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Title: Comparable benefits of land sparing and sharing indicated by bird responses to stand-level plantation intensity in Hokkaido, northern Japan

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Abstract

We examined potentially contrasting conservation benefits of land sparing (land-use specialization) and land sharing (multiple-use forestry) strategies in forested landscapes by investigating relationships between bird functional group densities and basal areas of coniferous trees (an index of plantation intensity) in Sakhalin fir (*Abies sachalinensis*) and Sakhalin spruce (*Picea glehnii*) plantations. Densities of most bird functional groups increased with decreasing plantation intensity in both plantation types. In many cases, linear models were best for descriptors of bird density–plantation intensity relationships, but statistical support of linear and nonlinear (quadratic) models was similar. This outcome indicates that ecological benefits of land sparing and land sharing are potentially comparable in the plantations we studied. In real landscapes, land-use decision making depends on a variety of factors other than biodiversity conservation (e.g., social and biophysical factors). Furthermore, niche theory also predicts that population densities could linearly respond to environmental gradients. When density–intensity relationships are linear, as in this study, land-sparing and land-sharing strategies provide similar benefits in terms of biodiversity conservation, and contrasting land-use strategies would be flexibly chosen to enhance the accommodation of biodiversity conservation to resource production.

KEY WORDS: broad-leaved trees; conifer plantations; land-use intensity; planted forest; response diversity

Introduction

Increasing human demands and consumptions of global natural resources are now the leading threats to the world's biodiversity (Dullinger *et al.* 2013; Ellis & Ramankutty 2008). How do we reconcile the use of natural resources with biodiversity conservation? Green *et al.* (2005) proposed a theoretical approach that examines land uses in a way that allows both biodiversity conservation and resource production; this proposal has generated great interest (e.g., Fischer *et al.* 2008). Within this framework, Green *et al.* (2005) considered two contrasting strategies for landscape use. One is an integration of biodiversity conservation and resource production on the same land, i.e., the land-sharing strategy (Phalan *et al.* 2011). Under this scheme, although the large area of target landscape is managed for resource production, the ecological impacts of production on biodiversity are minimized on a per-production area basis (also called "wildlife friendly farming" in agricultural landscapes: Green *et al.* 2005). In the alternate strategy, the spatial extent of resource production areas is minimized, and these areas are exploited as intensively as possible; this approach is known as the land-sparing strategy (Green *et al.* 2005). The land-sparing strategy conserves biodiversity by establishing areas free of production activity (e.g., a nature reserve) at the price of lost biodiversity in the production area (thus, land is spared for nature).

Should we spare land for nature or share land with nature? Within the theoretical model of Green *et al.* (2005), focal species are classified into those for which the optimal conservation strategy is land sparing and those for which land sharing is optimal. Classification of focal species in this way is based on functional relationships between species densities and land-use intensity or resource yields (Green *et al.* 2005; Phalan *et al.* 2011). Graphical plots of density responses on land-use intensity are divided into two classes: concave and convex curves. When the density–intensity relationship tracks a concave plot (i.e., density declines more steeply at a low level of the intensity), a species is classified as a

‘sparing best species’; when the plot is convex (i.e., density declines only at a high level of the intensity), a species is classified as a ‘sharing best species’ (Green *et al.* 2005). However, there may be a third relationship wherein wildlife density is linearly and negatively related to land-use intensity. Wildlife population density often responds linearly to environmental gradients (e.g., Austin 2002; Van Horne 2002). When this is the case for land-use intensity, the relative conservation benefits of land sparing and land sharing would be equivalent. When densities respond linearly to land-use intensity in real landscapes where a wide range of factors other than biodiversity conservation affect land-use decision making (e.g., social and biophysical factors: Fischer *et al.* 2008), the use of dichotomic models to identify single optimal conservation schemes is perhaps simplistic (cf. Wiens 2007), and other feasible conservation schemes may be considered for specific landscapes.

As the global demand for wood products is increasing rapidly, forestry plantations are expanding around the world (FAO 2010). Plantations have fewer plant species and simpler vertical structures than do natural forests, with negative effects on biological diversity (Gibson *et al.* 2011; Moore & Allen 1999). Thus, enhancement of stand complexity in plantations through retention of naturally occurring live or standing dead trees at the price of reduced wood production has been recommended (i.e., a land-sharing strategy: Brockerhoff *et al.* 2008; Hartley 2002). A contrasting strategy has also been recommended. Establishment of new intensive plantations would give protection from harvesting to remaining natural forests in the landscape (i.e., land sparing: Paquette & Messier 2010; Sedjo & Botkin 1997). These two contrasting views of forestry plantations (land-sparing vs. -sharing paradigms) raise issues of recent concern (Lindenmayer *et al.* 2012; Yamaura *et al.* 2012). However, although studies on the relative merits of the land sparing and sharing have been conducted in agricultural landscapes (e.g., Chandler *et al.* 2013; Hodgson *et al.* 2010), to our knowledge, the two approaches have yet to be considered for forested terrain (but see Edwards *et al.*

2014).

In this study, we examined functional relationships between bird density and the intensity of plantation forestry. Across the plantation–natural forest continuum, as a first step, we used the mature aged-plantation stands (31-49 years old), and basal area of planted conifers as an index of the intensity of the plantation enterprise because this index had a clear negative relationship with basal areas of broad-leaved trees in our surveyed sites (Fig. S1). Coniferous trees have fewer food resources (arthropods) and nesting cavities for birds than do broad-leaved trees (Chey *et al.* 1998; Newton 1994). We therefore predicted that densities of bird functional groups other than those with preferences for habitat associated with coniferous trees would decrease with increased plantation intensity.

Materials and methods

Study area

The study was conducted in Sakhalin fir (*Abies sachalinensis*) and Sakhalin spruce (*Picea glehnii*) plantations in the Chitose National Forest, located toward the eastern end of Lake Shikotsu in central Hokkaido, northern Japan (42°44'~42°50'N, 141°22'~141°37'E). For plantations, we used mature aged-stands to control stand structure and composition (Table S1). The study area was flat terrain, and we were able to select stands with similar conditions other than plantation intensity. *Abies sachalinensis* and *P. glehnii* are evergreen conifers that are major tree species in plantations on Hokkaido. The present natural forest in this region is deciduous broad leaved forest; it comprises Japanese oak (*Quercus crispula*), painted maple (*Acer momo*), monarch birch (*Betula maximowicziana*), Japanese maple (*Acer palmatum* var. *matsumurae*), and Korean whitebeam (*Sorbus alnifolia*). Mean temperature in the area was

6.7°C (1981–2010) and total precipitation was 1766 mm in 2010 at the Shikotsukohan metrological station. The elevation was approximately 290 m at the surface of Lake Shikotsu.

Sampling sites

We selected 25 survey sites (11 fir, 10 spruce, and 4 natural forest stands; 20 ± 9 ha (mean $\pm$ SD) and >5 ha; Table S1) with various proportions of broad-leaved trees (6–100%). The sites were chosen using aerial photographs and field surveys (Table S1). Proportions of conifers were quite low in four natural stands (0–2% in three stands and 24% in one), and accordingly, we categorized them as stands with the lowest plantation intensities. To avoid experimental confounding, sampling sites were spaced at least 500 m from one another.

Bird surveys

Birds were surveyed using the line-transect method (Bibby *et al.* 2000). One 200-m transect was established in each tree stand, and bird individuals were counted four times between sunrise and 09:00 in June 2012 (i.e., during the breeding season) under appropriate weather conditions. Individuals within a band of 50-m width on either side of each transect were identified and counted. As detectability rates for birds are high in the 3 hours after sunrise (Ralph *et al.* 1993), we conducted surveys in each stand at least once during this time window. Because it was difficult to visually distinguish marsh tit (*Poecile palustris*) from willow tit (*Poecile montanus*) in the field, these two species were pooled as marsh tits. For each stand, the maximum value among four recorded abundance during four stand visits was used as the index of species abundance for each bird species in each stand (Hausner *et al.* 2003; Yamaura 2013).

Vegetation survey

We conducted vegetation surveys in each sampling site from September to October 2012. First, we deployed five 5.64-m-radius sampling plots (100 m² in area) at intervals of 50 m along the bird survey line in each stand. When vegetation on the transect lines was disturbed (e.g., by trampling), sampling plots were moved 15 m from the transect lines. We identified all trees ≥ 1.3 m tall (excluding woody vines) to species in all sampling plots and recorded their diameters at breast height, the tree height, and the height of the crown base. Basal areas of trees were calculated from the diameters at breast height; the basal area of conifers in stands was used as an index of plantation intensity.

Bird categories

Bird species observed in the field were classified into six functional groups based on published reports (Fujimaki 2012; Yamaura *et al.* 2008a: Table S2). We first classified birds into categories of canopy foragers, cavity nesters, and flycatchers. Some species were assigned into multiple categories, for example, Narcissus flycatcher *Ficedula narcissina* is a flycatcher that nests in cavities. These groups are sensitive to forestry practices (Lindenmayer *et al.* 2002; Yamaura *et al.* 2008a). We excluded species with preferences for habitat associated with coniferous trees (hereafter ‘conifer species’) and analyzed them separately from other groups because their population size typically increases in conifer plantations (Yamaura *et al.* 2009). We recognized a ‘forest species’ group composed of the four preceding groups and non-classified species. We also grouped ‘broad-leaved species’ by excluding conifer species from the forest species. Four grassland species and one temporary migrant species were excluded from the analyses (Table S2).

Statistical analysis

Although generalized linear models (GLMs) with Poisson error distributions and log-link functions are standard analytical methods for count data, they are unsuitable for determining whether the shape of a function is linear. We therefore constructed linear models (LMs) with the ordinary least squares method (i.e., normal error distribution and an identity link), using the abundance of each bird functional group as a response variable and the basal area of conifers as an explanatory variable. We also constructed quadratic models (with simple and quadratic terms of the basal area as two explanatory variables) able to represent both concave and convex shapes. Our preliminary analyses showed that LMs and GLMs were little different in fitting the relationships between bird density and tree basal area (see Appendix), indicating that methodological differences between these two types of model did not significantly affect our general conclusions. We also constructed models using the same methods but with basal area of broad-leaved trees as an explanatory variable; the plots (Figs. S2-3) were almost mirror images of those with basal area of conifers as the explanatory variable (Fig. 1-2). The model with the smallest Akaike information criterion (AIC) was considered the best model. Analyses were conducted for each of two plantation types separately: fir plantation (11 fir plantation stands + 4 natural forest stands = 15 stands) and spruce plantation (10 spruce plantation stands + 4 natural forest stands = 14 stands). All statistical analyses were conducted with R ver. 2.15.1 software (R Development Core Team 2012).

Results

We recorded 39 bird species in the field surveys. Thirty-four were classified as forest species, 31 as broad-leaved species, 11 as canopy foragers, eight as cavity nesters, three as flycatchers, and three as conifer species (details in Table S2). The density of broad-leaved trees in each stand was 1010 ± 739 (mean $\pm$ SD, range: 40 – 2480) /ha, and tree basal area was 14.57 ± 9.86 (mean $\pm$ SD, range: 0.09 – 38.04) m²/ha (Table S1). In both fir and spruce plantations, strong negative correlations were found between basal areas of conifers and broad-leaved trees (Fig. S1).

Relationships between bird density and plantation intensity

In fir plantations, the abundances of birds classified as broad-leaved species, canopy foragers, and cavity nesters decreased with increasing plantation intensity (increasing basal area of conifers), though null models had comparable statistical supports relative to linear models, suggesting that the decreased tendencies were not so strong. On the other hand, abundances of bird species with conifer habitat preferences clearly increased with plantation intensity (Table 1, Fig. 1). For these functional groups not preferentially associated with conifer habitats, linear models were the best, but the difference in AIC (Δ AIC) between linear and quadratic model was <2 , indicating that the support for these two models was comparable. The null model was the best for forest bird species and flycatchers.

In spruce plantations, the abundances of bird species identified as broad-leaved, canopy forager, cavity nester, and flycatcher functional groups decreased with increasing plantation intensity, whereas abundances of bird species with a preference for conifer habitat increased with plantation intensity (Table 2, Fig. 2). For these functional groups, linear models were the best, but the Δ AIC between linear and quadratic models was <2 . The null model was best for forest bird species.

Discussion

As we had originally predicted, the density of most bird functional groups decreased with plantation intensity in two plantation types. In most cases, linear models were selected as the best by the principle of statistical parsimony, but statistical support for these models was not much different from support for quadratic models. When both models were statistically supported, their regression lines were similar. Thus, land sparing and land sharing had comparable ecological benefits for the forest birds, that is, both strategies would attain the similar bird abundances in the landscape. Although we only used the basal area of conifers as an intensity index directly relevant with plantation management, other variables related to stand structure and composition (e.g., development of understory) would have some roles for bird communities (e.g., Yamaura *et al.* 2008b), and future studies should consider their effects.

Within the framework of the land-sparing vs. -sharing paradigm, responses of wildlife populations to land-use intensity have been assigned to one of two types of response curve (concave or convex). As a consequence, either land sparing or land sharing has been determined as the best strategy for biodiversity conservation in each of the landscapes studied (Green *et al.* 2005; Mastrangelo & Gavin 2012; Phalan *et al.* 2011). Although our examination was conducted at stand-level in a single region, we showed that response curves could be linear, and that statistical supports of linear and non-linear responses could be similar. These indicate that dichotomic classification may be difficult. Animal population densities can linearly increase with increasing food and nesting resources (e.g., Newton 1998). In the forests we studied, decreasing plantation intensity increases the abundances of naturally

occurring broad-leaved trees, which have abundant food resources (Chey *et al.* 1998) and high probability of cavity occurrence (i.e., many potential nest sites: Kikuchi *et al.* 2013). Therefore, the extensive (less intensive) plantations we examined would have more abundant food and nesting resources than did intensive plantations. We suggest that land sparing and sharing may have comparable benefits when land-use intensity (or yield production) proportionally decreases the amounts of resources needed by wildlife. Land-use intensity is not necessarily proportionally related to resource availability in other cases. For example, the intensity of agriculture, such as fertilizer inputs and number of tillage operations, may not be directly related to food and nesting resources for birds, and there may not be linear relationships between land use intensity and food/nesting resources.

We showed that the introduction of broad-leaved trees into conifer plantations enhances bird diversity and supports previous management recommendations (e.g., increasing tree species richness: Brockerhoff *et al.* 2008; Hartley 2002). However, linear decreases in bird abundances with increasing plantation intensity indicate that there may be no clear thresholds in the abundance of broad-leaved trees required for the maintenance of bird densities. Thresholds may occur when the effects of land-use intensity span a broad spectrum of food and nesting resource volumes (cf., Austin 2002; Van Horne 2002). For example, wildlife individuals may require minimal resource quantities to allow habitat occupancy (Vance *et al.* 2003); habitats with certain amounts of resources may be saturated with wildlife individuals, and further increases in resources may not increase population densities (cf., Newton 1998). When such thresholds do exist, they can be used in planning management guidelines (Groffman *et al.* 2006). Accordingly, future studies should search for such thresholds in the relationships between wildlife densities and land-use intensities across a wide range of circumstances.

Bird species preferring conifer tree-associated habitat had unique responses; their

densities increased with plantation intensity, and they dominated bird communities in the intensive plantations (compare abscissas of conifer and forest species in Fig. 1-2). Therefore, densities of forest bird species, including birds associated with conifers, were relatively insensitive to the plantation intensity, suggesting that responses of birds associated with conifers masked the sensitivity of other bird species to land-use intensity. Similar cases have been reported in studies of habitat fragmentation (Cook *et al.* 2002), and the phenomenon has been termed ‘response diversity’ (Elmqvist *et al.* 2003). Biodiversity encompasses species with varied ecological traits, and some species are usually pre-adapted to anthropogenic environmental changes. We found that bird species with preferences for conifer habitat were pre-adapted to life in plantations of fir and spruce. Increases and decreases in resources associated with environmental change are crucial to the identification of species that are pre-adapted and maladapted, respectively.

Management implications

How do we reconcile the wood production with biodiversity conservation in forested landscapes? Edwards *et al.* (2014) recently showed that land-sparing is superior to land-sharing for a selective logging system in tropics. Our results showed that benefits of both land-use strategies can be comparable for plantation forestry. Further studies to compare these strategies are needed in forested landscapes; however, it is noted that the theoretical framework of land-sparing vs. land-sharing was originally developed for ‘static’ agricultural landscapes. Forests are dynamic systems involved with succession, and multiple functional groups (e.g., early-successional and mature forest species) can be of conservation concerns in the same landscapes (e.g., Toyoshima *et al.* 2013). In such cases, early-successional as well as mature-aged stages would also be considered. Nevertheless, comparable benefits of

land-sparing and land-sharing strategies our study showed suggest the importance of flexible management strategies taking advantages of both strategies depending on ecological, social and biophysical backgrounds (Fischer *et al.* 2008).

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Figure Legends

Fig. 1: Relationships between basal area of conifer trees and abundances of bird functional groups in a fir plantation. Solid and broken lines show linear and quadratic fits, respectively. Fitted lines are included for models with $\Delta AIC < 2$ and AIC smaller than that of null models.

Fig. 2: Relationships between basal area of conifer trees and abundances of bird functional groups in a spruce plantation. See Fig. 1 for details.

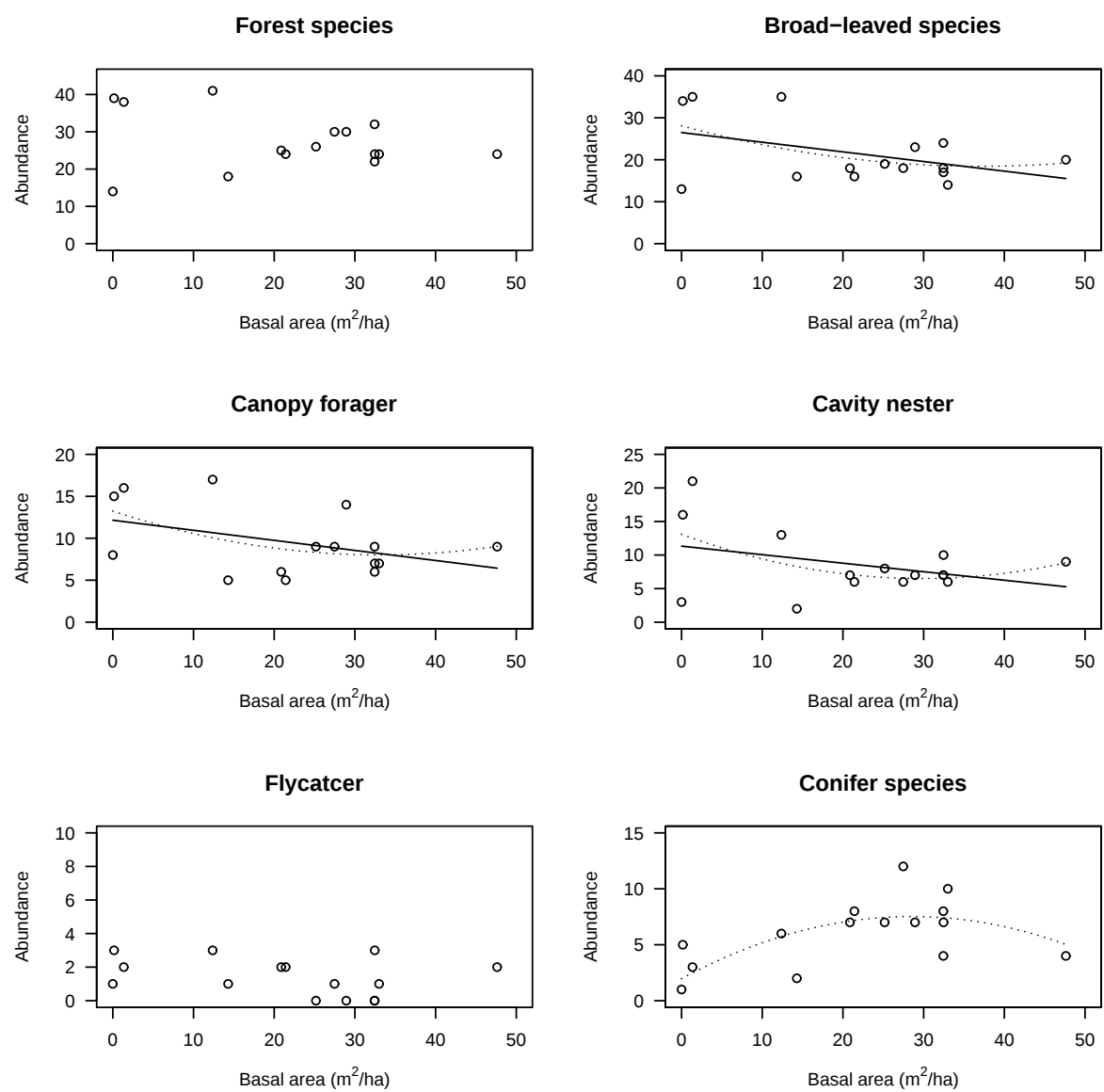


Fig. 1.

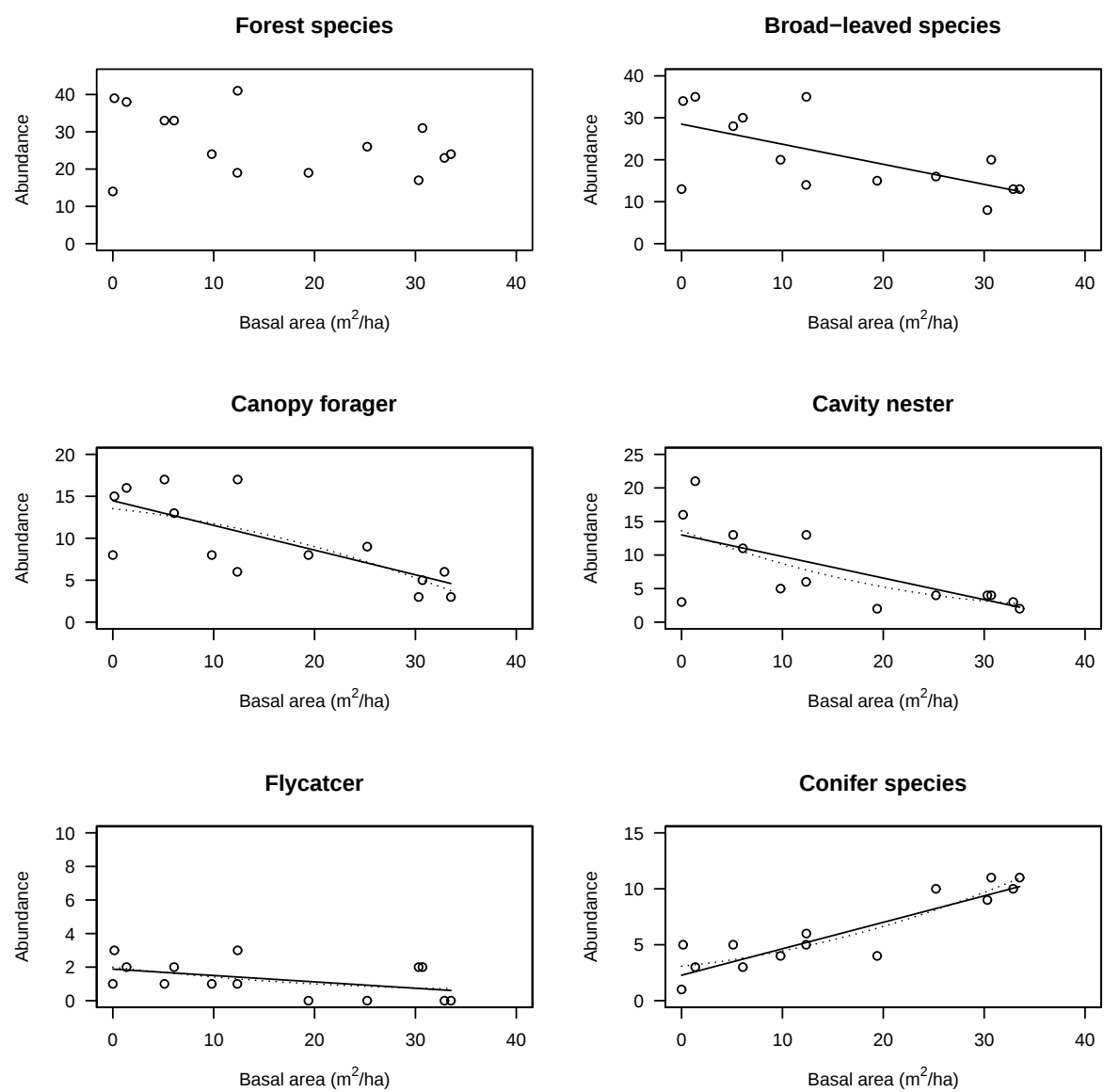


Fig. 2.

Table 1. Summary statistics for linear (LM), quadratic (QM), and null models used to explore the effects of conifer tree basal area in a fir plantation as an explanatory variable for abundances of bird functional categories.

Forest species	α	SE	p	β_1	SE	p	β_2	SE	p	AIC	Δ AIC	Akaike weight	R^2
Null	27.40	1.97	****							106.5	0.0	0.55	
LM	30.39	3.79	****	-0.14	0.15					107.6	1.0	0.33	0.06
QM	30.43	4.58	****	-0.14	0.44		1.81×10^{-4}	1.02×10^{-2}		109.6	3.0	0.12	0.06
Broad-leaved species													
Null	21.33	1.93	****							105.9	1.2	0.27	
LM	26.48	3.45	****	-0.23	0.13					104.7	0.0	0.48	0.19
QM	28.09	4.07	****	-0.52	0.39		7.01×10^{-3}	9.07×10^{-3}		106.0	1.3	0.25	0.23
Canopy foragers													
Null	9.47	1.05	****							87.5	0.9	0.28	
LM	12.15	1.88	****	-0.12	0.07					86.6	0.0	0.44	0.18
QM	13.24	2.19	****	-0.32	0.21		4.78×10^{-3}	4.88×10^{-3}		87.4	0.8	0.29	0.24
Cavity nesters													
Null	8.53	1.26	****							93.2	0.1	0.32	
LM	11.32	2.34	****	-0.13	0.09					93.1	0.0	0.34	0.13

QM	13.09	2.64	***	-0.44	0.26		7.74×10^{-3}	5.89×10^{-3}		93.1	0.0	0.34	0.24
Flycatchers													
Null	1.40	0.29	***							49.0	0.0	0.43	
LM	1.96	0.54	***	-0.03	0.02					49.4	0.4	0.35	0.10
QM	2.27	0.63	***	-0.08	0.06		1.37×10^{-3}	1.41×10^{-3}		50.2	1.3	0.23	0.17
Conifer species													
Null	6.07	0.77	***							78.1	4.9	0.07	
LM	3.91	1.35	**	0.10	0.05	*				76.5	3.3	0.15	0.21
QM	2.35	1.37		0.38	0.13	**	-6.83×10^{-3}	3.04×10^{-3}	**	73.2	0.0	0.78	0.45

α and β_1 means intercept and slope, respectively. β_2 is a quadratic term of non-linear (quadratic) models. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Table 2. Summary statistics for linear (LM), quadratic (QM), and null models used to explore the effects of conifer tree basal area in a spruce plantation as an explanatory variable for abundances of bird functional categories.

Forest species	α	SE	p	β_1	SE	p	β_2	SE	p	AIC	Δ AIC	Akaike weight	R^2
Null	27.21	2.32	***							103.2	0.0	0.44	
LM	31.00	3.66	***	-0.24	0.18					103.3	0.1	0.41	0.13
QM	31.38	4.93	***	-0.34	0.81		2.79×10^{-3}	2.32×10^{-2}		105.3	2.1	0.15	0.13
Broad-leaved species													
Null	21.00	2.53	***							105.6	5.5	0.04	
LM	28.49	3.26	***	-0.48	0.16	**				100.1	0.0	0.70	0.42
QM	28.30	4.40	***	-0.43	0.72		-1.38×10^{-3}	2.07×10^{-2}		102.1	2.0	0.26	0.42
Canopy foragers													
Null	0.57	1.35	***							88.1	9.1	0.01	
LM	14.18	1.53	***	-0.29	0.08	***				79.0	0.0	0.69	0.55
QM	13.52	2.05	***	-0.13	0.34		-4.87×10^{-3}	9.60×10^{-3}		80.7	1.7	0.30	0.56
Cavity nesters													
Null	7.64	1.61	***							93.0	6.6	0.02	
LM	12.68	2.00	***	-0.32	0.10	***				86.4	0.0	0.67	0.46
QM	13.62	2.66	***	-0.56	0.44		8.50×10^{-3}	1.25×10^{-3}		88.0	1.6	0.30	0.48

							10 ⁻⁴	10 ⁻²			
Flycatchers											
Null	1.29	0.29	***						44.6	1.2	0.28
LM	1.88	0.43	***	-0.04	-0.04				43.4	0.0	0.52 0.20
QM	2.00	0.58	***	-0.07	0.09		8.50 × 10 ⁻⁴	2.71 × 10 ⁻³	45.2	1.9	0.20 0.21
Conifer species											
Null	6.21	0.89	***						76.4	21.8	0.00
LM	2.51	0.64	***	0.24	0.03	***			54.6	0.0	0.57 0.82
QM	3.07	0.82	***	0.09	0.13		4.17 × 10 ⁻³	3.86 × 10 ⁻³	55.2	0.6	0.43 0.84