p*=0.58
			Pine	43	13	-0.68	-0.23	0.22	*Q42*=185.47, ***p*<0.0001**	
		Understorey	Cypress	52	23	-0.31	-0.03	0.26	*Q51*=447.24, ***p*<0.0001**	*Q1*=0.01, *p*=0.91
			Pine	21	6	-0.63	0.02	0.66	*Q20*=76.94, ***p*<0.0001**	
	Species richness	All taxa	Cypress	146	45	**-0.90**	**-0.68**	**-0.46**	*Q145*=559.53, ***p*<0.0001**	*Q1*=4.93, ***p*=0.03**
			Pine	114	32	-0.56	-0.28	0.00	*Q113*=573.28, ***p*<0.0001**	
		Vertebrate	Cypress	5	3	**-1.01**	**-0.55**	**-0.08**	*Q4*=6.02, *p*=0.20	*Q1*=0.87, *p*=0.35
			Pine	34	10	-0.65	-0.26	0.14	*Q33*=134.17, ***p*<0.0001**	
		Bird	Cypress	5	3	**-1.01**	**-0.55**	**-0.08**	*Q4*=6.02, *p*=0.20	*Q1*=0.60, *p*=0.44
			Pine	28	8	-0.82	-0.26	0.31	*Q27*=114.25, ***p*<0.0001**	
		Invertebrate	Cypress	60	17	**-0.86**	**-0.56**	**-0.26**	*Q59*=141.31, ***p*<0.0001**	*Q1*=3.14, *p*=0.08
			Pine	41	11	-0.49	-0.15	0.19	*Q40*=133.39, ***p*<0.0001**	
		Terrestrial arthropod	Cypress	37	12	**-1.08**	**-0.69**	**-0.30**	*Q36*=94.02, ***p*<0.0001**	*Q1*=4.50, ***p*=0.03**
			Pine	37	9	-0.47	-0.12	0.24	*Q36*=121.93, ***p*<0.0001**	
		Plant	Cypress	70	23	**-0.85**	**-0.53**	**-0.21**	*Q69*=333.68, ***p*<0.0001**	*Q1*=0.08, *p*=0.78
			Pine	39	12	-1.10	-0.42	0.25	*Q38*=281.15, ***p*<0.0001**	
		Understorey	Cypress	49	21	**-0.73**	**-0.41**	**-0.09**	*Q48*=204.91, ***p*<0.0001**	*Q1*=1.65, *p*=0.20
			Pine	22	8	-0.68	0.21	1.11	*Q21*=172.55, ***p*<0.0001**	

0.8<*g*
0.5<*g*<0.8
0.2<*g*<0.5
0<*g*<0.2
-0.2<*g*<0
-0.5<*g*<-0.2
-0.8<*g*<-0.5
g<-0.8

Planted tree species	Abundance	All taxa	Cedar	171	37	**-0.63**	**-0.45**	**-0.27**	*Q170*=703.78, ***p*<0.0001**	*Q4*=11.71, ***p*= 0.02**
			Cypress	28	11	-0.55	-0.23	0.08	*Q27*=54.19, ***p*=0.0014**	
			Larch	105	25	-0.26	-0.10	0.05	*Q104*=328.87, ***p*<0.0001**	
			Todo fir	25	13	-0.71	-0.20	0.32	*Q24*=88.57, ***p*<0.0001**	
			Red pine	20	6	-0.25	0.12	0.49	*Q19*=44.70, ***p*=0.0008**	
		Vertebrate	Cedar	22	6	**-0.85**	**-0.52**	**-0.20**	*Q21*=33.33, ***p*=0.04**	*Q3*=4.82, *p*= 0.19
			Cypress	0	0					
			Larch	50	10	-0.27	-0.14	0.00	*Q49*=150.69, ***p*<0.0001**	
			Todo fir	13	7	-0.94	-0.08	0.78	*Q12*=50.42, ***p*<0.0001**	
			Red pine	8	4	-0.55	-0.09	0.37	*Q7*=8.71, *p*=0.27	
		Bird	Cedar	4	2					*Q2*=0.15, *p*= 0.93
			Cypress	0	0					
			Larch	48	8	**-0.28**	**-0.15**	**-0.02**	*Q47*=137.12, ***p*<0.0001**	
			Todo fir	11	5	-1.26	-0.29	0.68	*Q10*=39.64, ***p*<0.0001**	
			Red pine	8	4	-0.55	-0.09	0.37	*Q7*=8.71, *p*=0.27	
		Invertebrate	Cedar	82	13	**-0.46**	**-0.26**	**-0.07**	*Q81*=141.59, ***p*<0.0001**	*Q2*=7.02, ***p*= 0.03**
			Cypress	6	3	-0.48	0.00	0.48	*Q5*=6.87, *p*=0.23	
			Larch	35	9	-0.08	0.21	0.50	*Q34*=80.85, ***p*<0.0001**	
			Todo fir	4	2					
			Red pine	0	0					
		Terrestrial arthropod	Cedar	28	8	**-0.81**	**-0.45**	**-0.10**	*Q27*=47.48, ***p*=0.009**	*Q1*=7.63, ***p*= 0.006**
			Cypress	3	2					
			Larch	34	8	-0.10	0.20	0.50	*Q33*=80.72, ***p*<0.0001**	
			Todo fir	4	2					
			Red pine	0	0					
		Plant	Cedar	51	16	**-0.98**	**-0.54**	**-0.10**	*Q50*=494.41, ***p*<0.0001**	*Q3*=2.23, *p*= 0.53
			Cypress	18	8	-0.79	-0.29	0.21	*Q17*=42.45, ***p*=0.0006**	
			Larch	20	6	-1.35	-0.65	0.06	*Q19*=83.11, ***p*<0.0001**	
			Todo fir	8	4	**-1.20**	**-0.78**	**-0.36**	*Q7*=10.42, *p*=0.17	
			Red pine	12	2					
		Understorey	Cedar	30	11	-0.66	-0.27	0.12	*Q29*=227.81, ***p*<0.0001**	*Q2*=8.10, ***p*= 0.02**
			Cypress	7	6	-0.25	0.23	0.70	*Q6*=6.63, *p*=0.36	
			Larch	1	1					
			Todo fir	7	3	**-1.15**	**-0.71**	**-0.27**	*Q6*=9.55, *p*=0.15	
			Red pine	10	1					

	Species richness	All taxa	Cedar	106	27	**-0.91**	**-0.65**	**-0.40**	*Q105*=412.36, ***p*<0.0001**	
			Cypress	12	8	-1.15	-0.34	0.48	*Q12*=46.14, ***p*<0.0001**	*Q3*=32.26,
			Larch	75	22	-0.72	-0.30	0.13	*Q74*=420.24, ***p*<0.0001**	***p*<0.001**
			Todo fir	12	7	0.01	0.12	0.22	*Q11*=19.52, *p*=0.052	
		Vertebrate	Cedar	2	1					
			Cypress	0	0					*Q1*=1.48,
			Larch	16	7	-1.79	-0.68	0.44	*Q15*=88.34, ***p*<0.0001**	*p*=0.23
			Todo fir	7	4	-0.64	0.19	1.02	*Q6*=16.60, ***p*=0.01**	
		Bird	Cedar	2	1					
			Cypress	0	0					*Q1*=0.99,
			Larch	14	5	-2.05	-0.67	0.71	*Q13*=79.03, ***p*<0.0001**	*p*=0.32
			Todo fir	6	3	-0.85	0.22	1.29	*Q5*=16.59, ***p*=0.0053**	
		Invertebrate	Cedar	49	12	**-1.01**	**-0.64**	**-0.27**	*Q48*=129.29, ***p*<0.0001**	
			Cypress	2	1					*Q1*=3.49,
			Larch	33	8	-0.52	-0.12	0.28	*Q32*=119.27, ***p*<0.0001**	*p*=0.06
			Todo fir	4	2					
		Terrestrial arthropod	Cedar	28	8	**-1.39**	**-0.86**	**-0.32**	*Q27*=82.48, ***p*<0.0001**	
			Cypress	2	1					*Q1*=4.41,
			Larch	32	7	-0.55	-0.13	0.28	*Q31*=118.95, ***p*<0.0001**	***p*=0.04**
			Todo fir	4	2					
		Plant	Cedar	51	13	**-0.93**	**-0.56**	**-0.20**	*Q50*=257.34, ***p*<0.0001**	
			Cypress	7	6	-0.43	0.40	1.24	*Q6*=15.16, ***p*=0.02**	*Q2*=4.33,
			Larch	26	7	-1.38	-0.34	0.70	*Q25*=211.87, ***p*<0.0001**	*p*=0.115
			Todo fir	1	1					
		Understorey	Cedar	36	12	**-1.07**	**-0.67**	**-0.28**	*Q35*=177.81, ***p*<0.0001**	
			Cypress	7	6	-0.43	0.40	1.24	*Q6*=15.16, ***p*=0.02**	*Q2*=8.62,
			Larch	11	4	-0.56	1.24	3.04	*Q10*=67.98, ***p*<0.0001**	***p*=0.01**
			Todo fir	1	1					
Season	Abundance	Vertebrate	Spring-summer	95	22	**-0.42**	**-0.28**	**-0.15**	*Q94*=260.81, ***p*<0.0001**	*Q1*=24.53,
			Autumn-winter	15	7	**0.03**	**0.11**	**0.19**	*Q14*=16.26, *p*=0.30	***p*<0.001**
		Bird	Spring-summer	79	16	**-0.41**	**-0.27**	**-0.13**	*Q78*=227.81, ***p*<0.0001**	*Q1*=6.60,
			Autumn-winter	5	3	-0.11	0.34	0.78	*Q4*=1.65, *p*=0.80	***p*=0.01**
	Species richness	Vertebrate	Spring-summer	28	11	-1.07	-0.51	0.05	*Q27*=117.71, ***p*<0.0001**	*Q1*=2.91,
			Autumn-winter	11	5	-0.14	-0.01	0.13	*Q10*=17.01, *p*=0.07	*p*=0.09
		Bird	Spring-summer	27	10	-1.06	-0.47	0.11	*Q26*=113.10, ***p*<0.0001**	*Q1*=4.40,
			Autumn-winter	6	4	-0.09	0.26	0.60	*Q5*=4.17, *p*=0.53	***p*=0.04**

Appendix S3.4.4. Details of results of the analysis for pseudo-replication

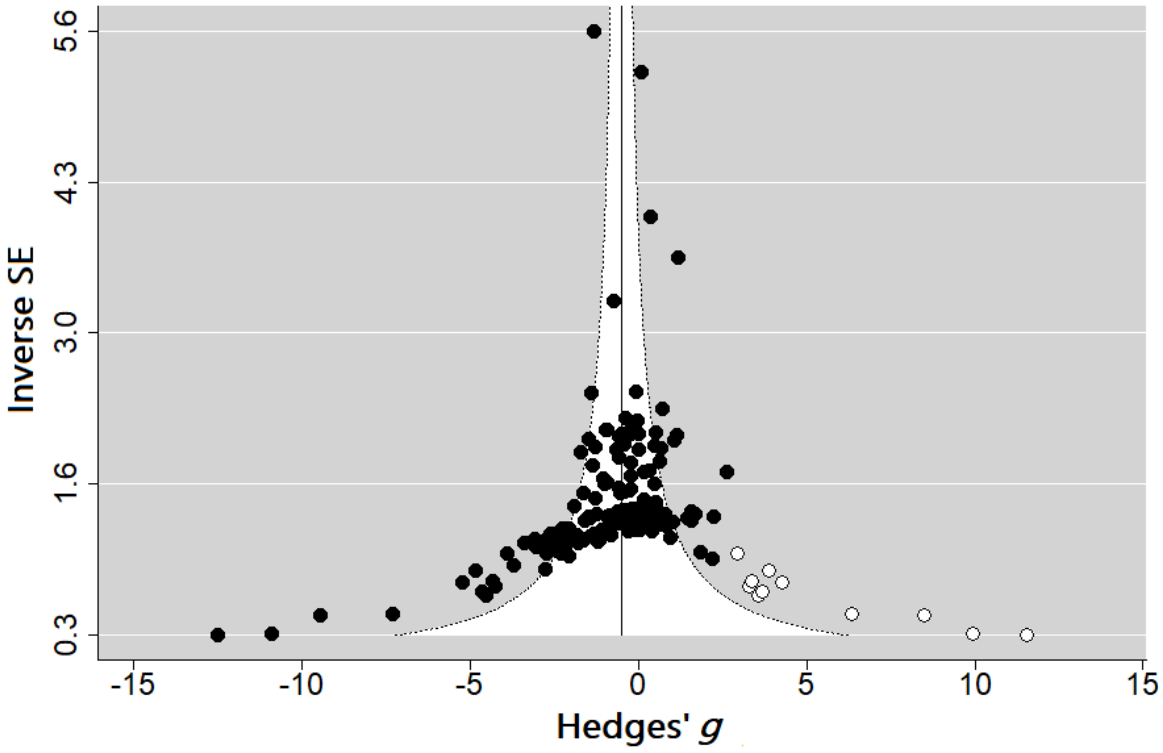


Fig. S3.9. Funnel plot correcting publication bias of studies on species richness of all taxa in cypress family plantations. The horizontal axis represents Hedges' *g*, and the vertical axis reprents the inverse standard error indicating sample size. Filled dots indicate observed comparisons, open dots indicate unpublished comparisons added by the trim-and-fill analysis.

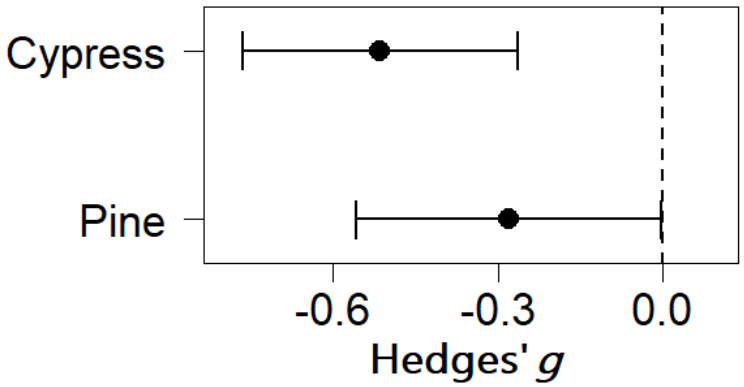


Fig. S3.10. Difference in averaged Hedges' *g* for species richness of all taxa between planted tree family after corrected publication bias for cypress family plantations by the trim-and-fill analysis. Filled dots and solid bars indicate the estimated means and its 95% confidence intervals, respectively. Cochran's Q test was conducted to examine the difference in estimates between planted tree families, however it is not significant.

Chapter 4

Conifer plantations as habitats for birds in breeding and wintering seasons: climate-dependent effects of stand age and broad-leaved tree proportion

4.1 Abstract

While plantations support less biodiversity compared to natural forests, existing studies have shown that mature plantations with abundant non-planted native trees can be alternative or comparable habitats to natural forests. Furthermore, young plantations can function as habitats for early-successional species that have decreased worldwide. However, the effects of stand age and the amount of non-planted trees on animal communities may differ among regions and seasons, reflecting changes in animal distribution, species composition and habitat selection. Here, I examined the effects of stand age and broad-leaved tree proportion in conifer plantations on bird species preferring broad-leaved natural forests (broad-leaved forest species) or early-successional forests across Hokkaido, northern Japan, in the breeding and wintering seasons. I examined the climate-dependent effects using interaction terms between climates and stand variables. Early-successional species occurred only in the breeding season, and the species richness and abundance were higher in younger plantations. Reflecting the differences in species compositions, its duration as a habitat for early-successional species was shorter in cooler regions. The effects of stand variables on broad-leaved forest species were consistent across Hokkaido in the breeding season, but differed among regions in the wintering season. Specifically, in the breeding season, the species richness and abundance increased with plantation age until 60-70 years. As the broad-leaved tree proportion within plantations increased, the species richness and abundance increased in stand classes with fewer broad-leaved trees, and remained almost unchanged in stand classes with more broad-leaved trees.

For the proportion, I found the threshold values of 25-50%. In the wintering season, as regional climatic conditions were more severe (lower temperature and deeper snow), the positive effects of stand age were weaker, and positive effects of the broad-leaved tree proportion were more obvious. Considering the regionality and seasonality is therefore necessary to implement regional plantation management for biodiversity conservation.

4.2 Introduction

Natural forests have been lost, and plantations have been expanding globally (FAO 2020). Plantations now account for 7% of the world's forests (FAO 2020), many of which have replaced natural forests (Puyravaud et al. 2010; Hua et al. 2018). In general, plantations support less biodiversity compared to natural forests (Brockerhoff et al. 2008; Chaudhary et al. 2016). However, several studies have shown that plantations can, in some contexts, serve as alternative or comparable habitats for species preferring natural forests (hereafter natural forest species) (Estades & Temple 1999; Faria et al. 2007; Irwin et al. 2014; Spake et al. 2016). In landscapes already or increasingly dominated by plantations, biodiversity conservation in plantations can be effective and important means (Yamaura et al. 2012a; Demarais et al. 2017; McFadden & Dirzo 2018). Elucidating the factors that determine the habitat function of plantations is therefore essential to reconcile both forestry and biodiversity conservation (Brockerhoff et al. 2008; Demarais et al. 2017; Castaño-Villa et al. 2019).

Stand age and the amount of non-planted native trees are important stand variables for biodiversity in plantations (Hartley 2002). Plantation age has positive effects on species dependent on mature forests (hereafter mature forest species; Castaño-Villa et al. 2019; Spake et al. 2019). Moreover, with increase in the amount of non-planted trees within plantations (e.g., broad-leaved trees within conifer plantations), the species richness and abundance of natural forest species (e.g., broad-leaved forest species, hereafter BL forest species) increase (Ohsawa 2007; Yoshii et al. 2015; Lindbladh et al. 2017). On the other hand, young plantations can

provide important habitats for early-successional species that have recently decreased in many parts of the world (Yamaura et al. 2012b; Toyoshima et al. 2013; Ram et al. 2020; Bakx et al. 2020). Not only natural forests, but also grasslands, wetlands, and farmlands have been replaced by plantations in many regions; plantations are expected to conserve both mature forest species and early-successional species (Yamaura et al. 2012a, 2012b; Iezzi et al. 2020).

Focusing on birds, most of these knowledge have been derived from intensive surveys in specific regions in the breeding season (e.g., Toyoshima et al. 2013; Lindbladh et al. 2017). However, species distributions, habitat selection, and species composition differ depending on regional contexts, including climatic conditions (Barbet-Massin et al. 2012; Crosby et al. 2019). Climates affect organisms not only directly via the physiology, such as maintaining body temperature (Cooper et al. 2006), but also indirectly via prey resources, vegetation, or disturbances (Huston & Wolverton 2009; Yamaura et al. 2011; Betts et al. 2019). Reflecting these climate effects, species or community responses to land-use changes would be climate-dependent as shown in recent studies (Amano et al. 2011; Betts et al. 2019; Spake et al. 2020). Furthermore, climatic conditions also change seasonally, and winter specific environments (e.g., low temperature or snow cover) strongly restrict the distribution or survival of organisms from the cool-temperate to the arctic zone (Leech & Crick 2007; Somveille et al. 2015). Many animal populations, especially birds with great ability to move, consequently alter their range, habitat use, behavior patterns, or food habits (Marchand 2014; Elsen et al. 2018; Kawamura et al. 2019). Thus, we should consider differences in regional climates and seasons when evaluating the

effects of stand age or the amount of non-planted trees in plantations.

In addition, setting minimum goals for conservation, i.e., 'how much is enough', is useful for plantation management that aim to enhance biodiversity while continuing timber production (Lindenmayer & Luck 2005; Moning & Müller 2009; Yamaura et al. 2012b). For community-level responses, the threshold values of stand variables have been rarely examined, although those of landscape-scale habitat loss or fragmentation have been examined well (Radford et al. 2005; Swift & Hannon 2010; Morante-Filho et al. 2015; but see Gúenette & Villard 2005; Moning & Müller 2009; Ellis & Betts 2011). Finding the threshold values of stand variables that can be applied to a large spatial extent would contribute to efficient biodiversity conservation in plantations (Suding & Hobbs 2009).

In Japan, conifer monoculture plantations have replaced broad-leaved natural forests and grasslands, mainly after World War II (1950-1980), and now consequently account for 41% of forest area (Yamaura et al. 2012a; Forestry Agency 2017a). Recently, large-scale clearcutting of mature plantations is occurring across Japan in effort to increase domestic wood supply (Forestry Agency 2019, 2020). At the same time, the expectation for enhancing biodiversity and ecosystem services in plantations has been increasing; Japanese forestry is at a turning point in management (Forestry Agency 2019; Kakizawa et al. 2018). Here, I evaluated the effects of stand age and the broad-leaved tree proportion within stands (hereafter BL tree proportion) on bird communities (BL forest species and early-successional species) in conifer plantations (Todo fir *Abies sachalinensis* and Japanese larch *Larix kaempferi)* and natural forests in the

breeding and wintering seasons across Hokkaido, northern Japan. Furthermore, I examined whether those effects differ depending on regional climates and the season, and explored the threshold values of stand variables.

4.3 Materials and Methods

4.3.1 Study area

This study was conducted across Hokkaido, northern Japan. Hokkaido is located in the transitional zone between cool-temperate and boreal zones, and previous studies on several bird species already revealed that climates affect the distribution of abundance across Hokkaido (Fujimaki 2007; Kawamura et al. 2016). The land area of Hokkaido is ~784 million hectares, 71% of which is covered by forests (Forestry Agency 2017a). In many regions, natural forests are dominated by deciduous broad-leaved trees, and the proportion of conifer trees is higher in cooler regions (Kira 1991). Among the forests, 27% are planted, relatively low in Japan; however, plantation area is the largest among prefectures in Japan (14% of plantations in Japan; Forestry Agency 2017a). Two major planted tree species in Hokkaido were Todo fir, a native species, and Japanese larch that was introduced from other parts of the country, and plantations of the two species account for ~80% of plantations, many of which have replaced natural broad-leaved forests (Forestry Agency 2017b; Yamaura et al. 2018).

To examine the effects of stand age and the amount of broad-leaved trees within stands on bird communities, I selected survey stands (> 3 ha) with a wide range of both stand variables

across Hokkaido, for Todo fir plantations (46 stands), Japanese larch plantations (45 stands), and natural forests (28 stands), and established a 3 ha transect (100 m × 300 m) in each stand (Appendix S4.1). As regards climatic factors that potentially affect bird distributions, I focused on the mean temperature in each season and snow depth, which have been shown to be important in previous studies in Japan or Hokkaido (Kawamura et al. 2016; Kawamura et al. 2019). The climates of each transect were calculated using the Mesh Climate Value 2010 (a contiguous nationwide grid of 1-km^2 squares with 30-year [1981–2010] mean monthly temperatures, snow depths, and other data provided by the Meteorological Agency of Japan; Appendix S4.1; https://nlftp.mlit.go.jp/ksj/gml/datalist/KsjTmplt-G02.html [in Japanese]). I confirmed stand type (plantations or natural forests), planted tree species (e.g., Todo fir or Japanese larch) and stand age by Hokkaido Government Opendata CC-BY4.0 (https://creativecommons.org/licenses/by/4.0/deed.ja). I selected study stands from regions with low elevation (< 600 m a.s.l.). To avoid multicollinearity, I selected transects of conifer plantations with low correlations ($|r|<0.5$) among environmental factors (the snow depth in the wintering season and the amount of broad-leaved trees were measured in field surveys, see details in the 'Field survey' section; Appendix S4.2-4.3; Dormann et al. 2013). Although the amount of broad-leaved trees within plantations generally increases with stand age (Yamaura et al. 2019), selecting young plantations with abundant broad-leaved trees (e.g., harvested stands with retained trees and unsuccessful plantations) and mature plantations with few broad-leaved trees enabled to analyze the effects of both stand variables, separately. I tried to make

the transects spatially independent by spacing at least 600 m. However, for efficiency in surveying across Hokkaido, I had to make three exceptions (each transect separated at least 300 m for two pairs of the transect, and was adjacent for one pair). I conducted these procedures using ArcGIS 10.2.2 (ESRI, CA, USA).

4.3.2 Field survey

I used line transect methods for the bird survey (Bibby et al. 2000). I slowly walked the 300 m line down the center of the transect (using ski in snowy regions in winters), and recorded the number of detected individuals of each species within the transect. I did not record birds flying over. I surveyed each stand twice in both the breeding season (from 14 May to 14 July) and the wintering season (from 13 December to 14 February). The surveys were conducted over two years, but two surveys in each stand were completed in one year to account for fluctuations in bird abundance among years (i.e., 60 plantation and six natural forest stands were surveyed from December 2017 to July 2018, and 29 plantation and 22 natural forest stands were done from December 2018 to July 2019). All stands were surveyed in both seasons except for four stands (i.e., two stands only in the breeding season, and the others only in the wintering season). In total, 89 plantation stands and 28 natural forest stands were surveyed in each season.

To avoid survey season bias, I conducted the second survey in each season after completing the first survey in all stands, at some intervals in each stand (>19 days in the breeding season, and >23 days in the wintering season). I conducted the survey in the morning

[sunrise (3:55) to noon] or in the evening [16:00 to sunset (19:05)] during the breeding season, and in the daytime [sunrise (6:55) to sunset (15:40)] during the wintering season. Bias in survey clock times was avoided by both changing the clock-time of our visits between two surveys, and surveying in the morning at least once in the breeding season (i.e., the mean difference in the survey clock times between the first and second surveys was 7.5 hours in the breeding season and 3.6 hours in the wintering seasons). No surveys were conducted when rain, heavy fog, strong winds, or heavy snow that could potentially interfere with observations.

I measured snow depth and the amount of broad-leaved trees within stands at six points set at equal intervals on each transect line (25, 75, 125, 175, 225, and 275 m points from the start) in each winter survey. For the amount of broad-leaved trees, I visually evaluated the coverage proportion of broad-leaved trees to conifer trees within a 25-m radius of each point in four parts (0-90, 90-180, 180-270, 270-360º) on a scale of 0, 5, 10, 20, 30, 40, 50, 60, 70, 80, 90, 95, and 100% (hereafter BL tree proportion). I could not calculate the basal areas of trees from the diameters at breast height due to time constraint for surveying, although it is one of the most common and accurate methods (Yoshii et al. 2015; Lindbladh et al. 2017). I did not differentiate broad-leaved trees by species or sizes, but recorded BL tree proportion as 50% when the overstory and understory was covered by broad-leaved trees and planted conifer trees, respectively, or vice versa. The values of snow depth and BL tree proportion for each stand were calculated by averaging the measured values at six points. In the second survey of some stands in the wintering season, BL tree proportion decreased than that of the first survey because

small broad-leaved trees were covered with snow. However, in the first survey in the wintering season, I could see almost all broad-leaved trees since snow depth was lower than that of broad-leaved trees even in regions with heavy snowfalls. Thus, I used the values of BL tree proportion that were measured in the first survey in wintering season for the analyses in the breeding season.

4.3.3 Bird categories

Based on the published literature, I classified bird species observed in the field into early-successional species and mature forest species, and then classified mature forest species into species that prefer conifer forests or not (hereafter conifer forest species and BL forest species; Yamaura et al. 2009; Kawamura et al. 2019; Appendix S4.4). Moreover, in the breeding season, I extracted cavity nesters, which depend on large and/or old trees with cavities, from BL forest species (Yamaura et al. 2008, 2009). Early-successional species occurred only in the breeding season. I classified two dominated species, the Black-faced Bunting *Emberiza spodocephala* and the Japanese Bush Warbler *Horornis diphone*, as generalists with no preference for stand age and BL tree proportion (Appendix S4.5). From the analyses, I excluded species which are too difficult to be detected by my method (nocturnal birds, raptors, and temporary migrants) or species that are strongly affected by non-forest variables (urban birds, waterbirds). I treated early-successional species and BL forest species, especially cavity nesters in the breeding season, as conservation targets, and conducted the analyses for these groups.

4.3.4 Statistical analysis

I used the generalized linear mixed models (GLMMs, Family = Poisson, link function = log) to examine the effects of stand age and BL tree proportion in plantations on bird communities. I separately analyzed for each group in each season (BL forest species in both seasons, and cavity nesters and early-successional species only in the breeding season). I considered the total abundance and species richness of all observed birds in each survey as response variables, and used the random site intercept accounting for pseudo-replication (89 plantation stands × 2 surveys = 178 samples). For the analyses of BL forest species and cavity nesters, I considered stand age, BL tree proportion, and the mean temperature in the breeding or wintering season as explanatory variables, and in the wintering season, I added snow depth at each survey. For the analyses of early-successional species, I considered only stand age and the mean temperature in the breeding season. Considering non-linearity of the responses to stand variables, I used logarithmically transformed variables [log(stand age) and log(BL tree proportion + 1), hereafter log form] in the analyses for BL forest species and cavity nesters, and added quadratic terms of stand variables [e.g., stand age + (stand age)2, hereafter quadratic form] in the analyses for early-successional species. Whether to use the log or quadratic forms was decided by comparing AIC of each models in the preliminary analyses (Appendix S4.6). Using the log form enable to express that the effects of stand variables are larger in the small ranges of the variables (Toyoshima et al. 2013). To consider climate-dependent effects of stand age and BL tree proportion, I used the interaction terms between these variables and climates (the mean

temperature in each season and snow depth). I constructed models for all possible combinations of these explanatory variables, and selected the model with the lowest Akaike's information criterion (AIC) as the best model (Burnham & Anderson 2002). Stand variables in the quadratic form, mean temperature in each season, and snow depth were standardized prior to analyses. In addition, in the wintering season, stand variables in the log form were also standardized for model convergence. For the abundance data in the wintering season, I excluded the Brambling *Fringilla montifringilla* that made extremely large flocks only in few surveys, and furthermore added the random survey intercept to account for over-dispersion caused by the large variation of bird abundance.

When any interaction terms with climate variables for each stand variable were not included in a best GLMM, I explored the threshold value of stand age or BL tree proportion that can be applied across Hokkaido, using the segmented regression (Muggeo 2003, 2008). In this analysis method, I could estimate the threshold values with the confidence interval (CIs) and treat the Poisson distribution, although could not consider the random effects. I targeted the non-transformed stand age or BL tree proportion for exploring the threshold value, and retained other explanatory variables same as the best GLMM. When both stand age and BL tree proportion were included in the best GLMM, I defined the threshold value of one variable at an analysis. I set the median values of stand variables as start point to search for the threshold values (default setting).

To examine whether the responses of many species were coincident with those of the

group, I used the GLMMs with the abundance of each species for each group as a response variable (hereafter multi-species GLMMs). I used only the data of species that occurred at least five surveys (Appendix S4.1). In these analyses, I included the random species intercepts and slopes to estimate average species responses considering the species differences in abundance or the responses to environments (Lehikoinen et al. 2019). To reduce the model complexity, I did not considered the interaction terms that were not included in the best GLMMs for the species richness and total abundance of the same group. As with the analyses for species richness and total abundance, I conducted the model selection by AIC. For all models, I retained all explanatory variables to be included in the random slopes because considering the species-specific effects.

When the strong interaction between stand variables and climates was detected in the analyses of species richness or total abundance, I reanalyzed after excluding the data that have potentially great effects on estimating the interaction (i.e., sensitivity analysis). Specifically, for the interaction between BL tree proportion and the mean temperature in the wintering season, I excluded the data of following four stands: i) two stands with the high temperature (−4.57 and −4.8ºC), low BL tree proportion (10.8 and 16.7%), and high richness and abundance of BL forest species (species richness: 7 and 9, total abundance: 123 and 84), and ii) two stands with the high temperature (−4.47 and −5.17 ºC), high BL tree proportion (97.5 and 76.7%), and low richness and abundance of the group (species richness: 1 and 2, total abundance: 1 and 1). Then, I conducted the model selection as with the original analyses.

Finally, I examined the effects of stand age on BL forest species in natural forests (28 stands × two surveys), using the similar method to that for plantations. I did not use BL tree proportion as explanatory variables since there were no natural forests with low BL tree proportion (mean: 90.09%, minimum: 40%). Moreover, I did not consider the interaction with climates because of its small sample size. To compare the habitat function for BL forest species between plantations and natural forests, I made figures in which the predicted values from the best GLMMs of both forest types were depicted. Moreover, in preliminary analyses, I examined the planted tree species effects and its interaction with stand variables; however, the effects were small (Appendix S4.7). I conducted all analyses using 'lme4' v. 1.1.21 (Bates et al. 2015), 'segmented' v. 1.2.0 (Muggeo 2003, 2008), 'MuMIn' v. 1.43.6 (Bartoń 2019) running in R v. 3.6.1 (R core team 2019).

4.4 Results

During the surveys in plantations in the breeding season, I recorded a total of 2,196 individuals of 36 BL forest species, 717 individuals of 5 conifer forest species, and 409 individuals of 11 early-successional species (the total number of individuals was the sum of the first and second surveys in all stands; Appendix S4.4). The three dominant species for each group were as follows; BL forest species: the Eastern Crowned Leaf Warbler *Phylloscopus coronatus* (628 individuals in 110 surveys), the Asian Stubtail *Urosphena squameiceps* (261 individuals in 72 surveys), and the Nurcissus Flycatcher *Ficedula narcissina* (202 individuals in 76 surveys),

conifer forest species: the Coal Tit *Parus ater* (347 individuals in 88 surveys), the Goldcrest *Regulus regulus* (240 individuals in 72 surveys), and the Sakhalin Leaf Warbler *Phylloscopus borealoides* (100 individuals in 36 surveys), and early-successional species: the Siberian Meadow Bunting *Emberiza cioides* (180 individuals in 43 surveys), the Oriental Greenfinch *Carduelis sinica minor* (75 individuals in 41 surveys), and the Olive-backed Pipit *Anthus hodgsoni* (69 individuals in 24 surveys). The two species of generalists were also abundant [the Black-faced Bunting (610 individuals in 88 surveys) and the Japanese Bush Warbler (182 individuals in 72 surveys)].

During the surveys in plantations in the wintering season, I recorded a total of 3,264 individuals of 23 BL forest species and 1,830 individuals of 3 conifer forest species (Appendix S4.4). The three dominant species for each group, except the Brambling that made extremely large flock but occurred in few surveys, as follows; BL forest species: the Willow Tit *Parus montanus* (596 individuals in 43 surveys), the Marsh Tit *Parus palustris* (218 individuals in 38 surveys), and the Long-tailed Tit *Aegithalos caudatus* (194 individuals in 30 surveys), conifer forest species: the Coal Tit (931 individuals in 62 surveys), the Eurasian Siskin *Spinus spinus* (475 individuals in 23 surveys), and the Goldcrest (424 individuals in 88 surveys).

4.4.1 Effects of stand age

In the breeding season, early-successional species occurred mainly in young plantations (<25 years old), and the species richness and total abundance decreased with stand age (Fig 4.1g-i,

Table 4.1a-c, Appendix S4.8a-c). For the best GLMMs, the interaction between the quadratic term of stand age and the mean temperature in the breeding season was significant, suggesting negative effects of stand age were weaker in warmer regions (i.e., early-successional species occurred in plantation with a relatively wide range of stand age; Fig 4.1g-h, Table 4.1a-b). In the best multi-species GLMM, the interaction term was not included (Table 4.1c). However, species compositions differed among regions with different temperature, and species that were occurred in cool regions (i.e., the Latham's Snipe *Gallinago hardwickii*, the Olive-backed Pipit, and the Stejneger's stonechat *Saxicola stejnegeri*) more strongly preferred younger plantations than species that were abundant in warm regions (i.e., the Siberian Meadow Bunting and the Oriental Greenfinch) (Fig 4.1i, Appendix S4.9a).

For BL forest species and cavity nesters, the species richness and abundance were higher in older plantations in the breeding season, and the responses were consistent across Hokkaido (Fig 4.1a-f; Table 4.1d-i, Appendix S4.8d-i). Segmented regressions indicated that, as stand age increased, the species richness and total abundance increased in younger stands, but the increase rate declined in older stands (> 60-70 years old) [the estimated threshold values; cavity nesters: 62.87 years (95%CI: 57.00-68.72) for species richness and 67.99 years (95%CI: 55.05-80.94) for total abundance (Fig 4.1a-b, d-e), BL forest species: 61.33 years (95%CI: 57.86-64.80) for total abundance but 20.74 years (95%CI: 13.68-27.81) for species richness], although the best GLMMs with the log form showed the almost linear increase patterns. In the best multi-species GLMM, the random species slopes of stand age suggested that there were

both species that showed the threshold pattern and the linear increase pattern (Fig 4.3f, i, Appendix S4.9b-c). Similarly, in the natural forests, the species richness and total abundance of these groups were higher in older stands; however, the increase rate declined in older stands (>70-80 years old; Appendix S4.10).

By contrast, in the wintering season, the effects of stand age differed depending on the mean temperature (Table 4.2a-b, Appendix S4.12); the species richness and abundance linearly increased with stand age in warmer regions, but in colder regions those increased only in the small range of stand age (<50 years old) (Fig 4.2a-b, Appendix S4.11). In the best multi-species GLMM, the interaction term was not included as a fixed effect (Table 4.2c). However, for nine of 12 species when considering the random slopes, the interaction term showed positive values, as with those of species richness and total abundance (Fig 4.2c, Appendix S4.13). Correlation among random slopes showed that the interaction tended to be more obvious for species of which abundance was higher in colder regions (Appendix S4.13, $r=-0.63$). Similarly, in the natural forests, the species richness and abundance were higher in older stands, although I did not consider the interaction with climates (Appendix S4.14).

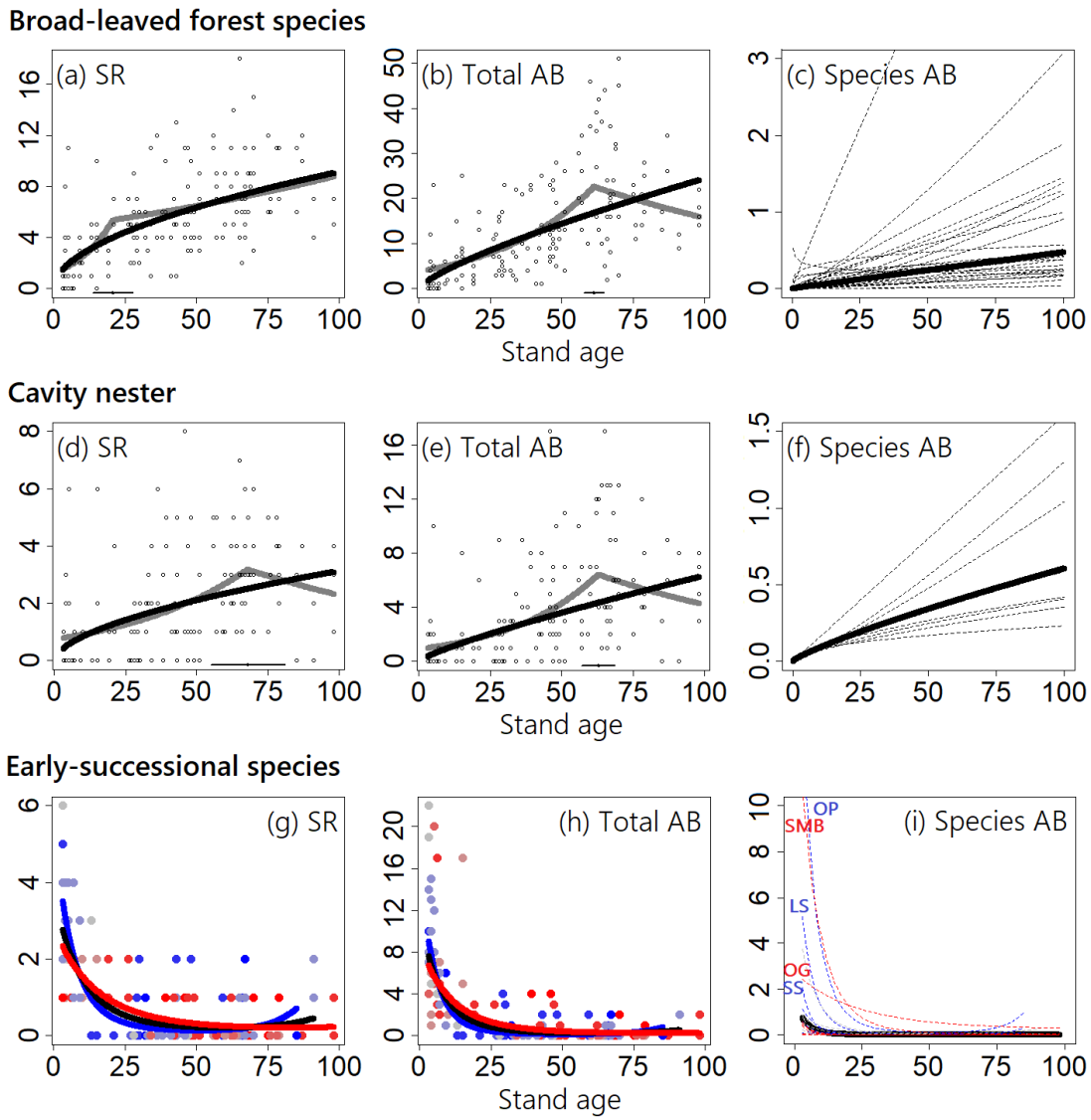


Fig. 4.1. Effects of stand age on bird communities in plantations in the breeding season [(a-c) broad-leaved forest species, (d-f) cavity nester, (g-i) early-successional species]. Results of (a, d, g) species richness, (b, e, h) total abundance, and (c, f, i) species-level abundance. Dots and black solid lines indicate data collected at each survey and the estimates afforded by the best GLMMs. (a-b, d-e) Grey solid lines indicate the estimates derived from the segmented regression. (c, f, i) Dotted lines represent the responses of each species considering the random intercepts and slopes. (g-i) For early-successional species that were affected by the interaction with the mean temperature in the breeding season, the differences in the temperature were shown by colors [blue: 5th percentile (11.07 ºC), black or grey: median (13.60 ºC), red: 95th percentile (15.37 ºC)]. The regional differences in dominant species of this group are shown in two capital letters for each species [warm regions (OG: the Oriental Greenfinch, SMB: the Siberian Meadow Bunting), cool regions (LS: the Latham's Snipe, OP: the Olive-backed Pipit, SS: the Stejneger's stonechat)]. The other explanatory variable was fixed to mean values in each figure (the broad-leaved tree proportion: 30.81%).

Table 4.1. The best GLMMs for the broad-leaved forest species in the wintering season [(a) species richness, (b) total abundance, (c) species-level abundance]. The estimates of SE (stand error), z value, Wald-*p* value for the fixed effects, and those of variance and SD (standard deviation) for the random effects. Abbreviations: L_Age; log(stand age), L_Broad; log(the broad-leaved tree proportion+1), Snow; snow depth at each survey, Temp; the mean temperature in the wintering season. Colons represent interactions. Blanks indicate not included in the model.

Early-successional species

Fixed effects	**(a) Species richness**				**(b) Total abundance**				**(c) Species-level abundance**			
	Estimate	SE	z value	*p*	Estimate	SE	z value	*p*	Estimate	SE	z value	*p*
Intercept	-1.32	0.20	-6.66		-1.14	0.23	-4.92		-6.59	1.55	-4.26	
Age	-0.91	0.10	-8.94	< 0.01	-1.28	0.13	-9.97	< 0.01	-2.75	0.90	-3.05	< 0.01
Age^2	0.64	0.12	5.31	< 0.01	0.83	0.14	5.89	< 0.01	1.35	0.42	3.25	< 0.01
Temp	0.32	0.18	1.81	0.07	0.46	0.19	2.41	< 0.01				
Age^2:Temp	-0.26	0.12	-2.10	0.04	-0.31	0.14	-2.16	0.03				

Random effects		Variance	SD	Variance	SD	Variance	SD
SiteID	Intercept	0.00	0.00	0.55	0.74	0.87	0.93
SpeciesID	Intercept					11.57	3.40
	Age					2.72	1.65
	Age^2					0.29	0.53
	Temp					1.88	1.37
	Age^2:Temp					0.11	0.33

Table 4.1, continued.

Broad-leaved forest species

Fixed effects	(d) Species richness				(e) Total abundance				(f) Species-level abundance			
	Estimate	SE	z value	*p*	Estimate	SE	z value	*p*	Estimate	SE	z value	*p*
Intercept	-1.05	0.23	-4.58		-1.73	0.30	-5.69		-7.19	0.88	-8.15	
L_Age	0.53	0.06	8.62	< 0.01	0.76	0.09	8.98	< 0.01	1.00	0.16	6.22	< 0.01
L_Broad	0.24	0.05	4.62	< 0.01	0.41	0.07	5.55	< 0.01	0.54	0.13	4.18	< 0.01
Temp									-0.29	0.19	-1.54	0.13
Random effects	Variance	SD			Variance	SD			Variance	SD		
SiteID Intercept	0.05	0.23			0.28	0.53			0.37	0.61		
SpeciesID Intercept									14.26	3.78		
L_Age									0.34	0.58		
L_Broad									0.20	0.44		
Temp									0.75	0.87		

Cavity nester

Fixed effects	(g) Species richness				(h) Total abundance				(i) Species-level abundance			
	Estimate	SE	z value	*p*	Estimate	SE	z value	*p*	Estimate	SE	z value	*p*
Intercept	-2.63	0.42	-6.33		-3.38	0.49	-6.96		-6.38	0.71	-8.96	
L_Age	0.57	0.11	5.32	< 0.01	0.82	0.13	6.43	< 0.01	0.82	0.17	4.73	< 0.01
L_Broad	0.33	0.09	3.56	< 0.01	0.42	0.11	3.92	< 0.01	0.60	0.19	3.12	< 0.01
Random effects	Variance	SD			Variance	SD			Variance	SD		
SiteID Intercept	0.1325	0.364			0.3995	0.632			0.45	0.67		
SpeciesID Intercept									0.93	0.96		
L_Age									0.08	0.28		
L_Broad									0.15	0.39		
Temp									0.10	0.31		

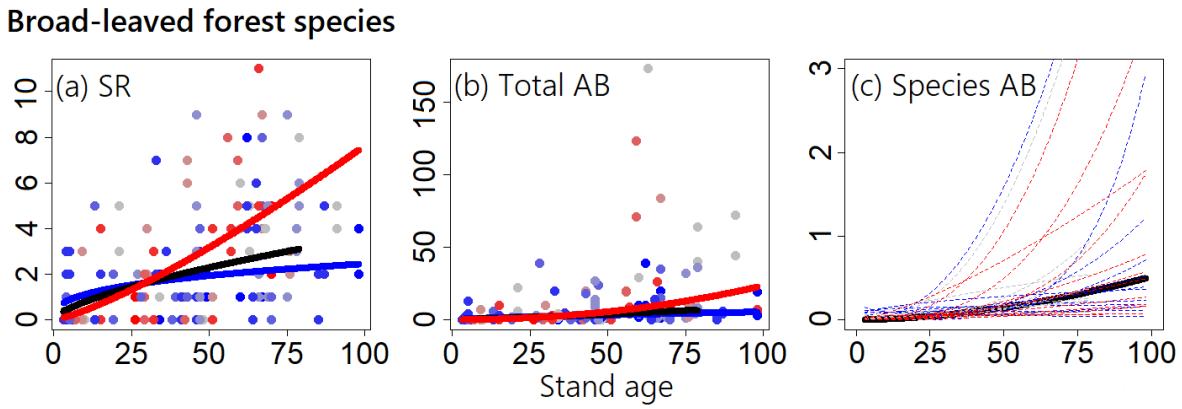


Fig. 4.2. Effects of stand age on broad-leaved forest bird species in plantations in the wintering season [(a) species richness, (b) total abundance, (c) species-level abundance]. Dots and black solid lines indicate data collected at each survey and the estimates afforded by the best GLMMs. (c) Dotted lines represent the responses of each species considering the random intercepts and slopes. The interaction with the mean temperature in the wintering season, the differences in the temperature were shown by colors [blue: 5th percentile (−8.17 ºC), black or grey: median (−6.70 ºC), red: 95th percentile (−3.90 ºC)]. The other explanatory variables were fixed to mean values in each figure (the broad-leaved tree proportion: 30.03%, snow depth: 83.19 cm).

Table 4.2. The best GLMMs for the broad-leaved forest species in the wintering season [(a) species richness, (b) total abundance, (c) species-level abundance]. The estimates of SE (stand error), z value, Wald-*p* value for the fixed effects, and those of variance and SD (standard deviation) for the random effects. Abbreviations: L_Age; log(stand age), L_Broad; log(the broad-leaved tree proportion+1), Snow; snow depth at each survey, Temp; the mean temperature in the wintering season. Colons represent interactions. Blanks indicate not included in the model.

Broad-leaved forest species

Fixed effects	**(a) Species richness**				**(b) Total abundance**				**(c) Species-level abundance**			
	Estimate	SE	z value	*p*	Estimate	SE	z value	*p*	Estimate	SE	z value	*p*
Intercept	0.41	0.17	2.36		0.25	0.11	2.31		-3.40	0.37	-9.20	< 0.01
L_Age	1.42	0.21	6.63	< 0.01	0.78	0.13	6.06	< 0.01	1.97	0.45	4.34	< 0.01
L_Broad	0.32	0.21	1.53	0.13	0.39	0.13	3.01	< 0.01	0.72	0.29	2.51	0.01
Snow	-0.22	0.16	-1.43	0.15					-0.51	0.25	-2.09	0.04
Temp	0.13	0.18	0.71	0.48	0.16	0.11	1.47	0.14				
L_Age:Temp	0.48	0.21	2.28	0.02	0.33	0.13	2.62	< 0.01				
L_Broad:Temp	-0.57	0.23	-2.46	0.01	-0.46	0.14	-3.31	< 0.01				
Random effects	Variance	SD			Variance	SD			Variance	SD		
SiteID Intercept	1.16	1.08			0.26	0.51			1.10	1.05		
Survey ID Intercept	0.83	0.91							1.38	1.18		
SpeciesID Intercept									0.96	0.98		
L_Age									1.59	1.26		
L_Broad									0.26	0.51		
Snow									0.32	0.57		
Temp									0.18	0.42		
L_Age:Temp									0.22	0.47		
L_Broad:Temp									0.11	0.34		

4.4.2 Effects of the broad-leaved tree proportion

In the breeding season, the species richness and total abundance of BL forest species were higher in plantations with higher BL tree proportion, and the responses were consistent across regions with different climates (Fig 4.3, Table 4.1d-e, g-h, Appendix S4.8d-e, g-h). I found the threshold values of 25-50% [the estimated threshold values; BL forest species: 21.67 (95%CI: 14.99-28.34) for species richness and 53.72 (95%CI: 49.23-58.21) for total abundance, cavity nesters: 21.67 (95%CI: 16.06-27.27) for species richness and 21.67 (95%CI: 16.94-26.39) for total abundance]. As the proportion increased, the species richness and abundance increased in stands with lower BL tree proportion, and remained almost unchanged in stands with higher BL tree proportion (Fig 4.3d-e, f-g). In the best multi-species GLMM, the similar patterns were shown for many species (Fig 4.3c, f, Table 4.1f, i, Appendix S4.8f, i, 4.9b-c).

By contrast, in the wintering season, the effects of BL tree proportion differed depending on the mean temperature (Table 4.2a-b). In colder regions, the positive effects of BL tree proportion were stronger, i.e., the species richness and total abundance linearly increased with the proportion (Fig 4.4a-b, Appendix S4.15). Even in the sensitivity analysis, the similar pattern was detected for species richness (Appendix S4.16). Moreover, for both the species richness and total abundance, the interaction with snow depth became significant; the positive effects of the BL tree proportion were more obvious in regions with deeper snow (Appendix S4.17). In the best multi-species GLMM, the interaction term with the temperature was not included as a fixed effect (Table 4.2c). However, seven of 12 species when considering the

random slopes, the estimates of interaction term were negative values, as with those of species richness and total abundance (Fig 4.4c, Appendix S4.13). For both seasons, in plantations where BL tree proportion exceeded 25%, the species richness and total abundance were comparable to those in broad-leaved natural forests under the fixed age condition (Appendix S4.18-4.19).

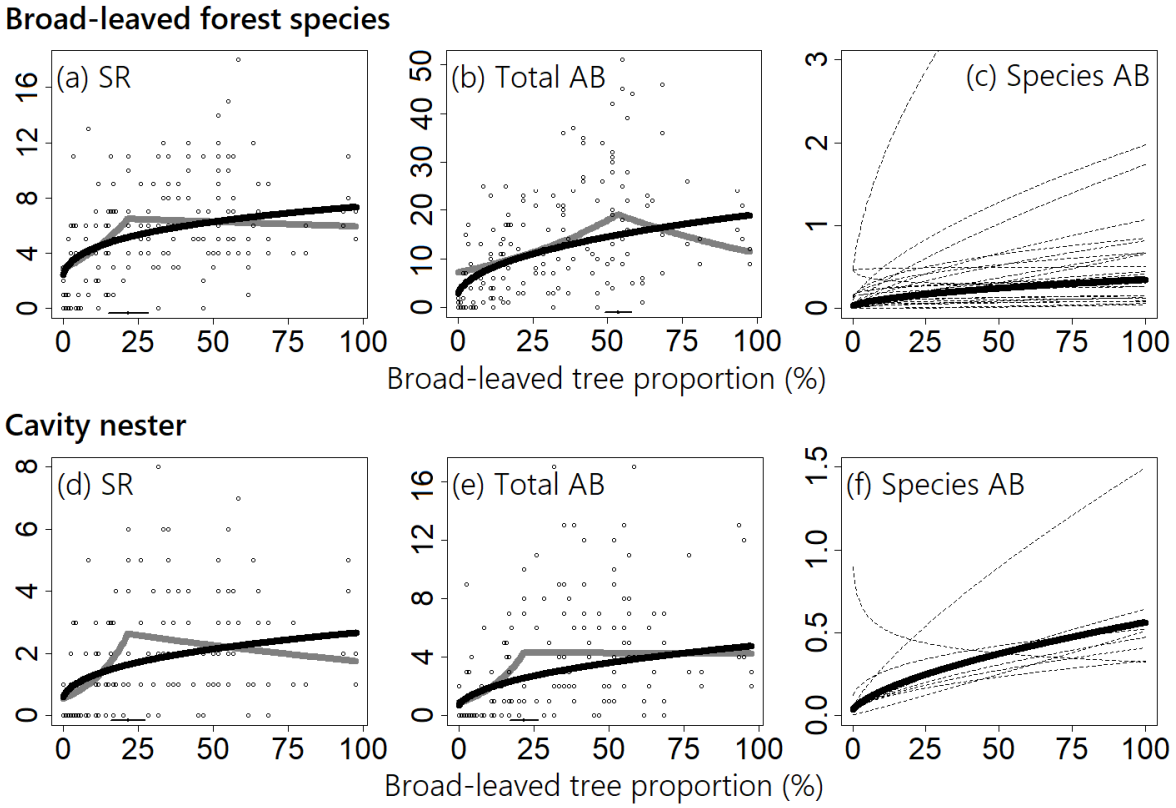


Fig. 4.3. Effects of the broad-leaved tree proportion on bird communities in plantations in the breeding season [(a-c) broad-leaved forest species, (d-f) cavity nester]. Results of (a, d) species richness, (b, e) total abundance, and (c, f) species-level abundance. Dots and black solid lines indicate data collected at each survey and the estimates afforded by the best GLMMs, respectively. (a-b, d-e) Grey solid lines indicate the estimates derived from the segmented regression. (c, f) Dotted lines represent the responses of each species considering the random intercepts and slopes. The other explanatory variables were fixed to mean values in each figure (stand age: 39.2, temperature: 13.40ºC).

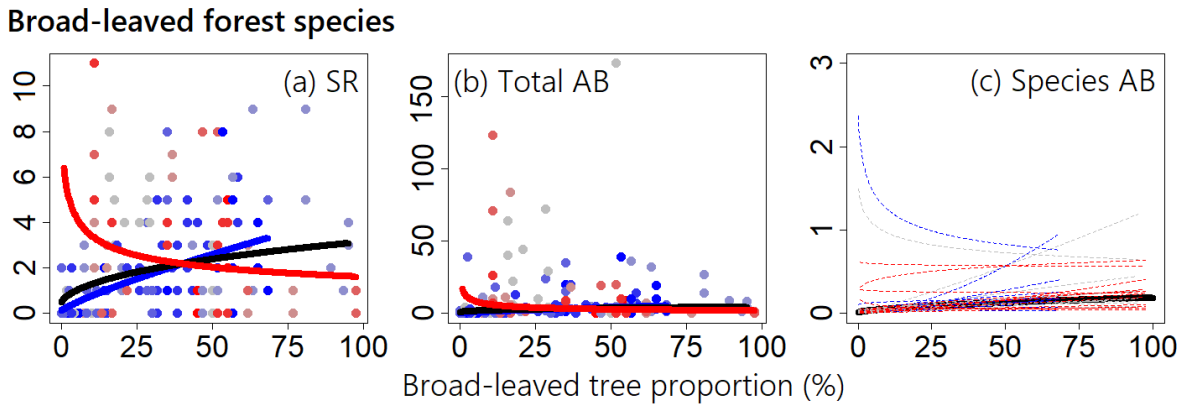


Fig. 4.4. Effects of the broad-leaved tree proportion on broad-leaved forest species in plantations in the wintering season [(a) species richness, (b) total abundance, (c) species-level abundance]. Dots and black solid lines indicate data collected at each site and the estimates afforded by the best GLMMs, respectively. (c) Dotted lines represent the responses of each species considering the random intercepts and slopes. The interaction with the mean temperature in the wintering season, the differences in the temperature were shown by colors [blue: 5th percentile (−8.17 ºC), black or grey: median (−6.70 ºC), red: 95th percentile (−3.90 ºC)]. The other explanatory variables were fixed to mean values in each figure (stand age: 39.83, snow depth: 83.19 cm).

4.5 Discussion

In the breeding season, the effects of stand age and BL tree proportion on BL forest species were consistent across Hokkaido. This means that plantation management based on stand age and BL tree proportion for breeding bird conservation is applicable across Hokkaido. By contrast, the species compositions of early-successional species in the breeding season differed depending on the regional temperature, leading to the differences in responses to stand age. Furthermore, in the wintering season, the effects of stand variables on BL forest species were also climate-dependent. These results suggest the importance of considering regional climates and seasonality to conserve biodiversity in plantations.

4.5.1 Effects of stand age

Early-successional species declined with stand age, and its species composition changed depending on the temperature. The Siberian Meadow Bunting and the Oriental Greenfinch, which were abundant in warm regions, occurred also in plantations with relatively higher stand age. These species nest on shrubs or low part of trees, and occur not only in open habitats, but also on forest edges (Nakamura & Nakamura 1995; Uchida 2019). In contrast, the Latham's Snipe, the Olive-backed Pipit, and the Stejneger's stonechat were abundant in especially younger plantations in cool regions. These bird species strongly depend on grassy plants because making the nest of grasses on the ground (Uchida 2019). In forest landscapes in Hokkaido, dwarf bamboos generally dominate the understory vegetation and make dense bushes; however, in cool regions, *Sasa nipponica* with lower height distributes (Toyooka et al. 1983). In regions with cooler breeding season, young plantations would not be suppressed by dwarf bamboos, likely leading to openness and high abundance and/or diversity of grass species (Nagai & Yoshida 2004; Itô & Hino 2007; Kudo et al. 2017). Thus, young plantations in cooler regions would serve as suitable habitats for the Latham's Snipe, the Olive-backed Pipit, and the Stejneger's Stonechat, although its duration as a habitat was shorter. However, the temperature in the breeding season positively correlated with snow depth in winter, and snow depth directly restrict the distributed bamboo species since snow cover protects the plant bodies from winter

coldness (Toyooka et al. 1983). Snow depth is more likely to be a strong driver influencing distribution of early-successional species.

For BL forest species in the breeding season, it was suggested that the increase rate of species richness and abundance with stand age declined in older stands (>60-70 years old in plantations and >70-80 years old in natural forests). This was consistent with the results of meta-analysis on studies in Japan (Spake et al. 2019). For Todo fir and Japanese larch plantations, the growth rate of tree height are known to decline in older stands (>~40 years old; Ishibashi et al. 2005; Takiya 2014). Most mature species were small birds and do not depend on old-growth forests, and thus, the increase rate of bird richness or abundance with the habitat space/niche expansion may also decline (Yui & Ishii 1991; Westworth 1993). However, the test using more abundant data from older plantations are needed to confirm this threshold pattern because the results of GLMMs with the log form showed the increase rate did not decline.

By contrast to the consistent effects of stand age on BL forest species in the breeding season across Hokkaido, in the wintering season, the effects of plantation age differed depending on the temperature; the species richness or total abundance linearly increased with stand age in warmer regions, but those increased only in the small range of stand age in colder regions. In mature plantations in warmer regions, I observed the large mixed-species flocks, which are anti-predator strategy in the wintering season (Morse 1970; Hino 2005). For especially the Long-tailed Tit and the Japanese Pygmy Woodpecker *Dendrocopos kizuki*, in addition the Great Spotted Woodpecker *Dendrocopos major* and the Dusky Thrush *Turdus*

eunomus, the positive effects of stand age were more obvious in warmer regions (Appendix S4.13). In colder regions, the starvation risk for wintering birds would be higher (Newton 1998). Participating the mixed-species flock would cause the decrease in available space per individual and the foraging efficiency of some species, due to forcing change in their foraging sites or movement speed (Morse 1970; Hutto 1988). Thus, for wintering birds in colder regions, it may be difficult to make large mixed-species flocks even when the habitat space or vertical niche diversity increases with stand age. It is also possible that new habitats (i.e., stands that is becoming mature) were quickly colonized by birds in colder regions because coldness would promote bird moving for search of prey (Latimer & Zuckerberg in press).

4.5.2 Effects of the broad-leaved tree proportion

In the breeding season, as BL tree proportion within plantations increased, the species richness and abundance increased until 25-50% of the proportion, but remained almost unchanged above the thresholds values. This pattern was also consistent across many species with different preference of climates. Furthermore, plantations where BL tree proportion was 25% supported comparable species richness and abundance to those of broad-leaved natural forests with the same stand age. In general, the amount of broad-leaved trees within plantations restrict prey resources and nest sites (e.g., cavity) for BL forest species (Yui & Ishii 1994; Newton 1998; Kikuchi et al. 2013). However, given that most bird species are territorial, there should be the upper limit for the abundance per area (Newton 1998; Comprodon et al. 2008). Moreover,

Japanese larch trees support many insect larvae, which are essential prey for breeding birds, comparable to that supported by broad-leaved trees (Yui & Ishii 1994). In addition, the invasion by broad-leaved trees to the canopy of plantations allow more light to reach the forest floor, supporting more abundant understory vegetation (the relative light intensity: Todo fir (2~8%) < Japanese larch < Birch (5~20%); Maebashi Forestry Office 1997). Therefore, the relatively small amount of broad-leaved trees would contribute to improving the habitat function of plantations for many species.

However, Yoshii et al. (2015) reported that the abundance of BL forest birds linearly increased with the basal area of broad-leaved trees within plantations in a landscape dominated by plantation in Hokkaido. This discrepancy with my results may be explained by the difference in the amount of surrounding BL forests. The amount of surrounding BL forests positively affect the density of BL forest birds in confer plantations (Yamaura et al. 2007). My survey sites, selected randomly in terms of surrounding BL forests, may be surrounded by more broad-leaved forests than those of Yoshii et al. (2015). Future studies should examine the cross-scale interaction of BL tree amount for planning effective stand management depending on landscape contexts (Mori et al. 2017).

In the wintering season, the effects of BL tree proportion differed depending on the temperature, or snow depth. BL tree proportion had greater positive effects in regions with more severe climates in winter (i.e., lower temperature or deeper snow). Bird survival is strongly limited by prey amount under the cold conditions, because birds require more energy to prevent

starvation, and at the same time, the prey availability decline (Gibb 1960; Yasué et al. 2003; Cresswell et al. 2009; Bonter et al. 2013). In regions where the productivity was low in winter, birds must persist on prey that were produced but unconsumed from spring to summer (Mönkkönen et al. 2006). Deciduous broad-leaved trees provide various prey, such as invertebrates, fruits, buds, and tree sap (Yui & Ishii 1994; Newton 1998; Pakkala et al. 2018). These trees also produce more cavities that allow cavity roosting species to consume less energy at night (Mayer et al. 1982; Cooper 1999; Paclík & Weidinger 2007). Thus, for BL forest species in regions with harsh winter climates, broad-leaved trees may be important in securing the energy required for overwintering. By contrast, no obvious effects in warm regions may be also explained by that the shelter function of conifer plantations with high tree density was more important than prey amount. Some studies in cold winter with abundant prey or high predation risk showed that birds tend to forage near or inside of dense structures (e.g., conifer crown and shrubs with many branches) that prevent to be attacked by predator (‘safety-first’ strategy; Suhonen 1993; Walther & Gosler 2001). Moreover, conifer plantations where trees stand in orderly lines have the high windbreak effects, potentially leading to bird survival in temporarily blizzards (Petit 1989; Rosenfeld et al. 2010).

4.5.3 Implications for bird conservation and forest management

Creating young stands by harvesting plantations was suggested to be effective for conservation of early-successional species across Hokkaido. However, the conserved species and the

duration as habitats were likely to be different among regions. Short-rotation forestry would be effective to conserve early-successional species, especially in regions with cool summer, where the duration as early-successional habitats was shorter.

For BL forest species in the breeding season, the species richness and abundance increased with plantation age until 60-70 years, and this pattern was consistent across Hokkaido. By contrast, in the wintering season, the species richness and abundance linearly increased with plantation age, but hardly increased in older plantations in colder regions. Therefore, long-rotation forestry is preferable for BL forest species, especially in regions with warm winter, where older plantations have important role as wintering habitats.

In the breeding season, plantations with 25% or more of BL tree proportion were suitable habitats for BL forest species, comparable to natural forests with the same stand age. For conservation of breeding bird communities in plantations, management that aim for this '25%' goal of BL tree proportion would be desirable wherever Hokkaido. However, in the wintering season, the species richness and abundance linearly increased with BL tree proportion in regions with severe climate (i.e., low temperature or deep snow). Especially in these regions, enhancing BL tree proportion would be the important mean for conserving BL forest species across seasons.

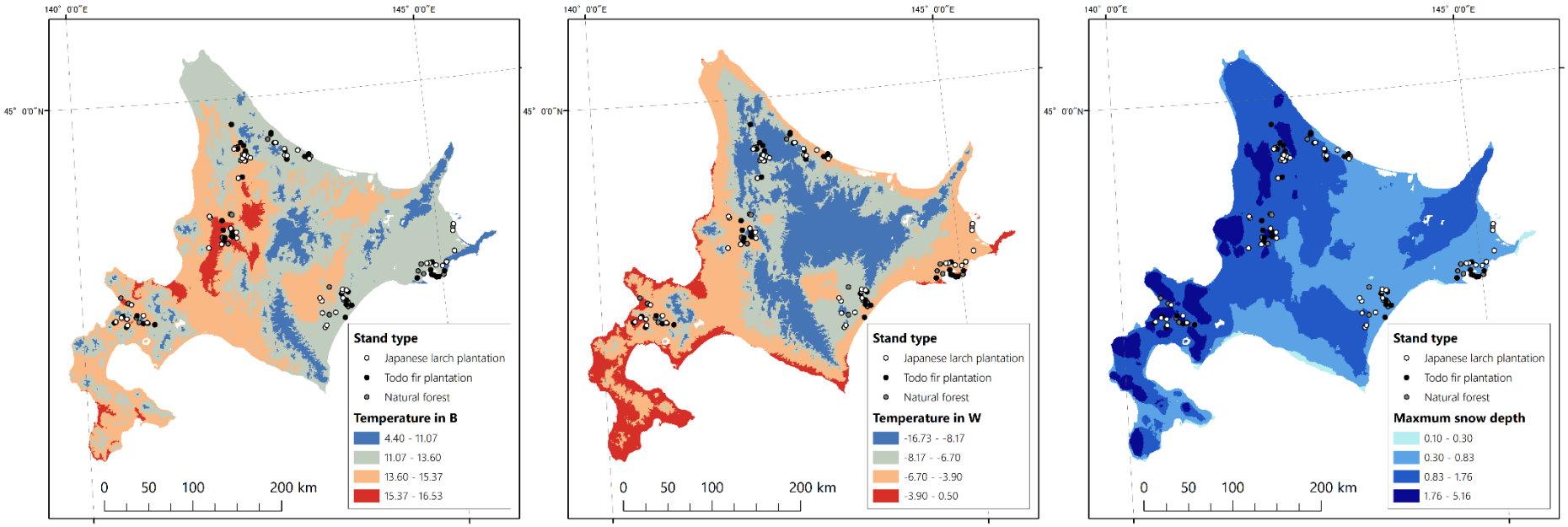
Although identifying which size and species of broad-leaved trees are more important is remained as research gaps, retaining the broad-leaved trees when harvesting or thinning would be the key to improving BL tree proportion according to the regional goals (Yamaura et

al. 2018; Yamaura et al. 2019). This study revealed the response of bird communities to stand age and BL tree proportion in plantations, considering regionality and seasonality, and informed regional management for bird diversity depending on the conservation target of seasons or groups (Table 4.3).

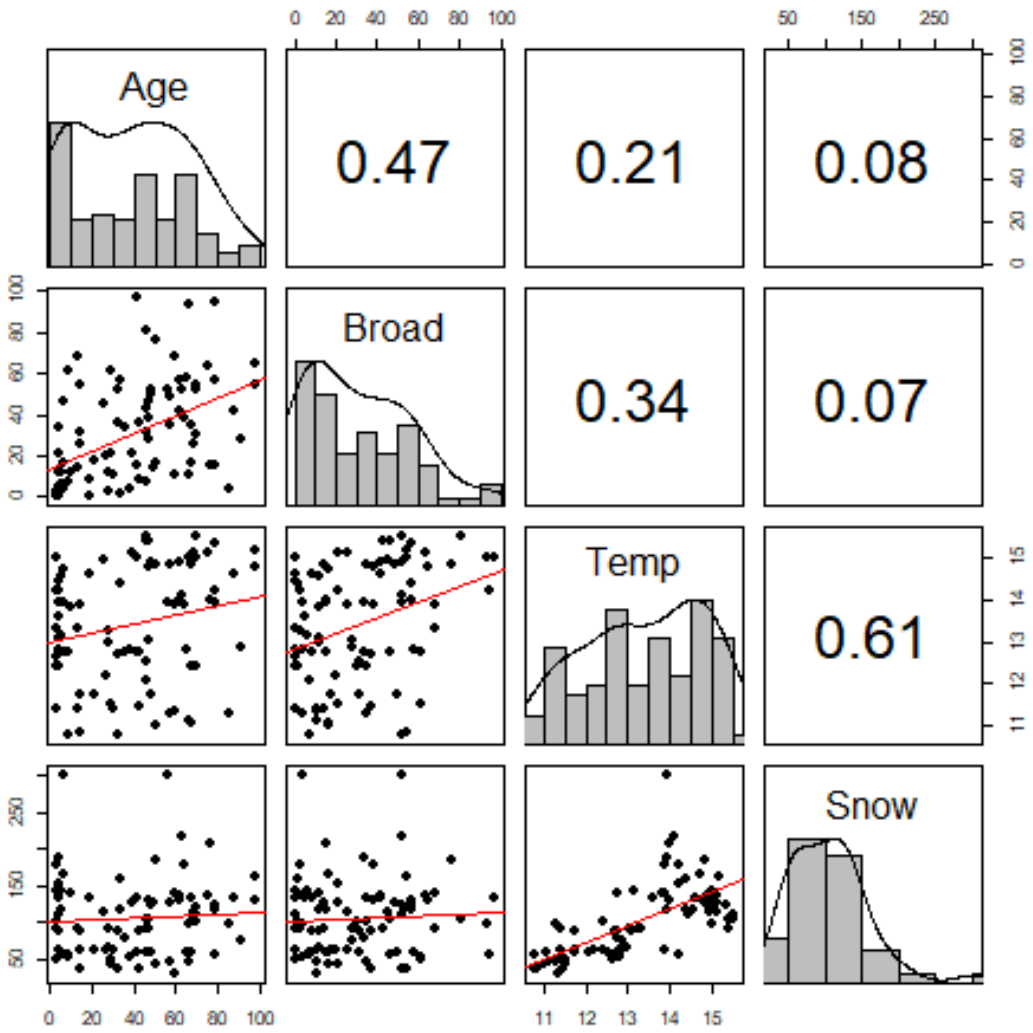
Table 4.3 Implication for regional plantation management for conservation of early-successional species in the breeding season and broad-leaved forest species (BL forest species), considering the regional difference in the effects of stand age and the broad-leaved tree proportion (BL tree proportion). Note that 25 % of BL tree proportion for conserving BL forest species in the breeding season across Hokkaido.

		Climates in the wintering season	
		Severe (low temperature, deep snow)	Mild (high temperature, shallow snow)
Temperature in the breeding season	Low	Inland of eastern Hokkado and Okhotsk regions Early-successional species ⇒Short-rotation forestry BL forest species in the wintering season ⇒Improving BL tree proportion	Coastland of eastern Hokkaido and Okhotsk region Early-successional species ⇒Short-rotation forestry BL forest species in the wintering season ⇒Long-rotation forestry
	High	Inland of northern and central Hokkaido Early-successional species ⇒Regular-rotation forestry BL forest species in the wintering season ⇒Improving BL tree proportion	Coastland of northern and central Hokkaido Pacific coastland of northern and central Hokkaido Early-successional species ⇒Regular-rotation forestry BL forest species in the wintering season ⇒Long-rotation forestry

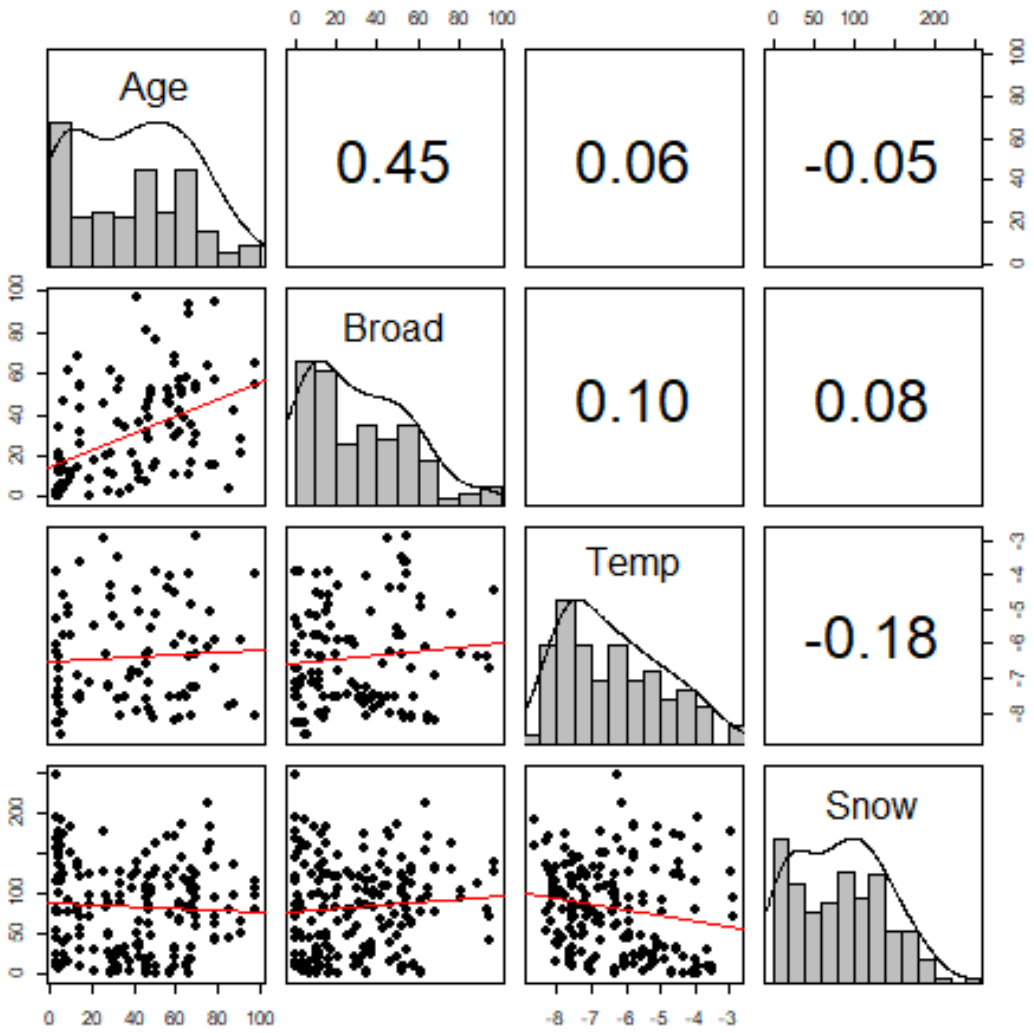
4.6 Appendices



Appendix S4.1. Distribution of survey stands and regional climates (left: the mean temperature in the breeding season, center: the mean temperature in the wintering season, right: the maximum snow depth).



Appendix S4.2. Relationships among environmental factors in plantations in the breeding season (Age: stand age, Broad: broad-leaved tree proportion, Temp: the mean temperature in the breeding season, Snow: the maximum snow depth). Panels below the diagonal show scatter plots of the pairs of factors (with regression lines). Pearson correlation values of the pairs are shown above the diagonal while histograms of each factors are shown at the diagonal. These plots were produced by 'pairs.panels' function of 'psych' package on R. I did not use the maximum snow depth for the analyses, but used for discussing that the effects of stand age on early-successional species differed depending on the temperature.



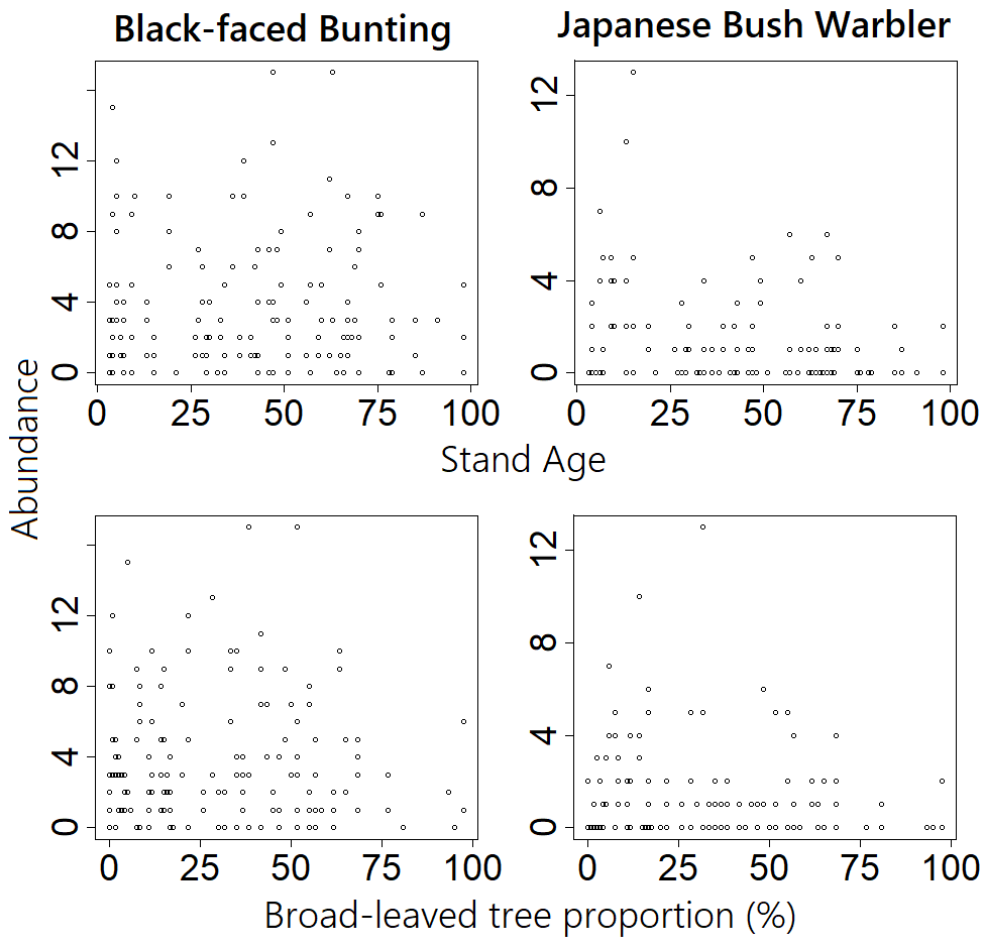
Appendix S4.3. Relationships among environmental factors in plantations in the wintering season (Age: stand age, Broad: broad-leaved tree proportion, Temp: the mean temperature in the wintering season, Snow: snow depth in each survey). See details in Appendix S4.2

Appendix S4.4. List of observed species in plantations. For each species, the habitat preferences [successional stage: early-successional (EA) or mature forests (MA), forest type: broad-leaved or conifer forests (BL and CO, respectively), and nesting sites: cavity nester or not)] and the number of individuals/surveys in each season are shown. GE indicates generalists. BS and WS mean the breeding and wintering season, respectively. Shaded species were excluded from the analyses.

Species ID	Common and scientific name	Successional stage	Forest type	Cavity ?	Number of individuals		Number of surveys		Note
					BS	WS	BS	WS	
1	Siberian Meadow Bunting *Emberiza cioides*	EA			180		43		
2	Oriental Greenfinch *Carduelis sinica minor*	EA			75	2	41	2	Categorized as BL in WS
3	Olive-backed Pipit *Anthus hodgsoni*	EA			69		24		
4	Stejneger's stonechat *Saxicola stejnegeri*	EA			32		9		
5	Bull-headed Shrike *Lanius bucephalus*	EA			19		9		
6	Latham's Snipe *Gallinago hardwickii*	EA			16		10		
7	Common Cuckoo *Cuculus canorus*	EA			7		4		
8	Long-tailed Rosefinch *Uragus sibiricus*	EA			6		5		
9	Grey's Grasshopper Warbler *Locustella fasciolata*	EA			3		3		
10	Chestnut-eared Bunting *Emberiza fucata*	EA			1		1		
11	Siberian Rubythroat *Luscinia calliope*	EA			1		1		
12	Eastern Crowned Leaf Warbler *Phylloscopus coronatus*	MA	BL		628		110		
13	Asian Stubtail *Urosphena squameiceps*	MA	BL		261		72		
14	Nurcissus Flycatcher *Ficedula narcissina*	MA	BL	yes	202		76		
15	Brown Flycatcher *Muscicapa dauurica*	MA	BL		117		60		
16	Willow Tit *Parus montanus*	MA	BL	yes	96	596	40	43	
17	Oriental Cuckoo *Cuculus saturates*	MA	BL		89		53		
18	Treecreeper *Certhia familiaris*	MA	BL	yes	79	67	44	43	
19	Oriental Turtle Dove *Streptopelia orientalis*	MA	BL		79		50		
20	Siberian Blue Robin *Luscinia cyane*	MA	BL		73		37		
21	Japanese Tit *Parus minor*	MA	BL	yes	54	90	33	22	
22	Brown-eared Bulbul *Hypsipetes amaurotis*	MA	BL		53	48	33	21	

23	Brown-headed Thrush *Turdus chrysolaus*	MA	BL		51		31		
24	Hawfinch *Coccothraustes coccothraustes*	MA	BL		45	4	25	4	
25	Japanese Grosbeak *Eophona personata*	MA	BL		45		23		
26	Great Spotted Woodpecker *Dendrocopos major*	MA	BL	yes	42	48	35	38	
27	Japanese Pygmy Woodpecker *Dendrocopos kizuki*	MA	BL	yes	37	72	28	44	
28	Marsh Tit *Parus palustris*	MA	BL	yes	34	218	22	38	
29	Nuthatch *Sitta europaea*	MA	BL	yes	31	67	25	43	
30	Grey Thrush *Turdus cardis*	MA	BL		29		17		
31	Eurasian Wren *Troglodytes troglodytes*	MA	BL		27	1	13	1	
32	Long-tailed Tit *Aegithalos caudatus*	MA	BL		23	194	15	30	
33	Blue-and-white Flycatcher *Cyanoptila cyanomelana*	MA	BL		16		13		
34	Japanese Robin *Erithacus akahige*	MA	BL		16		8		
35	Grey Bunting *Emberiza variabilis*	MA	BL		12		9		
36	Japanese Green Pigeon *Sphenurus sieboldii*	MA	BL		12		10		
37	Eurasian Jay *Garrulus glandarius*	MA	BL		11	24	10	18	
38	White's Thrush *Zoothera dauma*	MA	BL		8		3		
39	Russet Sparrow *Passer rutilans*	MA	BL	yes	7		4		
40	Hazel Grouse *Tetrastes bonasia*	MA	BL		5	2	4	2	
41	Grey-headed Woodpecker *Picus canus*	MA	BL	yes	4	2	2	2	
42	White-backed Woodpecker *Dendrocopos leucotos*	MA	BL	yes	2	2	2	2	
43	Chestnut-cheeked Starling *Sturnus philippensis*	MA	BL	yes	2		1		
44	Japanese White-eye *Zosterops japonicus*	MA	BL		2		1		
45	Grey Wagtail *Motacilla cinerea*	MA	BL		2		2		
46	Black Woodpecker *Dryocopus martius*	MA	BL	yes	1	2	1	2	
47	Varied Tit *Parus varius*	MA	BL	yes	1	2	1	2	
48	Brambling *Fringilla montifringilla*	MA	BL			1730		3	
49	Eurasian Bullfinch *Pyrrhula pyrrhula*	MA	BL			39		19	
50	Dusky Thrush *Turdus eunomus*	MA	BL			33		8	
51	Crossbill *Loxia curvirostra*	MA	BL			19		3	Temporary migrant in BS
52	Pallas's Rosefinch *Carpoducus roseus*	MA	BL			2		2	
53	Raven *Corvus corax*	MA	BL			2		2	
54	Coal Tit *Parus ater*	MA	CO		347	931	88	62	

55	Goldcrest *Regulus regulus*	MA	CO	240	424	72	88	
56	Sakhalin Leaf Warbler *Phylloscopus borealoides*	MA	CO	100		36		
57	Red-flanked Bush-robin *Tarsiger cyanurus*	MA	CO	19		7		
58	Eurasian Siskin *Spinus spinus*	MA	CO	11	475	2	23	
	Black-faced Bunting *Emberiza spodocephala*	GE	GE	610		140		
	Japanese Bush Warbler *Horornis diphone*	GE	GE	182		72		
	Jungle Crow *Corvus macrorhynchos*							Urban species
	Carrion Crow *Corvus corone*							Urban species
	Grey Starling *Sturnus cineraceus*							Urban species
	Kamchatka leaf Warbler *Phylloscopus examinandus*							Temporary migrant
	Eurasian Woodcock *Scolopax rusticola*							Nocturnal species
	Sparrowhawk *Accipiter nisus*							Raptor
	Black Kite *Milvus migrans*							Raptor
	Eastern Buzzard *Buteo japonicus*							Raptor



Appendix S4.5. Relationships between stand variables (stand age and broad-leaved tree proportion within plantations) and abundance of Black-faced Bunting and Japanese Bush Warbler. Dots indicate the results of each survey.

The responses of both species were not obvious.

Appendix S4.6. Comparison across models using logarithmically transformed forms (Log forms) or quadratic forms of stand variables. For four combinations of stand age and broad-leaved tree proportion (Log-Log, Log Quadratic, Quadratic-Log, Log-Log), I made the full model of the GLMM and conducted model selection. Then, I compared AIC of best models. Each full model contained not only stand variables but also climates and the interaction terms between stand and climate variables, as explanatory variables.

Age	Broad	Breeding						Wintering	
		Broad SR	Broad AB	Cavity SR	Cavity AB	Early SR	Early AB	Broad SR	Broad AB
Log	Log	**801.6**	**1204.7**	**552.6**	758.1	344.3	548.5	599.7	914.5
Log	Quadratic	805.3	1208.3	553.5	759.2			**597.6**	**913.8**
Quadratic	Log	807.0	1207.0	552.9	**755.8**	**341.9**	**547.0**	605.7	919.2
Quadratic	Quadratic	811.4	1211.2	553.7	756.9			602.2	918.1

For early-successional species, Log forms showed higher performances, so I used Log form in the analyses.

For broad-leaved forest species in the breeding season, models using Log forms for both stand age and broad-leaved tree proportion showed lowest AIC, and for cavity nesters, all models were almost identical. For broad-leaved forest species in the wintering season, AIC was lower when using Log form for stand age, but all models were almost identical for broad-leaved tree proportion. Based on these results, I used Log forms for both stand variables in the analyses of broad-leaved forest species and cavity nester.

Appendix S4.7. Model selection with planted tree species effects (Todo fir compared to Japanese larch) for total abundance of broad-leaved forest species in plantations. Results in (a) the breeding season and (b) the wintering season. Each row corresponds to each model with AIC < 2, and the estimated values of the included explanatory variables, AIC and delta AIC (the difference in AIC from best model with lowest AIC; delta in the table) are shown. Abbreviations; Age: log(stand age), Broad: log(broad-leaved tree proportion + 1), Temp: the mean temperature in the survey season, Todo: Todo fir plantation. Colons represent the interactions. Blanks indicate that these variables were not included in the model.

(a) Breeding season

Intercept	Age	Broad	Temp	Todo	Age:Temp	Age:Todo	Broad:Temp	Broad:Todo	AIC	delta
-1.73	0.76	0.41							1204.70	0.00
-1.69	0.76	0.40	0.03						1206.43	1.73
-1.74	0.76	0.41		0.02					1206.68	1.98

(b) Wintering season

Intercept	Age	Broad	Snow	Temp	Todo	Age:Snow	Age:Temp	Age:Todo	Broad:Snow	Broad:Temp	Broad:Todo	AIC	delta
0.41	1.42	0.32	-0.22	0.13			0.48			-0.57		914.48	0.00
0.43	1.44	0.26		0.19			0.47			-0.60		914.55	0.07
0.31	2.02	-0.10	-0.43	0.01	0.12		0.54	-1.05	0.36	-0.58	0.78	914.67	0.18
0.38	1.38	0.36	-0.30	0.10			0.49		0.27	-0.53		914.90	0.42
0.38	1.99	-0.13	-0.30	0.07	0.09		0.51	-0.94		-0.64	0.71	915.26	0.77
0.32	1.76	0.30	-0.28	0.13	0.16		0.45	-0.63		-0.62		916.10	1.62
0.26	1.76	0.35	-0.38	0.08	0.19		0.47	-0.68	0.31	-0.57		916.11	1.63
0.36	1.38	0.38	-0.28	0.11		-0.17	0.44		0.35	-0.52		916.26	1.78
0.41	1.42	0.32	-0.22	0.13		-0.02	0.48			-0.57		916.47	1.99
0.43	1.42	0.32	-0.23	0.13	-0.03		0.48			-0.57		916.47	1.99

Appendix S4.8. Model selection for plantations in the breeding season [(a-c) early-successional species, (d-f) broad-leaved forest species, (g-i) cavity nester]. Results of (a, d, g) species richness, (b, e, h) total abundance, (c, f, i) species-level abundance. Each row corresponds to each model with AIC < 2, and the estimated values of the included explanatory variables, AIC and delta AIC (the difference in AIC from best model with lowest AIC; delta in the table) are shown. Abbreviations; Age: stand age, Age^2: the quadratic term of stand age, L_Age: log(stand age), L_Broad: log(broad-leaved tree proportion + 1), Temp: the mean temperature in the breeding season. Colons represent the interactions. Blanks indicate that these variables were not included in the model, and crosses indicate those were not considered (e.g., not included in the full models).

Plantations in the breeding season

Early-successional species

(a) Species richness

Intercept	Age	Age^2	Temp	Age:Temp	Age^2:Temp	AIC	delta
-1.32	-0.91	0.64	0.32		-0.26	341.85	0.00
-1.30	-0.90	0.64	0.23	-0.14	-0.25	341.86	0.01
-1.29	-0.95	0.59				342.35	0.50

(b) Total abundance

Intercept	Age	Age^2	Temp	Age:Temp	Age^2:Temp	AIC	delta
-1.14	-1.28	0.83	0.46		-0.31	546.99	0.00
-1.14	-1.26	0.85	0.40	-0.17	-0.29	547.49	0.49
-1.17	-1.33	0.77				548.74	1.75

(c) Species-level abundance

Intercept	Age	Age^2	Temp	Age:Temp	Age^2:Temp	AIC	delta
-6.59	-2.75	1.35		×		1212.94	0.00
-6.95	-2.69	1.48	-0.49	×		1213.03	0.09

Broad-leaved forest species

(d) Species richness

Intercept	L_Age	L_Broad	Temp	L_Age:Temp	L_Broad:Temp	AIC	delta
-1.05	0.53	0.24				801.57	0.00
-1.08	0.53	0.25	-0.02			803.28	1.71

(e) Total abundance

Intercept	L_Age	L_Broad	Temp	L_Age:Temp	L_Broad:Temp	AIC	delta
-1.73	0.76	0.41				1204.70	0.00
-1.69	0.76	0.40	0.03			1206.43	1.73

(f) Species-level abundance

Intercept	L_Age	L_Broad	Temp	L_Age:Temp	L_Broad:Temp	AIC	delta
-7.19	1.00	0.54	-0.29	×	×	6553.12	0.00
-6.32	0.92	0.44		×	×	6553.46	0.34

Cavity nester

(g) Species richness

Intercept	LAge	L_Broad	Temp	L_Age:Temp	L_Broad:Temp	AIC	delta
-2.61	0.56	0.33				552.65	0.00
-2.69	0.57	0.35	-0.06			553.91	1.25
-2.74	0.56	0.38	0.55	-0.16		554.12	1.46

(h) Total abundance

Intercept	L_Age	L_Broad	Temp	L_Age:Temp	L_Broad:Temp	AIC	delta
-3.38	0.82	0.42				758.09	0.00
-3.29	0.81	0.40	0.06			759.66	1.56

(i) Species-level abundance

Intercept	L_Age	L_Broad	Temp	L_Age:Temp	L_Broad:Temp	AIC	delta
-6.38	0.82	0.60		×	×	2016.79	0.00
-6.42	0.82	0.60	-0.10	×	×	2018.36	1.57

Appendix S4.9. Responses of each species to explanatory variables in plantations in the breeding season [(a) early-successional species, (b) broad-leaved forest species, (c) cavity nester]. I calculated these values by summing the fixed effects and the random intercept/slopes, derived from the best models of GLMM with abundance of each species as response variables. Abbreviations; Age: stand age, Age^2: the quadratic term of stand age, L_Age: log(stand age), L_Broad: log(broad-leaved tree proportion + 1), Temp: the mean temperature in the breeding season. Colons represent the interactions. See details of species ID in Appendix S4.4.

(a) Early-successional species

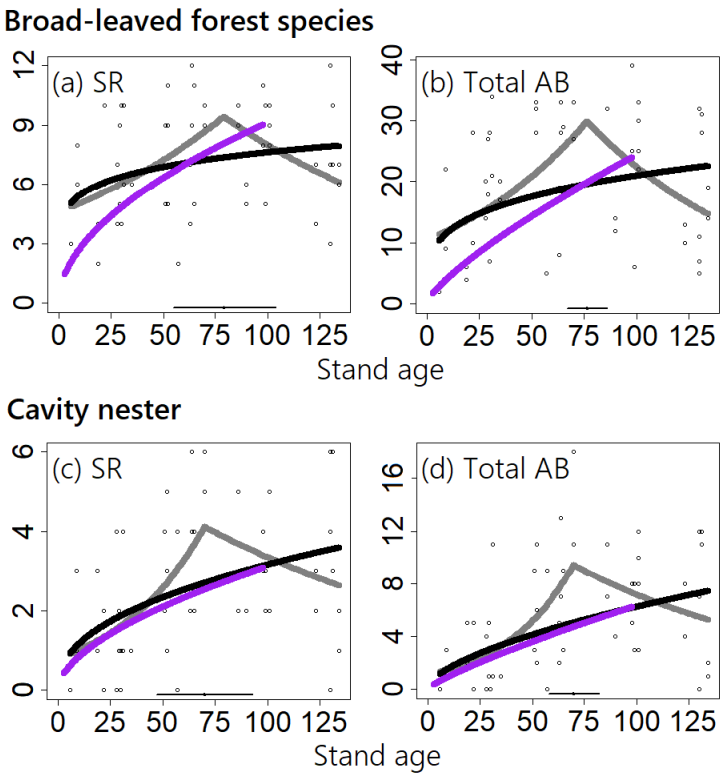
Species ID	Intercept	Age	Age^2	Temp	Age^2:Temp
1	-3.04	-2.06	0.91	1.04	-0.17
2	-2.44	-0.70	0.69	1.50	-0.38
3	-4.23	-1.39	0.95	-1.75	-1.75
4	-10.40	-4.96	2.01	-1.27	0.41
5	-7.21	-2.95	1.44	-0.15	0.04
6	-6.61	-1.52	1.21	-2.00	-0.26
8	-10.09	-3.95	1.86	0.15	0.29

(b) Broad-leaved forest species

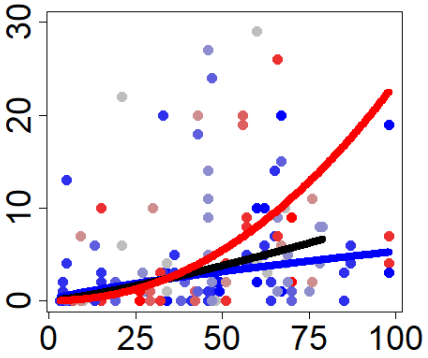
Species ID	Intercept	L_Age	L_Broad	Temp
12	-4.23	0.95	0.55	0.08
13	-6.85	1.25	0.63	0.47
14	-6.87	1.05	0.78	0.56
15	-5.81	1.05	0.39	0.30
16	-4.52	1.02	0.02	-0.23
17	-5.97	0.77	0.69	-0.06
18	-8.32	1.38	0.66	-0.33
19	-2.94	0.25	0.35	-0.04
20	-6.25	1.49	-0.12	0.28
21	-9.58	1.40	0.88	-0.20
22	-2.84	0.28	0.17	0.13
23	-3.79	0.54	0.15	-0.30
24	-2.41	0.11	0.14	-0.40
25	-2.51	-0.18	0.48	0.27
26	-5.53	0.62	0.53	-0.04
27	-7.21	0.95	0.62	-0.30
28	-7.51	0.54	1.11	-0.46
29	-7.07	0.96	0.51	-0.39
30	-7.55	1.27	0.22	0.56
31	-17.07	2.28	1.27	-2.76
32	-5.43	0.68	0.23	0.43
33	-7.48	1.12	0.27	-0.04
34	-16.60	1.62	1.65	-2.93
35	-7.96	1.26	0.19	-0.17
36	-8.27	0.95	0.60	-0.65
37	-8.80	1.23	0.40	-0.71

(c) Cavity nester

Species ID	Intercept	L_Age	L_Broad	Temp
14	-6.73	1.00	0.75	0.67
16	-4.55	1.21	-0.22	-0.16
18	-6.22	1.12	0.31	-0.04
21	-6.99	0.83	0.76	0.01
26	-6.06	0.65	0.63	-0.08
27	-6.25	0.72	0.59	-0.21
28	-7.15	0.45	1.05	-0.17
29	-6.02	0.70	0.51	-0.34



Appendix S4.10. Effects of stand age of natural forests on broad-leaved forest species in the breeding season [(a-b) broad-leaved forest species, (c-d) cavity nester], and the comparison with those of plantations. Results of (a,c) species richness and (b,d) total abundance. Each dot represents the observed values in each survey of natural forests, and black and purple solid lines indicate the predicted values derived from the best model of GLMM for natural forests and plantations, respectively. Grey lines indicated the predicted value from the segmented regression for natural forests. In each models, the other explanatory variables were fixed to mean values [(models for natural forests) broad-leaved tree proportion: 90.09 %, the mean temperature in the breeding season: 13.55 ºC, (for plantations) broad-leaved tree proportion: 30.81 %, the temperature: 13.40 ºC].



Appendix S4.11. Effects of stand age on broad-leaved forest bird species in plantations in the wintering season. This is the enlarged Fig. 4.2b in range of abundance from 0 to 30. See details in Fig. 4.2.

Appendix S4.12. Model selection for broad-leaved forest species in plantations in the wintering season [(a) species richness, (b) total abundance, (c) species-level abundance]. Each row corresponds to each model with AIC < 2, and the estimated values of the included explanatory variables, AIC and delta AIC (the difference in AIC from best model with lowest AIC; delta in the table) are shown. Abbreviations; L_Age: log(stand age), L_Broad: log(broad-leaved tree proportion+1), Snow: the snow depth in each survey, Temp: the mean temperature in the wintering season. Colons represent the interactions. Blanks indicate that these variables were not included in the model, and crosses indicate those were not included in the full models.

Plantations in the wintering season

Broad-leaved forest species

(a) Species richness

Intercept	L_Age	L_Broad	Snow	Temp	L_Age:Snow	L_Age:Temp	L_Broad:Snow	L_Broad:Temp	AIC	delta	weight
0.25	0.78	0.39		0.16		0.33		-0.46	599.73	0.00	0.28
0.24	0.77	0.41	-0.10	0.13		0.34		-0.45	600.40	0.67	0.20
0.21	0.75	0.45	-0.17	0.11		0.34	0.18	-0.42	600.49	0.76	0.19

(b) Total abundance

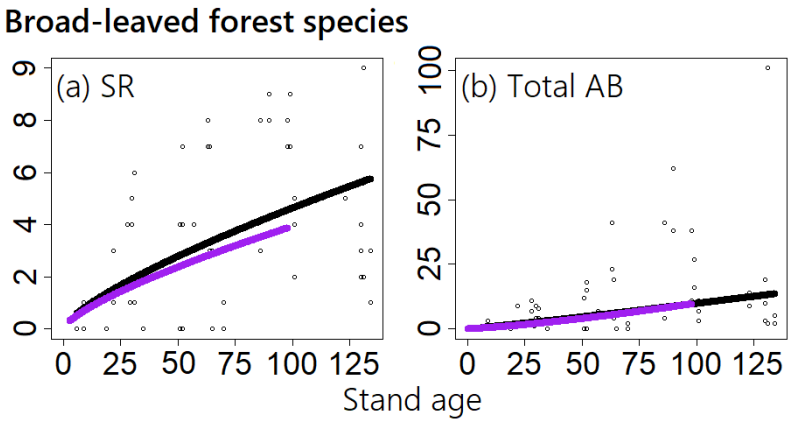
Intercept	L_Age	L_Broad	Snow	Temp	L_Age:Snow	L_Age:Temp	L_Broad:Snow	L_Broad:Temp	AIC	delta	weight
0.41	1.42	0.32	-0.22	0.13		0.48		-0.57	914.48	0.00	0.13
0.43	1.44	0.26		0.19		0.47		-0.60	914.55	0.07	0.12
0.38	1.38	0.36	-0.30	0.10		0.49	0.27	-0.53	914.90	0.42	0.10
0.36	1.38	0.38	-0.28	0.11	-0.17	0.44	0.35	-0.52	916.26	1.78	0.05
0.41	1.42	0.32	-0.22	0.13	-0.02	0.48		-0.57	916.47	1.99	0.05

(c) Species-level abundance

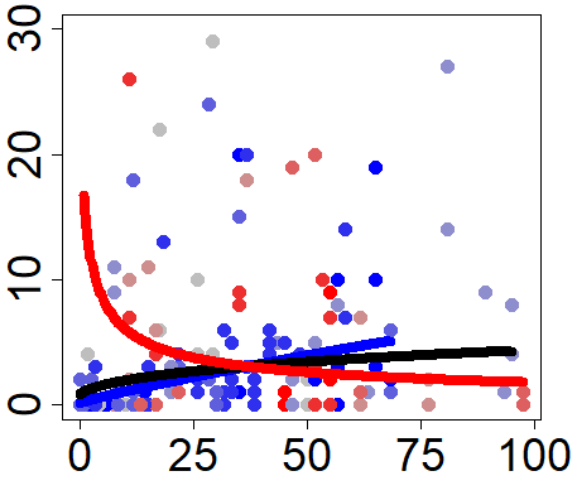
Intercept	L_Age	L_Broad	Snow	Temp	L_Age:Snow	L_Age:Temp	L_Broad:Snow	L_Broad:Temp	AIC	delta	weight
-3.40	1.97	0.72	-0.51		×		×		4043.16	0.00	0.26
-3.35	1.92	0.71	-0.48	0.32	×		×	-0.40	4044.63	1.47	0.12
-3.42	2.02	0.72	-0.50	0.12	×		×		4044.77	1.62	0.12

Appendix S4.13. Responses of each species of broad-leaved forest species to explanatory variables in plantations in the wintering season. I calculated these values by summing the fixed effects and the random intercept/slopes, derived from the best models of GLMM with abundance of each species as response variables. Abbreviations; Age: stand age, Age^2: the quadratic term of stand age, L_Age: log(stand age), L_Broad: log(broad-leaved tree proportion + 1), Snow: the snow depth at each survey, Temp: the mean temperature in the wintering season. Colons represent the interactions. See details of species ID in Appendix S4.4.

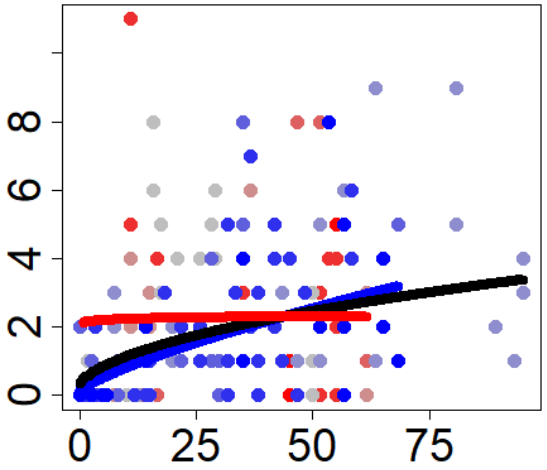
Species ID	Intercept	L_Age	L_Broad	Snow	Temp	L_Age:Temp	L_Borad:Temp
16	-1.17	2.62	-0.20	0.13	-0.25	0.12	0.10
18	-3.25	1.84	0.95	-0.69	-0.10	0.09	0.06
21	-5.12	4.62	0.82	-0.37	0.41	-0.63	0.46
22	-2.97	1.28	0.40	-0.65	-0.52	0.15	0.20
26	-2.84	0.91	0.85	-0.20	-0.41	0.35	0.08
27	-2.66	0.92	1.09	-0.20	-0.16	0.62	-0.26
28	-3.29	3.01	0.62	-0.98	0.44	0.06	-0.38
29	-3.74	2.38	0.85	-0.89	0.35	-0.37	-0.05
32	-1.90	0.86	1.27	-0.61	0.36	0.34	-0.61
37	-3.35	0.90	0.21	-0.19	0.37	-0.42	-0.36
49	-2.69	0.12	0.36	0.46	-0.13	0.04	-0.17
50	-3.98	0.62	1.47	-1.68	-0.45	0.82	-0.22



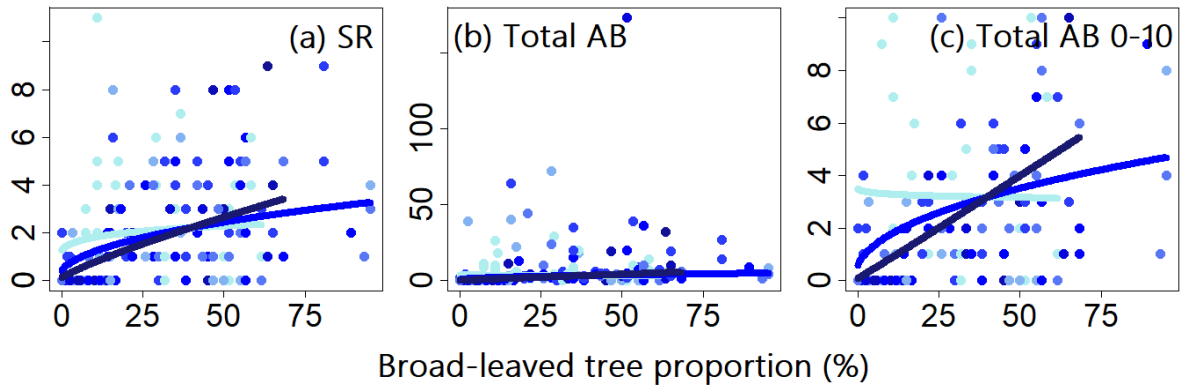
Appendix S4.14. Effects of stand age of natural forests on broad-leaved forest species in the wintering season [(a) species richness, (c-d) total abundance], and the comparison with those of plantations. In each model, the other explanatory variables were fixed to mean values [(models for natural forests) broad-leaved tree proportion: 89.99 %, (for plantations) broad-leaved tree proportion: 31.03 %, the mean temperature in the wintering season: −6. 38 ºC]. See details in Appendix S4.10.



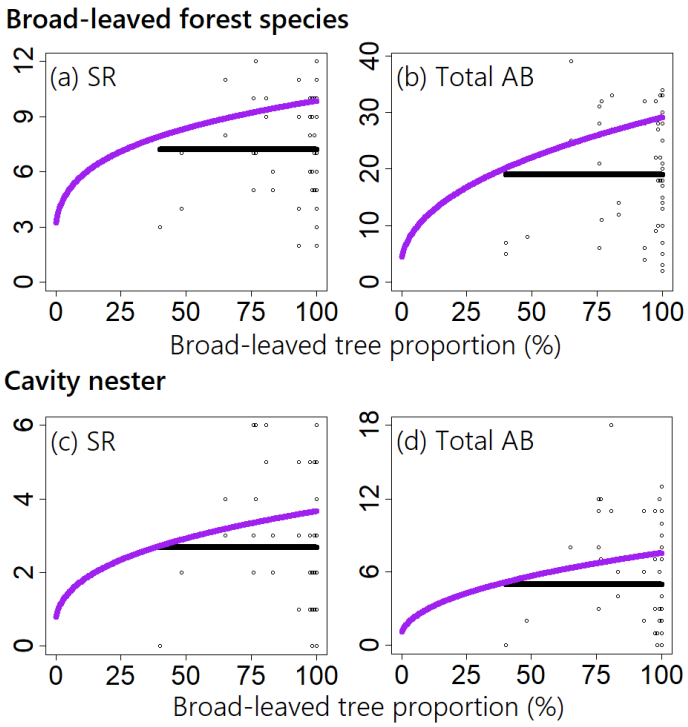
Appendix S4.15. Effects of broad-leaved tree proportion (horizontal axis) on abundance of broad-leaved forest bird species (vertical axis) in plantations in the wintering season. This is the enlarged Fig 4.4b in range of abundance from 0 to 30. See details in Fig 4.4.



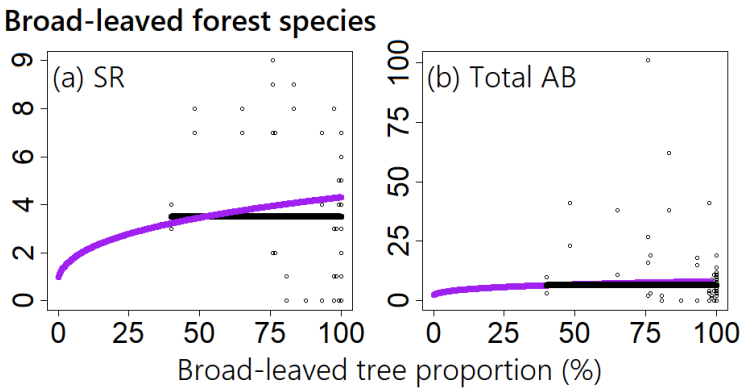
Appendix S4.16. Temperature-dependent effects of broad-leaved tree proportion (horizontal axis) on species richness of broad-leaved forest species (vertical axis) in the wintering season in the sensitivity analysis. The interaction with the mean temperature in the wintering season, the differences in the temperature were shown by colors [blue: 5th percentile (−8.17 ºC), black or grey: median (−6.73 ºC), red: 95th percentile (−3.90 ºC)]. The other explanatory variables were fixed to mean values in each figure (stand age: 39.13, snow depth: 83.19 cm). See details in Fig. 4.4.



Appendix S4.17. Snow depth-dependent effects of broad-leaved tree proportion on broad-leaved forest species in the wintering season in the sensitivity analyses. Dots and solid lines indicate data collected at each survey and the estimates afforded by the best GLMMs, respectively. The interaction with the snow depth, the differences in the snow depth were shown by colors [light blue: 5th percentile (4.41 cm), blue: median (83.25 cm), dark blue: 95th percentile (175.79 cm)]. The other explanatory variables were fixed to mean values in each figure (stand age: 39.13, the mean temperature in the wintering season: −6.46 ºC).



Appendix S4.18. Effects of broad-leaved tree proportion within natural forests on broad-leaved forest species in the breeding season [(a-b) broad-leaved forest species, (c-d) cavity nester], and the comparison with those of plantations. Results of (a,c) species richness and (b,d) total abundance. Each dot represents the observed values in each survey of natural forests, and black and purple solid lines indicate the predicted values derived from the best model of GLMM for natural forests and plantations, respectively. In each model, stand age was fixed to the mean value in natural forests (68.07 years). In models for natural forests, the mean temperature was fixed to mean values in natural forests (13.55 ºC).



Appendix S4.19. Effects of broad-leaved tree proportion within natural forests on broad-leaved forest species in the wintering season, and the comparison with those of plantations. Results of (a) species richness and (b) total abundance. In each model, stand age was fixed to the mean value in natural forests (68.07 years). In models for natural forests, the mean temperature was fixed to mean values in natural forests (−6.46 ºC). See details in Appendix S4.18.

Chapter 5 --- General discussion and conclusion

In Chapter 2, I revealed that the species richness of forest birds and early-successional birds differed among regions and seasons. Cool regions or highlands were important as breeding grounds, and warm regions with little snow or lowlands had also important roles as wintering sites. In Chapter 3, I showed that the function of plantations in Japan for biodiversity conservation varied depending on the planted tree species and season. Specifically, I found that the habitat function of plantations was higher when planting pine family species (e.g., Japanese larch, Todo fir, and Japanese red pine) rather than cypress family (cedar and cypress), and in the wintering season than in the breeding season. In Chapter 4, focusing on bird communities in Todo fir and Japanese larch plantations across Hokkaido, results revealed as follows: 1) the species richness and abundance of early-successional species in the breeding season were high in younger plantations, but the duration as habitats was shorter in cooler regions; 2) in the breeding season, the richness and abundance of broad-leaved forest species increased with stand age, and increased with broad-leaved tree proportion within plantations until 25-50%, but remained almost unchanged above the thresholds values; 3) for this group in the wintering season, in regions with more severe climates, the positive effects of stand age were weaker, and the positive effects of the broad-leaved tree proportion were more obvious. Based on these results, I discuss the plantation management to conserve biodiversity considering regionality and seasonality, and show the future directions.

5.1 Biodiversity conservation in plantations across Japan

Cool regions (i.e., northern Japan and highlands) were important for both forest and early-successional birds in the breeding season (Chapter 2). Pine family plantations which occur widely in these regions had the high function for biodiversity conservation (Chapter 3). Moreover, in Hokkaido in the breeding season, young plantations of Todo fir and Japanese larch functioned as habitats for early-successional species, and mature plantations with 25% or more of the broad-leaved tree proportion served as suitable habitats for broad-leaved forest species (Chapter 4). Results on the effects of these stand variables were coincident to those from previous studies on many taxa including birds, insects, and plants in Japanese larch plantations in many regions, e.g., Hokkaido, Iwate, Nagano, and Yamanashi prefectures (Nagaike et al. 2003; Yoshida et al. 2005; Ohsawa 2007; Yamaura et al. 2008; Yamaura et al. 2012b). In addition, recent studies showed that cool regions and highlands hold more old natural forests, and the amount of broad-leaved trees within plantations was also higher in these regions (Yamaura et al. 2019; Yamaura et al. 2020). Therefore, reconciling both forestry and conservation of both forest and early-successional species in these regions would be achieved by retaining abundant broad-leaved trees within and surrounding plantations and avoiding extremely short- or long-rotation forestry (e.g., using multiple-rotation forestry; Lindenmayer & Franklin 2002). In eastern Hokkaido, younger plantations were used by early-successional species whose Japanese populations breed mainly in Hokkaido (the Latham's Snipe, the Stejneger's stonechat, and the Long-tailed Rosefinch *Uragus sibiricus*; Biodiversity Center of

Japan 2004), and the Olive-backed Pipit that is recently decreasing (Bird Atlas Japan 2019), although the duration as early-successional habitats was shorter. In regions where BL forest species can be adequately conserved in abundant natural forests, or where young plantations have important roles for population size of early-successional species, short-rotation forestry can be effective conservation means.

By contrast, southern Japan and lowlands, with high temperature and less snow, were important wintering grounds (Chapter 2). Plantations of cedar and cypress, which are abundant in such regions, had generally the low function for biodiversity conservation; however, there were also many studies showing opposite patterns in the meta-analysis and the analysis on publication bias suggested the presence of unpublished studies with higher species richness in plantations (Chapter 3). These results indicated the room for improving the habitat function of cypress family plantations. Indeed, thinning and long-rotation forestry can promote the recruitment and growth of broad-leaved trees in cypress family plantations (Utsugi et al. 2006; Igarashi & Kiyono 2008; Yamaura et al. 2019). Furthermore, studies on vertebrates including birds in plantations were scarce in southern Japan, although the habitat function of plantations was higher in the wintering season than in the breeding season (Chapter 3). In future studies, the effects of stand age and the amount of broad-leaved trees, or the function as wintering habitats should be clarified for cypress family plantations, which account for 70% of plantation areas in Japan.

5.2 Importance of studying in winter

The effects of landscape context (surrounding habitat amount), forest type (natural forests/plantations), and stand variables (stand age and the broad-leaved tree proportion within plantations) were different between the breeding and wintering seasons, suggesting the importance of considering seasonality in various scales (Chapter 2-4). The effects of landscape context and forest type were less obvious in the wintering season than in the breeding season (Chapter 2-3). These patterns were also reported in previous studies (e.g., Yahner 2000). The effects of stand variables on bird communities in the wintering seasons differed depending on regional winter climates across Hokkaido; the positive effects of stand age were weaker and the positive effects of the broad-leaved tree proportion were stronger in colder regions (Chapter 4). Moreover, the variation in bird density among stands was larger in winter. Specifically, many birds occurred in any plantations in the breeding season, but there were stands with almost no birds in the wintering seasons. In the wintering season in cold regions, local environments may be more important for birds, likely because of prey resources and strategy for predator or micro/temporary climates, rather than the habitat amount or type that are commonly used in macroecological analyses (Walther & Gosler 2001; Yoshikawa et al. 2017; Latimer & Zuckerberg 2019).

For migratory birds, improving wintering environments in warm regions would lead to the recovery of breeding populations in cool regions, vice versa (Norris et al. 2004; La Sorte et al. 2017; Dokter et al. 2018). Moreover, the effects across regions and seasons may influence

communities and ecological functions (Bauer & Hoye 2014). Given the high proportion of migrants to breeding bird communities in cool regions (Chapter 2, 4), the increase in population size of migrants mean the increase in total abundance of breeding bird communities in cool regions, likely leading to higher ecological functions of birds (Fristoe 2015). Furthermore, it is possible that birds in the wintering season have specific function. For instance, bird predation on insects in the wintering season, when insect abundance is low, may have pest control function different from those in the breeding season (Gibb et al. 1960; Higashiura 1989). The seed dispersal function via bird foraging fruits and seeds from autumn to winter cannot be substituted by birds in other seasons (Hirata et al. 2006; Yoshikawa & Osada 2015). Proceeding studies in the wintering season would enable to understand the role of plantations for maintaining biological communities, especially animals with high mobility, but also their prey (e.g., invertebrates and plants) throughout the year.

5.3 Toward plantation management for biodiversity conservation with consideration for regionality and seasonality

Climates affect organism distributions not only directly via the physiology, such as maintaining body temperature (Cooper et al. 2006), but also indirectly via prey resources, vegetation, or disturbances (Huston & Wolverton 2009; Yamaura et al. 2011; Betts et al. 2019). Results from Chapter 2-4 suggested that its effects and processes differed depending on the spatial scale and the season. Considering these differences would be important for conserving animal

communities in multiple seasons at multiple scales, such as a country, regions, and stands. The analysis for existing macro-scale data are suitable for quantifying regionality and seasonality in animal distributions and examining thereof determining factors (Chapter 2-3). On the other hand, for the large-scale survey, selecting survey sites with low correlation among variables allow us to analyze the relative importance of variables and their interactions (Kawamura et al. 2016; Chapter4). The approach taking advantages of both the analysis on the existing macro-scale data and the large-scale survey focusing on local variables enables to plan local-scale conservation considering macroecological environments.

In this thesis, I revealed the importance of climates as the drivers of regionality and seasonality in bird communities of Japan (Chapter 2), and the high potential of pine family plantations in cool regions for biodiversity conservation (Chapter 3). Then, considering regional climates and the interaction with stand variables, I proposed bird conservation methods for Todo fir and Japanese larch plantations in each region across Hokkaido (Chapter 4). For conservation of broad-leaved forest birds in the breeding season, it would be desirable to manage that the broad-leaved tree proportion within plantations is at least 25%. To conserve early-successional birds in the breeding season, short-rotation forestry is likely to be effective, especially in cool regions where the duration as a habitat was shorter (e.g., eastern Hokkaido). Additionally, broad-leaved forest birds in the wintering season can be conserved by enhancing the broad-leaved proportion within plantations in regions with severe climates, and by long-rotation forestry in regions with mild climates. In Japan where vast plantations are expanded across the

country, surveying plantation biodiversity at a large scale in both the breeding and wintering seasons are necessary to effectively conserve forest biodiversity considering the differences in climates and seasons.

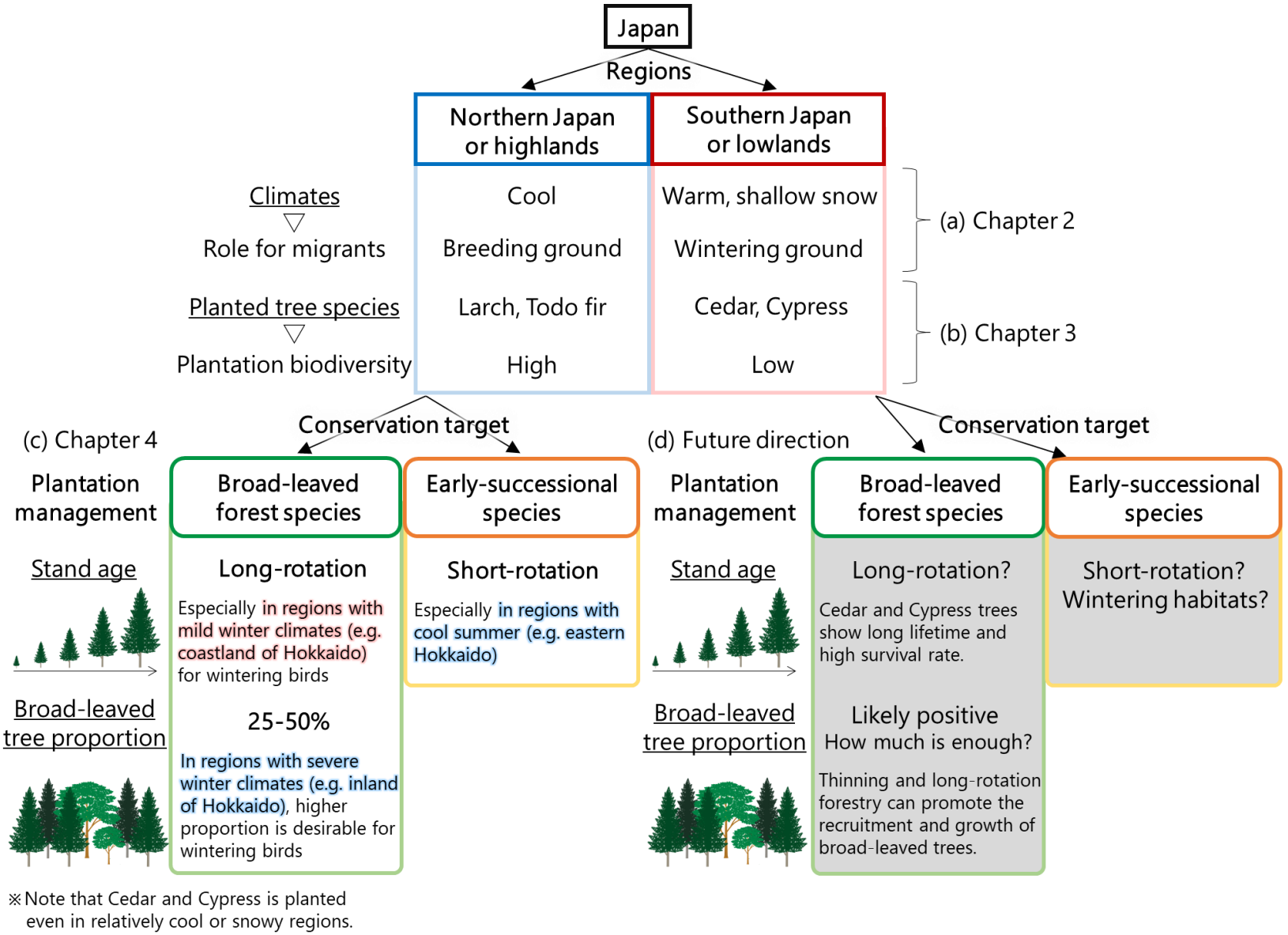

Japan
Regions
Northern Japan or highlands
Southern Japan or lowlands
Climates
Role for migrants
Cool
Breeding ground
Warm, shallow snow
Wintering ground
(a) Chapter 2
Planted tree species
Plantation biodiversity
Larch, Todo fir
High
Cedar, Cypress
Low
(b) Chapter 3
Conservation target
(c) Chapter 4
Plantation management
Broad-leaved forest species
Early-successional species
Stand age
Long-rotation
Especially in regions with mild winter climates (e.g. coastland of Hokkaido) for wintering birds
Short-rotation
Especially in regions with cool summer (e.g. eastern Hokkaido)
Broad-leaved tree proportion
25-50%
In regions with severe winter climates (e.g. inland of Hokkaido), higher proportion is desirable for wintering birds
※Note that Cedar and Cypress is planted even in relatively cool or snowy regions.
(d) Future direction
Conservation target
Plantation management
Broad-leaved forest species
Early-successional species
Stand age
Long-rotation?
Cedar and Cypress trees show long lifetime and high survival rate.
Short-rotation?
Wintering habitats?
Broad-leaved tree proportion
Likely positive
How much is enough?
Thinning and long-rotation forestry can promote the recruitment and growth of broad-leaved trees.

Fig. 5.1. Graphical summary of this thesis. (a) Chapter 2: Across Japan, the seasonal roles as bird habitats differed depending on regional climates. (b) Chapter 3: In addition, the function of biodiversity conservation in plantations also differed depending on planted tree species used in each region. (c) Chapter 4: In plantations of Japanese larch (Larch in the figure) and Todo fir in northern Japan and highlands, which are expected to serve as bird breeding sites, long-rotation forestry and managing the broad-leaved tree proportion within plantations to be 25-50% were suggested to be important means for conserving broad-leaved forest species. These methods were also basically effective in the wintering season; however, the magnitude of those effects in this season differed among regions in Hokkaido. Moreover, when conserving early-successional species in these plantations, short-rotation forestry would be effective. To conserve both forest and early-successional species within a landscape, avoiding extremely short- or long-rotation forestry across the landscape are needed. (d) Future direction: Not only in Hokkaido, but also in other regions, including southern Japan where abundant plantations of cedar and cypress are expected to function as wintering habitats, the effects of stand age and the broad-leaved tree proportion on bird communities in multiple seasons are necessary to explore.

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