



Climate and topography drives macroscale biodiversity through land-use change in a human-dominated world

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Drivers of biodiversity at macroscales have long been of interest in ecology, and climate and topography are now considered to be major drivers. Because humans have transformed most of the Earth's land surface, land use may play a significant role as a driver of biodiversity at a macroscale. Here we disentangle the relationships among climate, topography, land use, available energy (measured by the normalized difference vegetation index [NDVI]), and species richness of Japanese forest birds. Species richness was better explained at 40- and 80-km resolutions than at 5-, 10- and 20-km resolutions; it was explained by climate, topography, and land use, and the effects of land use were fully incorporated into those of climate and topography. As temperature increased and elevation decreased, natural forest area decreased, and this decrease intensified in warm lowland areas. With the loss of natural forest, species richness decreased below a certain threshold. As temperature increased and elevation decreased, species richness and NDVI increased slightly or were unchanged in cool highland areas and decreased in warm lowland areas. Species richness increased linearly with the increase in NDVI. Most effects of climate/topography on species richness in warm lowland areas were shared by those of land use, suggesting that the decrease in species richness in warm lowland areas has been caused by loss of natural forest. Therefore, it is suggested that climate and topography determined land use intensity, which in turn, drove species richness through the depletion of available energy. Increasing temperature and decreasing elevation leads to both benefits (increase in potential available energy) and costs (depletion of energy by human land-use change) for forest birds. These costs seem to override benefits in warm lowland areas.

Drivers of biodiversity at macroscales (e.g. nations or continents) have long been of interest in ecology (Janzen 1967, Gaston 2000). Many studies have investigated this topic, and climate and topography are now considered major drivers (Hawkins et al. 2003, Rahbek et al. 2007). Human domination of the Earth and concomitant global environmental changes have also made these basic topics important from applied perspectives (Kerr et al. 2007). The role of land use has been a focus of attention at smaller scales such as local sites or landscapes, and their effects on biodiversity are now widely acknowledged (Fischer and Lindenmayer 2007). As humans have transformed more than 75% of the Earth's ice-free land surface (Ellis and Ramankutty 2008), their effects on biodiversity may now scale up to a macroscale (Foley et al. 2005, Yamaura et al. 2009).

Accordingly, the relative importance of climate, topography, and land use to macroscale biodiversity is of great concern (Jetz et al. 2007, Dormann et al. 2008). Recent studies have shown that the effects of land use are weaker than those of climate and topography (Davies et al. 2007, Pompe et al. 2008). Moreover, land use explains little additional variation

in organismal distribution beyond what climate and topography explain (Thuiller et al. 2004, Luoto et al. 2007).

However, the role of land use may have been underestimated for the following reasons: (1) the spatial resolutions in previous studies ($>50 \times 50$ km) are much coarser than are those at which land use is known to affect biodiversity ($<20 \times 20$ km; Radford et al. 2005). At coarse resolutions, even in extensively transformed regions, large areas of relatively undisturbed habitat/biota within the grids would generate species richness/occupancy estimates similar to those driven by climate and topography (see also Pautasso 2006). Hence, effects of land use might become apparent at finer resolutions, as reported by Luoto et al. (2007). (2) An important, but often overlooked, issue is the close relationships among land use, climate, and topography (Thuiller et al. 2004, Luoto et al. 2007). Interactions among them may lead to distortion (or mediation) of climate/topography and species richness relationships by land use. Energy theory predicts that species richness increases with the amount of available energy (or resource availability), which is typically approximated by increases and decreases in temperature

and elevation, respectively (Evans et al. 2005). However, the energy available to biodiversity is not necessarily high in productive areas. Land use can be viewed as human appropriation/preemption of energy/resources (Haberl et al. 2007), and takes place in productive regions of the Earth (Ellis and Ramankutty 2008). After human appropriation, the amount of energy left for other species may be quite low. For example, forest loss, one of the biggest threats to biodiversity (Foley et al. 2005), could be considered to negatively affect forest species through depletion of available energy within landscapes (Wright 1983, Honkanen et al. 2010). Climate and topography may drive biodiversity in a manner that is dependent on land-use change, particularly in productive areas.

With these considerations in mind, we make three predictions about the relationships among climate/topography, land use, energy availability, and species richness. (1) Effects of land use on species richness are not independent of climate and topography due to the dependency of land use on climate and topography (*sensu* Legendre and Legendre 1998). Rather, the effects of climate and topography will be partly explained by (or shared/confounded with) those of land use. (2) The effects of climate and topography on species richness are nonlinear (Fig. 1). Increases in site/regional productivity (e.g. with increasing temperature and decreasing altitude) may increase species richness in unproductive areas. But the relationship will become weak or reversed through land-use changes in productive areas. (3) Consequently, the effects of climate and topography on remaining energy are also nonlinear, and there is a positive relationship between energy and species richness. Here, we test these predictions for Japanese forest birds across five grid sizes (scales) of spatial resolution (5×5 , 10×10 , 20×20 , 40×40 and 80×80 km) to understand the role of land use in a human-dominated region. We used the normalized difference vegetation index (NDVI) as an index of the amount of remaining energy within grids (Evans et al. 2005). We also searched for thresholds in the relationships among climate/topography, land use, NDVI, and species richness. Japan is an ideal study area because it has a long history of forest use (>1000 years) (Totman 1989) and wide climatic and topographic gradients (the archipelago extends from cold temperate to subtropical latitudes; the landscape ranges from high mountains to coastal plains). Urban and agricultural areas created by forest clearance

typically occur in lowlands. We examined the species richness of two major functional groups of birds, viz. foliage gleaners (predators of herbivorous insects) and frugivores (seed dispersers) (Şekercioğlu 2006). Because high species richness is likely to result from large population sizes (Evans et al. 2005), we assumed that large numbers of species in each functional group of birds would be indicative of important ecological roles or services within the respective grids.

Methods

Bird data

The Japanese Ministry of the Environment has conducted a National Survey of the Natural Environment every five years since 1973. We used the results of the sixth (most recent) survey of birds (Biodiversity Center of Japan 2004), which was one of two surveys that systematically examined bird distributions nationwide (Yamaura et al. 2009). The bird censuses were conducted using transect surveys and questionnaires, although we excluded the questionnaire data. More than 1000 trained volunteers participated in this survey, and each transect was visited by a volunteer once between 1 April and 31 August in the years 1998–2002. More than 2000 line transects (3 km long) were established such that two transects were included in every 20-km grid section in Japan. The volunteers recorded all bird species encountered (regardless of the observers' distances from the birds), while walking at 2 km h⁻¹ along the transect. The records were ranked by estimated reproductive state (four ranks: A–D; Appendix 1). Similar surveys were also conducted during 30-min periods at the beginning and end of each transect. The volunteers recorded the proportions of the 3-km transects covered by each of eight habitat types, including forest (Appendix 2).

We obtained the above data from the Ministry of the Environment. We reduced 2317 transects along which birds were recorded to 1878 transects by excluding the following: (1) transects without records of bird reproductive status, (2) transects whose locations (5-km grids within which transects were located) were not specified in the Geographical Information System (GIS), (3) transects whose habitat type proportions were not recorded, and (4) transects that intersected multiple 5-km grids. The last category was excluded because the finest spatial resolution at which we examined bird-environment relationships was 5-km grid, and we used the environmental data within each grid. We excluded bird records when the status of reproduction entry indicated that the birds did not reproduce in the location (i.e. rank D). We re-sampled these bird data at five resolutions (5-, 10-, 20-, 40- and 80-km grids). It was possible for one grid to contain multiple transects. Although the 3-km-long census lines did not necessarily capture all birds inhabiting grids, we explored the relationships between these aggregated bird data and environment variables from the grids because the specific locations of census lines (i.e. line vectors) were not specified in GIS (but identities of the grids in which lines were located were specified). We instead calculated the lengths of transect line(s) (km) covered by forest within each grid and used this as census effort in the analysis. Although 218 species were recorded, we targeted 94 that are diurnal,

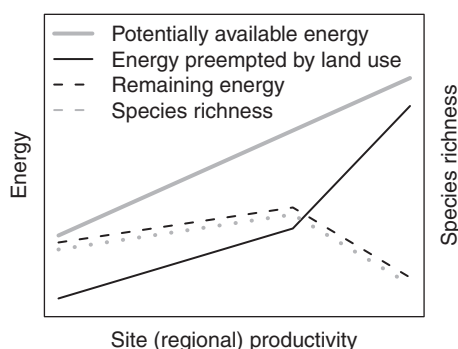


Figure 1. Hypothetical relationships among site (regional) productivity, energy, and species richness. Species richness may be highest in sites with intermediate productivity due to energy depletion in productive sites by human land use.

native, dependent on mature forest, and reproduce within Japan (hereafter forest species: Appendix 3). We further grouped species by foraging substrate, and included 34 foliage gleaners and 47 frugivores in the analysis. We obtained traits of bird species from previous studies (Yamaura et al. 2009). Foliage gleaners included canopy gleaners, shrub gleaners, and omnivores. Frugivores included obligate and opportunistic frugivores. We calculated species richness for three functional bird groups (forest species, foliage gleaners, and frugivores) within each grid.

Climate, topography and NDVI

We obtained three temperature (annual temperature, temperature within breeding and wintering seasons) and three precipitation (annual precipitation, precipitation within breeding and wintering seasons) variables from Mesh Climate Value 2000 provided by the Meteorological Agency of Japan, and two topography variables (mean elevation and range of elevation) from the Digital National Land Information project of the Japanese Ministry of Land, Infrastructure, Transport, and Tourism (Appendix 4). In this study, we classified breeding and wintering seasons as May–July and December–February, respectively. The climate data records of Mesh Climate Value 2000 were 30-year means of monthly/annual values (for the period 1971–2000) within 1-km² grids spread through a contiguous nationwide grid. We obtained each month's NDVI at 1-km² grids measured in 2000 by SPOT-Vegetation, and calculated three average values in each grid (average through 12 months, averages in breeding and wintering seasons). We re-sampled these variables at five resolutions using ArcGIS ver. 9.1.

Land-use

We obtained areas of seven land-use types within each grid (Appendix 4) from vegetation maps in the fifth Japanese National Survey of the Natural Environment (1994–1998). The survey resulted in the production of a nationwide 1:50 000-scale actual vegetation map. Generally, land-use patches larger than 0.25 ha were identified on these maps. We consolidated all vegetation map legends and aggregated them in the following seven land-use types (Appendix 5): (1) natural forest, (2) conifer plantation, (3) arable field, (4) paddy field, (5) xeric grassland, (6) mesic grassland, and (7) urban. We did not consider some minor vegetation types, and these were excluded from the analyses (e.g. plantations of broad-leaf tree species, bamboo forests). We re-sampled these land-use types at five resolutions.

Data reduction

We used grids for only the four largest islands in the Japanese archipelago (Honshu, Hokkaido, Kyushu and Shikoku), and smaller islands were excluded to control for island-size effects. We further excluded any grid in which land occupied less than half the grid area. Hence, we used 1724 5-km grids, 1633 10-km grids, 868 20-km grids, 234 40-km grids, and 59 80-km grids.

We excluded redundant explanatory variables from the analysis. Among the climate and topography variables, some

were highly correlated ($|r| > 0.75$) at all resolutions (Appendix 6), and for this reason, we selected just four as explanatory variables for detailed analyses: annual temperature (ATP; °C), annual precipitation (APP; mm), mean elevation (ELV; m), and range of elevation (RngELV; m). Precipitation in the wintering season was correlated with annual precipitation ($r \approx 0.55$), and was excluded because preliminary analysis indicated that it was not an important variable. Range of elevation was closely correlated with mean elevation (5-km: $r = 0.78$; 10-km: $r = 0.81$; 20-km: $r = 0.83$; 40-km: $r = 0.85$; 80-km: $r = 0.87$); previous studies have repeatedly demonstrated its importance (Davies et al. 2007). We therefore used range of elevation as an explanatory variable and examined whether its effect differed from that of mean elevation.

Because correlations among the seven land-use variables were not high at any resolution ($|r| < 0.5$), we excluded only two variables (xeric and mesic grasslands) and retained the other five variables (area: m²) in the analysis (natural forest [NATL], conifer plantation [CONF], arable field [ARABL], paddy field [PADDY], and urban [URBAN]); the first two were minor land uses in the grids.

Statistical analysis

Variation in census effort and spatial autocorrelation

Transect length covered by forest (hereafter, forest length) varied among transects, and the number of transects within grids varied among grids. To control for bias caused by these variations in census effort among grids (Haila 1990), we always used forest length (km) summed within grids (Effort) as an explanatory variable (covariate), and quantified or controlled the effects shared with other explanatory variables using partial regression analysis or multiple regression analysis, respectively. Because forest length correlated with natural forest area, we did not remove its effects before the analysis because such procedures could result in the underestimation of the effects of natural forest area (Freckleton 2002). Because species richness increased asymptotically with forest length, we used simple and quadratic terms of forest length as explanatory variables (i.e. Effort and Effort²). We assumed that species richness was normally distributed after inspection of its distribution (Dormann et al. 2008).

The distributions of organisms are usually spatially autocorrelated, which can lead to misinterpretation of the effects of environmental variables (Dormann et al. 2007). We used centroids of grids as the grid coordinates (x, y) and regressed forest species richness against simple and quadratic terms of the 10 explanatory variables (Effort, ATP, APP, ELV, RngELV, NATL, PLANT, ARABL, PADDY and URBAN; the variables that were used in the analysis). We generated correlograms of the regression residuals using the *ncf* R package ver. 1.1-3 (Bjørnstad 2009); a positive autocorrelation was found within ten-fold grid size changes, especially at finer resolutions. We then used a spatial simultaneously autoregressive error model (SAR_{err}; hereafter, SAR; Kissling and Carl 2008) rather than ordinary least squared (OLS) models, unless noted otherwise using the *spdep* R package ver. 0.5-4 (Bivand et al. 2010). Spatial neighbors between which autocorrelation was expected were grids within ten times the grid size (e.g. 10 × 5-km for 5-km grid resolution). We weighed closer grids more heavily by using a spatial decay function of the form

$w_{ij} = 1/d_{ij}^\alpha$ (Rangel et al. 2006), where α was set to 1. We did not use any standardization techniques for neighbor weights, such as row standardization, therefore sums of weights could differ among grids according to the number of neighboring grids (Bivand et al. 2008).

Partial regression analysis

We examined the relative importance of climate/topography (ATP, APP, ELV and RngELV) and land use (NATL, PLANT, ARABL, PADDY and URBAN) while explicitly considering their relationships and their shared effects with census effort (Effort) through partial regression analysis (Legendre and Legendre 1998) under spatial regression, SAR. We used simple and quadratic terms for each variable (e.g. ATP and ATP²), resulting in 20 explanatory variables with which to explore the nonlinear effects of climate, topography, and land-use variables. We evaluated the importance of each variable set (i.e. climate/topography and land use variable sets) using Nagelkerke pseudo-R² (hereafter, R²; Faraway 2006). We partitioned the total effects of each explanatory variable set by conducting multiple SARs with different explanatory variables (Legendre and Legendre 1998). The total effect was the variation in the response variable (R²) explained by each explanatory variable set, and encompassed variation explained only by each variable set (i.e. independent effects) as well as variation also explained by the other variable sets (shared or confounding effects). Shared effects occurred when different explanatory variable sets co-varied and explained the same variation in the response variable. Therefore, shared effects could not be attributed exclusively to a single explanatory variable set. Specifically, we partitioned total effects of each variable set into four fractions. For example, total effects in the land-use variable set included (1) independent effects of land use, (2) shared effects with climate/topography, (3) shared effects with census effort, and (4) shared effects with climate/topography and census effort. We also partitioned total effect of each explanatory variable (e.g. only ATP and ATP²) into four fractions: (1) independent effects, (2) shared effects with the other eight variables, (3) shared effects with census effort, and (4) shared effects with the other eight variables and census effort. Further, we examined the total effect of each NDVI variable and partitioned this into independent effect and shared effect with census effort. Our response variables were species richness of three bird species groups. We did not examine interactions between climate/topography and land-use variables because the latter had small independent effects. We did not conduct path analysis because (1) it is difficult to build quadratic relationships into a path diagram, and (2) small independent effects of land-use variables would not allow path analysis to identify the land use-mediated climate/topography effects (Legendre and Legendre 1998).

Piecewise regression analysis

Because nonlinear relationships were found among the variables, we searched for thresholds at which relationships shifted. We conducted this analysis at the resolutions at which species richness was well explained and there was sufficient sample size, namely 40-km. We searched for thresholds (ψ) in the effects of each explanatory variable on richness of forest species because richness of this group was the best explained.

We conducted analyses for annual temperature (ATP), mean elevation (ELV), natural forest area (NATL), conifer plantation area (PLANT), and NDVI in breeding season because these variables explained species richness fairly well. We also searched for thresholds in the effects of ATP and mean elevation on NATL and NDVI in the breeding season. Because it is difficult to conduct segmented regression that can estimate thresholds and their confidence intervals (Muggeo 2003) under an SAR framework, we fitted piecewise regression (Crawley 2007) in which species richness, natural forest area, or NDVI was a response variable and climate/topography, NDVI, or land use was the single explanatory variable. We fit 999 piecewise regressions with 999 different break points created by dividing the range of the explanatory variables into 1000 equal-length segments. We used the break points with the highest R² as estimated thresholds. We examined support for the thresholds by comparing the performance of the best-fitted piecewise models, linear models (with only a single simple term), and quadratic models (with simple and quadratic terms). We compared the models with the Akaike information criterion (AIC), R², and w_i (Akaike weight), which indicate the probability of one model being the best among the candidate models (Burnham and Anderson 2002). Threshold analyses identified the natural forest area below which forest species richness decreased (minimum natural forest area). We obtained annual temperature and elevation with minimum natural forest area through quadratic models that included natural forest area as an explanatory variable (i.e. NATL and NATL²) and annual temperature or elevation as a response variable. In regression analyses with species richness as a response variable, we always used census effort as an explanatory variable (i.e. Effort and Effort²). After estimating the thresholds of annual temperature and elevation for species richness, we divided the data at the thresholds. We conducted partial regression analysis for each segment to determine whether the effects of climate/topography and land-use variables shifted before and after the thresholds. All statistical analyses other than spatial analysis were conducted with R ver. 2.11.0.

Results

In the spatial regression analysis, quadratic models were always more supported than linear models except for the relationship between forest species richness and NDVI in spring ($AIC_{\text{quadratic}} < AIC_{\text{linear}}$; Appendix 7), suggesting that most relationships among climate/topography, land use, NDVI, and species richness were nonlinear. We subsequently used both simple and quadratic terms in partial regression analysis to determine whether the effects of climate/topography and land-use variables may be attributed exclusively to single variables. Results were similar among the three species groups at the finest resolutions (5-, 10-, and 20-km; Fig. 2a–c). Species richness was best explained at the coarsest two resolutions (40- and 80-km), and richness of forest species was well explained among the three groups. Total effects of climate/topography and land use were comparable at the finest three resolutions, and their effects were well shared with each other and census effort at these resolutions. Almost all of the effects of land use were shared with climate/topography

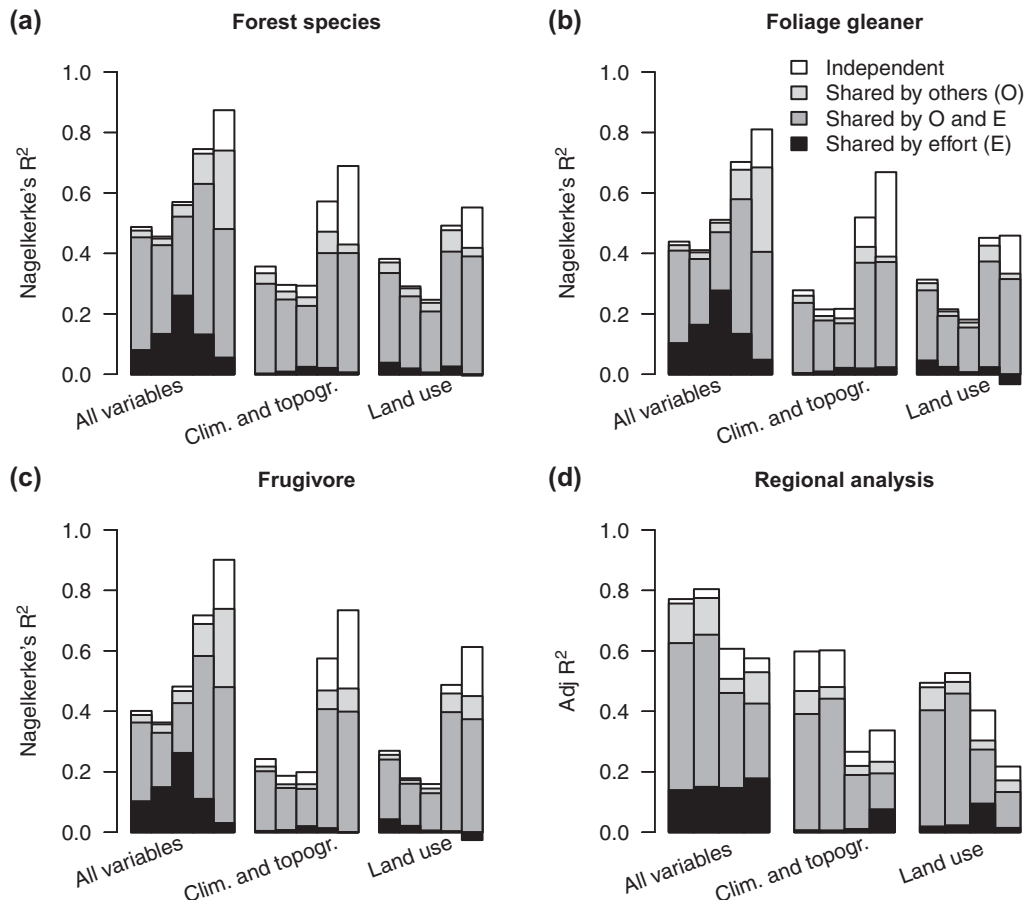


Figure 2. Effects of nine climate/topography and land-use variables on forest bird species richness. (a–c) Effects of each variable set at 5-, 10-, 20-, 40-, and 80-km resolutions, respectively, are shown in groups arranged from left to right. White, light gray, dark gray, and black bars represent independent effects of land use, independent effects of climate/topography, shared effects among land use, climate/topography, and census effort, and independent effects of census effort, respectively. (d) Effects of climate/topography and land-use variables on species richness in four regions at 40-km resolution. Effects in warm, lowland, cool, and highland areas are shown in groups arranged from left to right. Negative shared effects occur in the cases where positively correlated explanatory variables have effects of opposite signs on response variables (Legendre and Legendre 1998).

except for at the coarsest two resolutions, indicating that the effects of land use were fully included by those of climate/topography. Climate/topography had some independent effects at the finest three resolutions, and their independent effects increased at the coarsest two resolutions, especially at 80-km. Among the ten explanatory variables, the effects of annual temperature (ATP), mean elevation (ELV), and range of elevation (RngELV) were strongest (Appendix 8). The effects of natural forest area (NATL) were secondary, following by those of plantation forest (PLANT). The pattern in the effects of mean elevation were hardly different from those of range of elevation. These results suggest that the effects of temperature, mean elevation, and natural forest area determined the effects of climate/topography and land use, respectively. Among three NDVI variables, NDVI in breeding season (spring) almost always best explained species richness of three groups across five resolutions, especially at 40-km resolution (Appendix 9).

Subsequently, we inspected relationships among climate, topography, land use, NDVI, and forest species richness at 40-km resolution. Piecewise regression was always better supported than linear and quadratic models ($AIC_{\text{piecewise}} <$

$AIC_{\text{linear/quadratic}}$; Appendix 7), with the exception of two relationships. In the species richness-annual temperature relationship, support for quadratic and piecewise models were comparable, indicating that the threshold in the species richness-temperature relationship was vague. In the species richness-NDVI (spring) relationship, the linear model had more support than the quadratic and piecewise models, indicating that species the richness-NDVI relationship was rather linear (Fig. 3). Nevertheless, the existence of thresholds was somewhat supported in most relationships.

Although non-spatial OLS regression produced similar regression lines in almost all relationships (not shown), different relationships were found only in the natural forest area-temperature relationship. In this case, SAR and OLS identified thresholds in cool and warm areas, respectively, suggesting that natural forest area declined precipitously at both ends of the temperature regions. The threshold found under the natural forest area-elevation and natural forest area-elevation relationship shows that the decrease in natural forest area with increasing temperature and decreasing elevation was typically marked in warm lowland areas (Fig. 3). As temperature increased and elevation decreased in cool

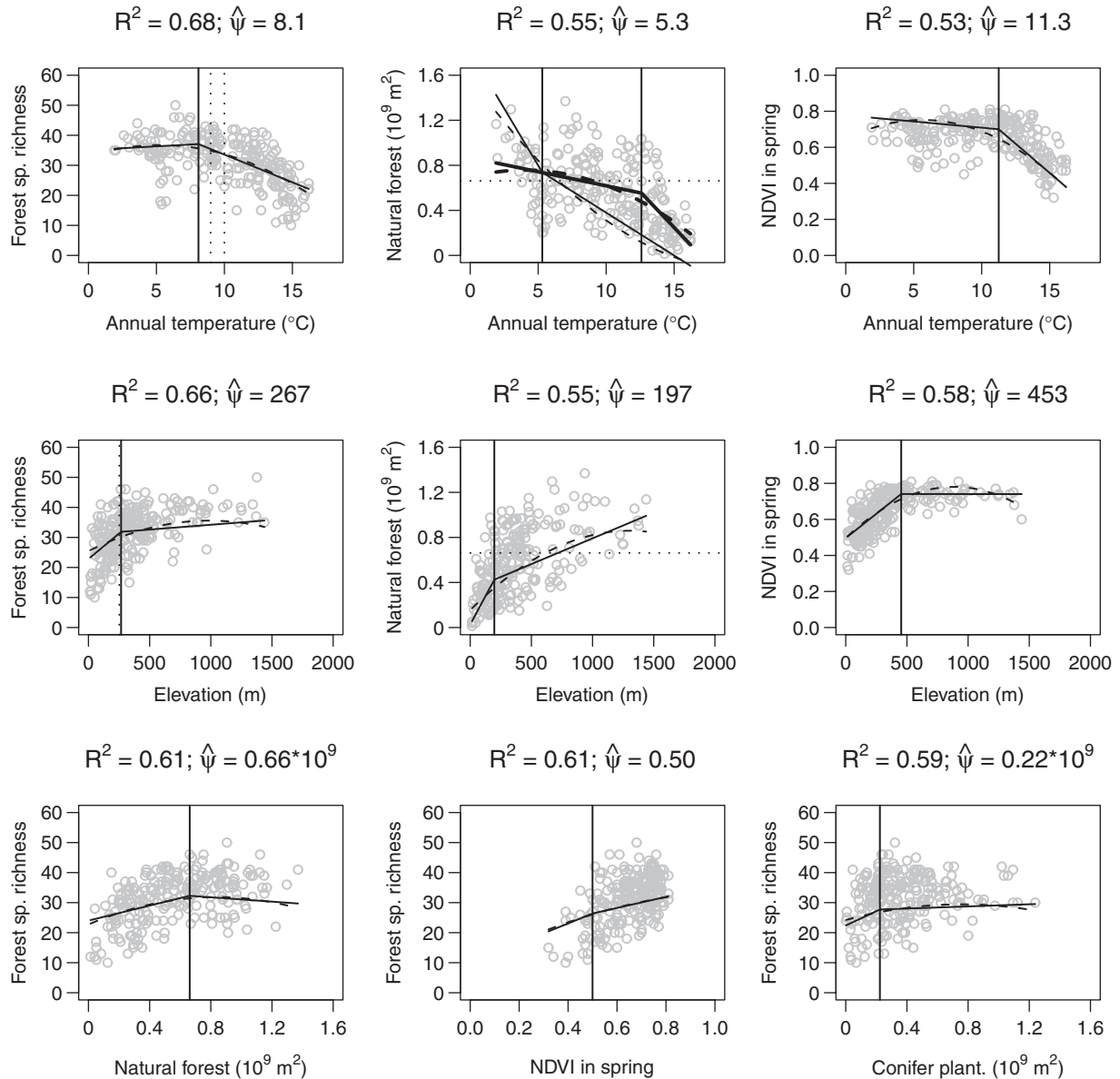


Figure 3. Relationships among climate/topography, land-use, NDVI, and forest bird species richness at 40-km resolution. Nagelkerke pseudo- R^2 and estimated thresholds ($\hat{\psi}$) are shown above the panels. Solid and broken lines indicate piecewise and quadratic regression lines, respectively. Wide regression lines are depicted by OLS regression for the natural forest area-temperature relationship. Vertical solid lines indicate estimated thresholds. Dotted horizontal lines show $\hat{\psi}$ in the effects of natural forest area on forest species richness (minimum natural forest area). Dotted vertical lines show values of annual temperature (SAR: 10.0°C ; OLS: 9.0°C) and elevation (252 m) having minimum natural forest area. Fitted regression lines of species richness are depicted by models in which census effort was held to the average value. In the spatial regression (SAR), spatial error terms were set to zero. It is noted that the explained variation in the response variables (R^2) includes not only effects of explanatory variables but also effects of spatial error terms.

highland areas, species richness was unchanged or increased slightly, and finally decreased in warm lowland areas (Fig. 3). The thresholds at which species richness began to decrease occurred at 8.1°C and 267 m elevation. Species richness also decreased with decreasing natural forest area, and this decrease was observed where natural forest covered $<662 \text{ km}^2$, which was the case in $\sim 41\%$ of the 40-km grids. If we call this threshold the minimum (required) natural forest area, this area had been lost before the marked loss of natural forest area occurred with increasing temperature and decreasing elevation. Thresholds at which species richness started to decrease with increasing temperature and

decreasing elevation corresponded roughly with temperature and elevation at which natural forest area declined to the minimum natural forest area. The decrease in species richness with declining conifer plantation area was observed only where conifer plantation area covered $<223 \text{ km}^2$, which corresponded to 14% of the grid area.

We divided the data at thresholds of temperature (8.1°C) and elevation (267 m), and conducted partial regression analysis on the divided data sets (Fig. 2d). More than half of the effects of climate/topography were shared with land use in the warm lowland data. Although the effects of climate/topography were much smaller in the cool highland data, the

proportion of independent effects increased in the highland data. In the cool area data, the effects of climate/topography were smallest and there were few independent effects, which is logical because species richness hardly changed with temperature in this range.

Similar to natural forest area and species richness, NDVI also showed stark decreases in warm lowland areas. As temperature increased and elevation decreased in cool highland areas, NDVI slightly increased in cool highland areas, peaked with intermediate temperature and elevation, and finally decreased in warm lowland areas (Fig. 3). There was a positive linear relationship between species richness and NDVI.

Discussion

Land use as a driver of macroscale biodiversity

As we predicted, the effects of land use on species richness were fully included in those of climate and topography, and the effects of climate and topography on species richness were nonlinear. Land use was strongly dependent on climate and topography. Natural forest area decreased with an increase in annual temperature and decrease in elevation, and this decrease was marked in warm lowland areas. Although the effects of climate/topography, land use, and NDVI were confounded with census effort, they explained nontrivial variation of forest species richness ($R^2 > 40\%$), and regression models with census effort as covariates showed clear changes in forest species richness with their trends.

We found thresholds in the effects of climate/topography and land use on species richness. Forest species richness decreased precipitously below 41% of natural forest area, which we termed the minimum natural forest area. With increasing temperature and decreasing elevation, forest species richness increased slightly or was unchanged in cool highland areas, and then decreased precipitously in warm lowland areas. Such thresholds in temperature and elevation corresponded roughly with the temperature and elevation at which minimum natural forest area was maintained. Further, most of the effects of climate and topography were shared by land use in warm lowland areas. As we also predicted, the amounts of energy measured by NDVI were conserved in cool highland areas, and distinctly decreased in warm lowland areas, similar to the pattern of natural forest area, and there was a positive linear relationship between species richness and NDVI. These results suggest that the decrease in species richness in warm lowland areas was actually caused by depletion of energy through land-use change. Therefore, land use was not merely a redundant driver of species richness for climate and topography. Rather, it was a critical driver that distorted (or mediated) the relationships between climate/topography and species richness. The role of land use as a driver of macroscale biodiversity would have been underestimated by overlooking land use-mediated climate and topography effects.

Determining the relative importance of land use versus climate is not a simple issue because land use mediates climate (and topography) effects. Increasing temperature and decreasing elevation leads to not only benefits (increase in potentially available energy) but also costs (depletion of

energy by human land-use change) for forest birds. These costs seem to override benefits in warm lowland areas. Unimodal responses of species richness to increases in productivity have sometimes been reported (Gaston 2000), and their mechanisms have attracted interest (Rosenzweig 1992). Ironically, humans have generated a novel mechanism for reducing species richness in productive warm lowland areas through transformation of these land areas (see also Nogués-Bravo et al. 2008). Because the remaining energy embodied by the interactions between climate/topography and land use eventually drives species richness, if prediction of species richness is a sole objective, we may circumvent these interactions by using available energy (e.g. NDVI) as a predictor.

Piecewise regression under SAR found a precipitous decline in natural forest area with increasing temperature in cool areas. Division of the data by temperature before and after the threshold showed that a loss of natural forest in cool areas occurred on Hokkaido Island (Fig. 4a). This region is unique in having a low temperature, nevertheless it has lowland plains with vast agricultural areas. In other parts of Japan, cool areas typically exist in mountainous forested highlands. Aside from Hokkaido, steep decreases in species richness with increasing temperature started before the threshold from which forest area started to decline steeply. This is probably because minimum natural forest area was reached before the natural forest area-temperature threshold, which suggests that creeping land-use change is sufficient to cause a precipitous decline in species richness. There may be other anthropogenic drivers working independently or synergistically with land-use change to reduce species richness along with climate/topography. Indeed, the decrease in species richness with increasing temperature and decreasing elevation was not fully explained by land-use. Candidate drivers include fragmentation of natural forests and the simplification of vegetation composition and structure (Foster et al. 2003).

It is noted that maximum/minimum values of the explanatory variables were dropped from our analysis and grids were less frequently dominated by a single land use at coarser resolutions (Appendix 10–11). Decreases in species richness at such values (e.g. cool highland areas), which were observed with finer resolutions, became diluted at coarser resolutions (Appendix 10–11). However, the diluted decrease in species richness in cool highland areas may have occurred because such areas are more productive than was previously thought (Huston and Wolverton 2009). In Japan, deciduous broadleaved forests establish in cool highland areas (Taoda 1998). Deciduous broadleaved forests may be the most productive forests during the growing season (Blondel et al. 1993), and forest birds may migrate to deciduous broadleaved forests to take advantage of the greater amount of leaf production, creating an association for herbivores within breeding season, called a flush/pulse (Huston and Wolverton 2009). Forest species richness was better explained by NDVI in the breeding season than during the full 12 months or the wintering season (Appendix 9). Reduced species richness in warm lowland areas may be partly explained by small amounts of deciduous broadleaved forests in these areas.

For human-dominated regions, our results suggest that in warm lowland areas where species richness was once greatest, natural habitats have been modified or lost, and anthropogenic



Figure 4. Distributions of regions divided by piecewise regression thresholds. (a) Warm (white) and cool (gray) areas divided by the threshold in the natural forest area–annual temperature relationship under SAR piecewise regression. (b) Anthropogenic (white) and productivity (gray) domains were divided by annual temperature (8.1°C). (c) Two domains were divided by elevation (267 m). The spatial resolution is 40×40 km.

impacts constrain species richness. Although anthropogenic impacts would have long-delayed effects on species richness (cf. Vellend et al. 2006), warm lowland areas of Japan have had a long history of intensive forest use (Totman 1989), and loss of species richness would have already occurred in these areas. In cool highland areas where forest use is limited and the history of human effects is short, high species richness would be maintained by productivity itself (i.e. potentially available energy). Therefore, warm lowland areas and cool highland areas may be considered anthropogenic and productivity domains, respectively. We found the thresholds of these domains, suggesting that regions except for northern and mountainous areas of Japan are in the anthropogenic domain (Fig. 4b–c).

It is surprising that forest species richness was better explained by land use at coarser resolutions (40- and 80-km) than at resolutions where the role of land use has been focused (e.g. 5-, 10- and 20-km). Increased effects of land use may be due to an increased number of 3-km census lines being included in coarser grids, which captured more bird species inhabiting grids. Indeed, census effort did not explain species richness well at a resolution of 80-km (Fig. 2; Appendix 8). However, because census effort explained species richness at 40-km and at finer resolutions, the increased effects of land use at 40-km may not be a sampling artifact. There is considerable evidence that forest birds are influenced by land use at much finer resolutions (Radford et al. 2005), even at 50-m

(Desrochers and Hannon 1997). However, forest birds may disperse longer distances than was previously thought (Tittler et al. 2009), and there may be additional, larger spatial scales at which land-use change drives forest bird diversity.

Conservation implication

Our results have several implications for conservation. First, although any remaining natural habitats in warm lowland areas and the restoration of such areas have important roles, we should focus on biodiversity conservation in cool highland areas. Species richness of functional groups is likely an index of the magnitude of their functions. The effects of climate/topography and land-use on species richness of the two functional groups examined here (foliage gleaners and frugivores) were similar to the effects on forest species richness. Therefore, present and future biodiversity and its function/services (e.g. predation on herbivorous insects by foliage gleaners and seed dispersal by frugivores) within regions are likely maintained by restricted cool highland areas rather than by the whole region equally. Such areas are remnant refugia of biodiversity because of high remaining energy. High amounts of potentially available energy and resultant high species richness have been lost in warm lowland areas where humans have dominated and altered the landscape for long periods. As global warming may make such remnant refugia more productive, species richness may increase in the future. However, at the same time, global warming may also make such land tracts more suitable for humans, who would push these areas into the anthropogenic domain.

Another implication is that threshold effects from the amount of habitat may exist at the community level, although such threshold effects have been examined at the species level (Betts et al. 2007). We found thresholds in the effects of natural and plantation areas on forest species richness. Such threshold effects may be generated through aggregation of similar species responses to habitat availability at some spatial resolutions, e.g. 40×40 km. Indeed, Radford et al. (2005) also found threshold effects of forest area on forest bird species richness. Population abundance of many species and associated function/services may be greatly reduced below thresholds (Swift and Hannon 2010). The vagueness in thresholds that we found in this study might stem from regional variation in thresholds (Rhodes et al. 2008). The small threshold values for plantation area suggest that plantation area may contribute to species richness only when plantation area is small. Adding plantations to regions where they were previously absent (including regions with no forests) would only slightly increase regional species richness. The expansion of plantations would reduce regional species richness by replacing natural forest area.

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Appendix

Appendix 1. Reproductive status criteria recorded in the bird census.

Rank	Criterion
A	Reproduction was confirmed
B	There was a possibility of reproduction
C	Reproduction was uncertain
D	Bird would not reproduce

Appendix 2. Details of eight habitat types recorded in the bird census.

Habitat type	Composite sub-habitat classes
Forest	Broadleaved forest, conifer forest, mixed forest, shrubland
Farmland	Arable field, paddy field, excluding abandoned paddy field (included in grasslands or bare grounds)
Xeric grassland	Grassland except for marsh and swamp, clear-cut, mountaintop grassland, roadside grassland
Mesic grassland	Grassland in marsh and swamp
Open water	River, pond, lake
Xeric bare ground	Rock land, bald mountain
Mesic bare ground	Tidal land, sand, cliff adjacent to open water, polder, bare island
Other	Urban area, residential area, industrial area, urban park

Appendix 3. Ecological traits of bird species. We considered only species that depend on mature forests, are diurnal and native, and reproduce within Japan. We first excluded species that are nocturnal and nonnative, and that do not reproduce within Japan, and next excluded non-forest species. We grouped the forest species by their preferred successional stage, and excluded early-successional species. We also considered foliage gleaners and frugivores among the mature forest species.

Common name	Scientific name	Diurnal and native	Forest-dependent	Successional stage	Foraging substrate	Frugivore
Japanese green woodpecker	<i>Picus awokera</i>	Yes	Yes	Mature forest	Stem	Yes
Grey heron	<i>Ardea cinerea</i>	Yes				
Black-faced bunting	<i>Emberiza spodocephala</i>	Yes	Yes	Early succ		
Brown hawk owl	<i>Ninox scutulata</i>					
Japanese green pigeon	<i>Sphenurus sieboldii</i>	Yes	Yes	Mature forest		Yes
Common redshank	<i>Tringa totanus</i>	Yes				
Red-necked grebe	<i>Podiceps grisegena</i>	Yes				
Great spotted woodpecker	<i>Dendrocopos major</i>	Yes	Yes	Mature forest	Stem	Yes
Izu Island thrush	<i>Turdus celaenops</i>	Yes	Yes	Mature forest	Ground	Yes
Ruddy kingfisher	<i>Halcyon coromanda</i>	Yes	Yes	Mature forest	Ground	
Brown thrush	<i>Turdus chrysolaus</i>	Yes	Yes	Mature forest	Ground	Yes
Ryukyu robin	<i>Erithacus komadori</i>	Yes	Yes	Mature forest	Ground	
Brown shrike	<i>Lanius cristatus</i>	Yes	Yes	Early succ		
Cattle egret	<i>Bubulcus ibis</i>	Yes				
White-rumped swift	<i>Apus pacificus</i>	Yes				
Amami woodcock	<i>Scolopax mira</i>					
Eurasian wryneck	<i>Jynx torquilla</i>	Yes	Yes	Mature forest	Ground	Yes
Iijima's willow warbler	<i>Phylloscopus ijimae</i>	Yes	Yes	Mature forest	Foliage glean	
Masked grosbeak	<i>Eophona personata</i>	Yes	Yes	Mature forest	Foliage glean	
Long-billed plover	<i>Charadrius placidus</i>	Yes				
Crossbill	<i>Loxia curvirostra</i>	Yes	Yes	Mature forest		
Common sandpiper	<i>Actitis hypoleucos</i>	Yes				
Blue rock thrush	<i>Monticola solitarius</i>	Yes				
Goden eagle	<i>Aquila chrysaetos</i>	Yes	Yes	Mature forest	Edge predator	
Asian house martin	<i>Delichon dasypus</i>	Yes				
Alpine accentor	<i>Prunella collaris</i>	Yes	Yes	Early succ		
Japanese bush warbler	<i>Cettia diphone</i>	Yes	Yes	Mature forest	Foliage glean	Yes
Eurasian bullfinch	<i>Pyrrhula pyrrhula</i>	Yes	Yes	Mature forest	Foliage glean	Yes
Styan's grasshopper warbler	<i>Locustella pleskei</i>	Yes	Yes	Mature forest	Foliage glean	
Rhinoceros auklet	<i>Cerorhinca monocerata</i>	Yes				
Japanese cormorant	<i>Phalacrocorax capillatus</i>	Yes				
Black-tailed gull	<i>Larus crassirostris</i>	Yes				

(Continued)

Common name	Scientific name	Diurnal and native	Forest-dependent	Successional stage	Foraging substrate	Frugivore
Grey's grasshopper warbler	<i>Locustella fasciolata</i>	Yes	Yes	Early succ		
Eastern pale-legged leaf warbler	<i>Phylloscopus borealoides</i>	Yes	Yes	Mature forest	Foliage glean	
Hazel grouse	<i>Tetrastes bonasia</i>	Yes	Yes	Mature forest	Ground	Yes
Long-tailed tit	<i>Aegithalos caudatus</i>	Yes	Yes	Mature forest	Foliage glean	Yes
Black-naped tern	<i>Sterna sumatrana</i>	Yes				
White-backed woodpecker	<i>Dendrocopos leucotos</i>	Yes	Yes	Mature forest	Stem	Yes
Collared scops owl	<i>Otus lempiji</i>					
Latham's snipe	<i>Gallinago hardwickii</i>					
Reed bunting	<i>Emberiza schoeniclus</i>	Yes	Yes	Early succ		
Slaty-backed gull	<i>Larus schistisagus</i>	Yes				
Japanese marsh warbler	<i>Locustella pryeri</i>	Yes				
Northern goshawk	<i>Accipiter gentilis</i>	Yes	Yes	Mature forest	Edge predator	
Common coot	<i>Fulica atra</i>	Yes				
Great reed warbler	<i>Acrocephalus arundinaceus</i>	Yes				
Blue-and-white flycatcher	<i>Cyanoptila cyanomelana</i>	Yes	Yes	Mature forest		Yes
Gadwall	<i>Anas strepera</i>	Yes				
Mandarin duck	<i>Aix galericulata</i>	Yes	Yes	Mature forest	Ground	Yes
White-tailed eagle	<i>Haliaeetus albicilla</i>	Yes	Yes	Mature forest	Edge predator	
Azure-winged magpie	<i>Cyanopica cyana</i>	Yes	Yes	Mature forest	Foliage glean	Yes
Little grebe	<i>Tachybaptus ruficollis</i>	Yes				
Eurasian jay	<i>Garrulus glandarius</i>	Yes	Yes	Mature forest	Foliage glean	Yes
Magpie	<i>Pica pica</i>	Yes	Yes	Mature forest	Foliage glean	Yes
Rustic bunting	<i>Emberiza rustica</i>					
Brown booby	<i>Sula leucogaster</i>	Yes				
Common cuckoo	<i>Cuculus canorus</i>	Yes	Yes	Early succ		
Chinese thrush	<i>Garrulax canorus</i>					
Japanese accentor	<i>Prunella rubida</i>	Yes	Yes	Early succ		
Japanese wood pigeon	<i>Columba janthina</i>	Yes	Yes	Mature forest		Yes
Spot-billed duck	<i>Anas poecilorhyncha</i>	Yes				
Goosander	<i>Mergus merganser</i>	Yes				
Great cormorant	<i>Phalacrocorax carbo</i>	Yes				
Brown dipper	<i>Cinclus pallasii</i>	Yes	Yes	Mature forest		
Common kingfisher	<i>Alcedo atthis</i>	Yes				
Oriental greenfinch	<i>Carduelis sinica minor</i>	Yes	Yes	Early succ		
Great crested grebe	<i>Podiceps cristatus</i>	Yes				
Crested serpent eagle	<i>Spilornis cheela</i>	Yes	Yes	Mature forest	Edge predator	
Goldcrest	<i>Regulus regulus</i>	Yes	Yes	Mature forest	Foliage glean	
Common pheasant	<i>Phasianus colchicus</i>	Yes	Yes	Early succ		
Oriental turtle dove	<i>Streptopelia orientalis</i>	Yes	Yes	Mature forest	Ground	Yes
Grey wagtail	<i>Motacilla cinerea</i>	Yes	Yes	Mature forest	Ground	
Tree creeper	<i>Certhia familiaris</i>	Yes	Yes	Mature forest	Stem	
Narcissus flycatcher	<i>Ficedula narcissina</i>	Yes	Yes	Mature forest		Yes
Tufted duck	<i>Aythya fuligula</i>	Yes				
Pine grosbeak	<i>Pinicola enucleator</i>	Yes	Yes	Mature forest	Foliage glean	Yes
Emerald dove	<i>Chalcophaps indica</i>	Yes	Yes	Mature forest	Ground	Yes
Water rail	<i>Rallus aquaticus</i>	Yes				
Black woodpecker	<i>Dryocopus martius</i>	Yes	Yes	Mature forest	Stem	
Hodgson's hawk-eagle	<i>Spizaetus nipalensis</i>	Yes	Yes	Mature forest	Edge predator	
Common noddy	<i>Anous stolidus</i>	Yes				
Pacific reef egret	<i>Egretta sacra</i>	Yes				
Grey bunting	<i>Emberiza variabilis</i>	Yes	Yes	Early succ		
Grey thrush	<i>Turdus cardis</i>	Yes	Yes	Mature forest	Ground	Yes
Spectacled guillemot	<i>Cephus carbo</i>	Yes				
Grey-headed lapwing	<i>Vanellus cinereus</i>	Yes				
Lesser spotted woodpecker	<i>Dendrocopos minor</i>	Yes	Yes	Mature forest	Stem	Yes
Little tern	<i>Sterna albifrons</i>	Yes				
Black-crowned night heron	<i>Nycticorax nycticorax</i>					
Green-winged teal	<i>Anas crecca</i>	Yes				
Willow tit	<i>Parus montanus</i>	Yes	Yes	Mature forest	Foliage glean	Yes
Japanese pygmy woodpecker	<i>Dendrocopos kizuki</i>	Yes	Yes	Mature forest	Stem	Yes
Little egret	<i>Egretta garzetta</i>	Yes				
Brown flycatcher	<i>Muscicapa dauurica</i>	Yes	Yes	Mature forest		

(Continued)

Common name	Scientific name	Diurnal and native	Forest- dependent	Successional stage	Foraging substrate	Frugivore
Red-rumped swallow	<i>Hirundo daurica</i>	Yes				
Nuthatch	<i>Sitta europaea</i>	Yes	Yes	Mature forest	Stem	Yes
Chinese bamboo partridge	<i>Bambusicola thoracica</i>					
Japanese reed bunting	<i>Emberiza yessoensis</i>	Yes	Yes	Early succ		
Little ringed plover	<i>Charadrius dubius</i>	Yes				
Common scops owl	<i>Otus scops</i>					
Mute swan	<i>Cygnus olor</i>	Yes				
Japanese robin	<i>Erithacus akahige</i>	Yes	Yes	Mature forest	Ground	Yes
Chestnut-cheeked starling	<i>Sturnus philippensis</i>	Yes	Yes	Mature forest	Foliage glean	Yes
Black-browed reed warbler	<i>Acrocephalus bistrigiceps</i>	Yes	Yes	Early succ		
Siberian blue robin	<i>Luscinia cyane</i>	Yes	Yes	Mature forest	Ground	
Green-backed heron	<i>Butorides striatus</i>					
Grey-faced buzzard	<i>Butastur indicus</i>	Yes	Yes	Mature forest	Edge predator	
Sooty flycatcher	<i>Muscicapa sibirica</i>	Yes	Yes	Mature forest		
Eurasian bittern	<i>Botaurus stellaris</i>	Yes				
Black paradise flycatcher	<i>Terpsiphone atrocaudata</i>	Yes	Yes	Mature forest		
Ashy minivet	<i>Pericrocotus divaricatus</i>	Yes	Yes	Mature forest	Foliage glean	
Great tit	<i>Parus major</i>	Yes	Yes	Mature forest	Foliage glean	Yes
Harlequin duck	<i>Histrionicus histrionicus</i>	Yes	Yes	Mature forest		
Yellow-breasted bunting	<i>Emberiza aureola</i>	Yes	Yes	Early succ		
Nutmeg mannikin	<i>Lonchura punctulata</i>					
Middendorff's grasshopper warbler	<i>Locustella ochotensis</i>	Yes	Yes	Early succ		
Hawfinch	<i>Coccothraustes coccothraustes</i>	Yes	Yes	Mature forest	Foliage glean	Yes
Horsfield's hawk-cuckoo	<i>Cuculus fugax</i>	Yes	Yes	Mature forest	Foliage glean	
Sand martin	<i>Riparia riparia</i>	Yes				
Collared turtle dove	<i>Streptopelia decaocto</i>	Yes	Yes	Early succ		
Chinese bulbul	<i>Pycnonotus sinensis</i>	Yes	Yes	Mature forest	Foliage glean	Yes
Kentish plover	<i>Charadrius alexandrinus</i>	Yes				
Pale thrush	<i>Turdus pallidus</i>	Yes	Yes	Mature forest	Ground	Yes
White-breasted waterhen	<i>Amaurornis phoenicurus</i>	Yes	Yes	Early succ		
Whistling green pigeon	<i>Treron formosae</i>	Yes	Yes	Mature forest		Yes
Malaysian night heron	<i>Gorsachius melanolophus</i>					
Greater scaup	<i>Aythya marila</i>	Yes				
Eurasian tree sparrow	<i>Passer montanus</i>	Yes	Yes	Early succ		
Black-winged stilt	<i>Himantopus himantopus</i>	Yes				
Indian cuckoo	<i>Cuculus micropterus</i>					
Japanese wagtail	<i>Motacilla grandis</i>	Yes	Yes	Early succ		
Fan-tailed warbler	<i>Cisticola juncidis</i>	Yes	Yes	Early succ		
Eastern crowned leaf warbler	<i>Phylloscopus coronatus</i>	Yes	Yes	Mature forest	Foliage glean	
Pecking robin	<i>Leiothrix lutea</i>					
Great egret	<i>Egretta alba</i>	Yes				
Common snipe	<i>Gallinago gallinago</i>					
Greater painted snipe	<i>Rostratula benghalensis</i>					
Japanese crane	<i>Grus japonensis</i>	Yes				
Hobby	<i>Falco subbuteo</i>	Yes	Yes	Mature forest	Edge predator	
Thick-billed shrike	<i>Lanius tigrinus</i>	Yes	Yes	Mature forest	Ground	
Red-faced cormorant	<i>Phalacrocorax urile</i>	Yes				
Intermediate egret	<i>Egretta intermedia</i>	Yes				
Eastern marsh harrier	<i>Circus spilonotus</i>	Yes				
Kestrel	<i>Falco tinnunculus</i>	Yes	Yes	Mature forest	Edge predator	
Dusky thrush	<i>Turdus naumanni</i>					
Oriental cuckoo	<i>Cuculus saturatus</i>	Yes	Yes	Mature forest	Foliage glean	
House swallow	<i>Hirundo rustica</i>	Yes				
Oriental pratincole	<i>Glareola maldivarum</i>	Yes				
Japanese sparrowhawk	<i>Accipiter gularis</i>	Yes	Yes	Mature forest	Edge predator	
Yellow wagtail	<i>Motacilla flava</i>	Yes	Yes	Early succ		
Domestic pigeon	<i>Columba livia</i>	Yes				
Black kite	<i>Milvus migrans</i>	Yes	Yes	Mature forest	Edge predator	
White's thrush	<i>Zoothera dauma</i>					
Long-eared owl	<i>Asio otus</i>					
Russet sparrow	<i>Passer rutilans</i>	Yes	Yes	Early succ		
Okinawa woodpecker	<i>Sapheopipo noguchii</i>	Yes	Yes	Mature forest	Stem	Yes

(Continued)

Common name	Scientific name	Diurnal and native	Forest-dependent	Successional stage	Foraging substrate	Frugivore
Siberian rubythroat	<i>Luscinia calliope</i>	Yes	Yes	Early succ		
Japanese yellow bunting	<i>Emberiza sulphurata</i>	Yes	Yes	Early succ		
Common buzzard	<i>Buteo buteo</i>	Yes	Yes	Mature forest	Edge predator	
Stonechat	<i>Saxicola torquata</i>	Yes	Yes	Early succ		
Sparrowhawk	<i>Accipiter nisus</i>	Yes	Yes	Mature forest	Edge predator	
White wagtail	<i>Motacilla lugens</i>	Yes				
Northern shoveler	<i>Anas clypeata</i>	Yes				
Marsh tit	<i>Parus palustris</i>	Yes	Yes	Mature forest	Foliage glean	Yes
Jungle crow	<i>Corvus macrorhynchos</i>	Yes	Yes	Mature forest	Foliage glean	Yes
Carrion crow	<i>Corvus corone</i>	Yes	Yes	Mature forest	Foliage glean	Yes
Oriental honey buzzard	<i>Pernis ptilorhynchus</i>	Yes	Yes	Mature forest	Edge predator	
Peregrine falcon	<i>Falco peregrinus</i>	Yes	Yes	Mature forest	Edge predator	
White-throated needle-tailed swift	<i>Hirundapus caudacutus</i>	Yes	Yes	Mature forest		
Muscovy duck	<i>Cairina moschata</i>	Yes				
Common moorhen	<i>Gallinula chloropus</i>	Yes				
Coal tit	<i>Parus ater</i>	Yes	Yes	Mature forest	Foliage glean	
Ruddy crane	<i>Porzana fusca</i>					
Common skylark	<i>Alauda arvensis</i>	Yes	Yes	Early succ		
House swift	<i>Apus affinis</i>	Yes				
Pelagic cormorant	<i>Phalacrocorax pelagicus</i>	Yes				
Brown-eared bulbul	<i>Hypsipetes amaurotis</i>	Yes	Yes	Mature forest	Foliage glean	Yes
Olive-backed pipit	<i>Anthus hodgsoni</i>	Yes	Yes	Early succ		
Ural owl	<i>Strix uralensis</i>					
Doller bird	<i>Eurystomus orientalis</i>	Yes	Yes	Mature forest		
Roseate tern	<i>Sterna dougallii</i>	Yes				
Long-tailed rosefinch	<i>Uragus sibiricus</i>	Yes	Yes	Early succ		
Chestnut-eared bunting	<i>Emberiza fucata</i>	Yes	Yes	Early succ		
Siberian meadow bunting	<i>Emberiza cioides</i>	Yes	Yes	Early succ		
Nutcracker	<i>Nucifraga caryocatactes</i>	Yes	Yes	Mature forest	Foliage glean	
Common pochard	<i>Aythya ferina</i>	Yes				
Little cuckoo	<i>Cuculus poliocephalus</i>	Yes	Yes	Mature forest	Foliage glean	
Mallard	<i>Anas platyrhynchos</i>	Yes				
Lanceolated grasshopper warbler	<i>Locustella lanceolata</i>	Yes	Yes	Early succ		
Siskin	<i>Carduelis spinus</i>	Yes	Yes	Mature forest		
Siberian Thrush	<i>Turdus sibirica</i>	Yes	Yes	Mature forest	Ground	Yes
Bridled tern	<i>Sterna anaethetus</i>	Yes				
Osprey	<i>Pandion haliaetus</i>	Yes				
Japanese night heron	<i>Gorsachius goisagi</i>					
Winter wren	<i>Troglodytes troglodytes</i>	Yes	Yes	Mature forest	Ground	
Barred button quail	<i>Turnix suscitator</i>	Yes	Yes	Early succ		
Grey starling	<i>Sturnus cineraceus</i>	Yes	Yes	Early succ		
Purple heron	<i>Ardea purpurea</i>	Yes				
Bonin Islands white-eye	<i>Apalopteron familiare</i>	Yes	Yes	Mature forest	Foliage glean	Yes
Japanese white-eye	<i>Zosterops japonicus</i>	Yes	Yes	Mature forest	Foliage glean	Yes
Arctic warbler	<i>Phylloscopus borealis</i>	Yes	Yes	Mature forest	Foliage glean	
Bull-headed shrike	<i>Lanius bucephalus</i>	Yes	Yes	Early succ		
Fairy pitta	<i>Pitta brachyura</i>	Yes	Yes	Mature forest	Ground	Yes
Short-tailed bush warbler	<i>Urosphena squameiceps</i>	Yes	Yes	Mature forest	Foliage glean	
Varied tit	<i>Parus varius</i>	Yes	Yes	Mature forest	Foliage glean	Yes
Grey-headed woodpecker	<i>Picus canus</i>	Yes	Yes	Mature forest	Stem	Yes
Eurasian woodcock	<i>Scolopax rusticola</i>					
Greater pied kingfisher	<i>Ceryle lugubris</i>	Yes	Yes	Mature forest		
Copper pheasant	<i>Syrnaticus soemmerringii</i>	Yes	Yes	Mature forest	Ground	
Okinawa rail	<i>Gallirallus okinawae</i>	Yes	Yes	Mature forest	Ground	Yes
Falcated teal	<i>Anas falcata</i>	Yes				
Chinese little bittern	<i>Ixobrychus sinensis</i>					
Jungle nightjar	<i>Caprimulgus indicus</i>					
Rock ptarmigan	<i>Lagopus mutus</i>	Yes	Yes	Early succ		
Ryukyu scops owl	<i>Otus elegans</i>					
Pacific swallow	<i>Hirundo tahitica</i>	Yes				
Lidth's jay	<i>Garrulus lidthi</i>	Yes	Yes	Mature forest	Foliage glean	Yes
Red-flanked bushrobin	<i>Tarsiger cyanurus</i>	Yes	Yes	Mature forest	Ground	Yes

Appendix 4. Ranges of response and explanatory variables.

	Min	25%	50%	75%	Max
(a) 5 × 5 km (n = 1724)					
Species richness					
Forest species	0	11	15	19	39
Foliage gleaner	0	7	9	11	20
Frugivore	0	8	10	13	23
Transect length covered by forest (Effort) (km)	0	1.2	2.1	2.7	3.3
Climate and topography					
Annual temperature (ATP) (°C)	−0.1	7.3	10.7	13.5	17.6
Temperature in breeding season (BTP) (°C)	8.5	14.8	17.9	20.1	23.1
Temperature in wintering season (WTP) (°C)	−12.8	−3.3	0.4	3.7	9.4
Annual precipitation (APP) (mm)	680	1289	1604	2110	3922
Precipitation in breeding season (BPP) (mm)	159	359	490	687	1552
Precipitation in wintering season (WPP) (mm)	53	151	224	318	1196
Mean elevation (ELV) (m)	0	74	242	529	2328
Range of elevation (RngELV) (m)*	1	119	265	442	1606
NDVI					
Average through twelve months (ANDVI)	0.01	0.46	0.53	0.65	0.82
Average in breeding season (BNDVI)	0.01	0.62	0.72	0.77	0.85
Average in wintering season (WNDVI)	−0.01	0.18	0.34	0.55	0.83
Land-use (area: m ²)					
Natural forest (NATL)	0	3852929	8816639	13846570	25728507
Conifer plantation (PLANT)	0	1552796	5125902	9654441	24422137
Arable field (ARABL)	0	69368	603565	2113387	17894370
Paddy field (PADDY)	0	14013	1098700	3585584	24869167
Xeric grassland (XLCGRS)	0	220532	812051	2089034	18907761
Mesic grassland (MSCGRS)	0	0	0	62077	10896666
Urban (URBAN)	0	19856	291699	1540173	25871501
(b) 10 × 10 km (n = 1633)					
Species richness					
Forest species	0	11	15	19	39
Foliage gleaner	0	7	9	11	20
Frugivore	0	8	11	13	23
Transect length covered by forest (Effort) (km)	0	1.2	2.1	2.7	5.7
Climate and topography					
Annual temperature (ATP) (°C)	−1	7	11	14	18
Temperature in breeding season (°C)	8	15	18	20	23
Temperature in wintering season (°C)	−14	−4	1	4	10
Annual precipitation (APP) (mm)	700	1294	1603	2111	3647
Precipitation in breeding season (mm)	179	363	492	695	1526
Precipitation in wintering season (mm)	56	153	222	317	1173
Mean elevation (ELV) (m)	1	95	263	509	2208
Range of elevation (m)	4	243	463	722	2012
NDVI					
Average through twelve months	0.09	0.46	0.52	0.64	0.81
Average in breeding season (or spring)	0.12	0.60	0.71	0.76	0.86
Average in wintering season (or winter)	0.00	0.18	0.34	0.54	0.82
Land-use (area: m ²)					
Natural forest (NATL)	0	17071870	35333807	54262088	100912463
Conifer plantation (PLANT)	0	8431595	20254698	36111836	92493686
Arable field (ARABL)	0	904284	3054737	9457089	76645205
Paddy field (PADDY)	0	802221	6112228	16401878	82650051
Xeric grassland	0	1543293	3695209	7732118	71679575
Mesic grassland	0	0	29710	391338	24879159
Urban (URBAN)	0	309723	1619679	6718484	94836718
(c) 20 × 20 km (n = 868)					
Species richness					
Forest species	1	15	20	25	41
Foliage gleaner	0	9	11	14	20
Frugivore	1	11	13	16	25
Transect length covered by forest (Effort) (km)	0	2.25	3.3	4.8	9.9

(Continued)

Appendix 4. (Continued)

	Min	25%	50%	75%	Max
Climate and topography					
Annual temperature (ATP) (°C)	-1	7	10	13	17
Temperature in breeding season (°C)	9	15	18	20	23
Temperature in wintering season (°C)	-13	-4	0	4	9
Annual precipitation (APP) (mm)	710	1295	1582	2103	3556
Precipitation in breeding season (mm)	181	358	486	677	1392
Precipitation in wintering season (mm)	59	156	225	323	1117
Mean elevation (ELV) (m)	3	131	282	522	2115
Range of elevation (m)	16	476	728	1046	3212
NDVI					
Average through twelve months	0.21	0.45	0.51	0.62	0.79
Average in breeding season (or spring)	0.24	0.60	0.70	0.75	0.84
Average in wintering season (or winter)	0.02	0.17	0.32	0.52	0.80
Land-use (area: m ²)					
Natural forest (NATL)	0	78315138	143194286	212829510	368454652
Conifer plantation (PLANT)	0	43014948	80339630	137781831	337865822
Arable field (ARABL)	0	4769534	14303169	35565851	287387809
Paddy field (PADDY)	0	5953225	28636902	61979366	285204658
Xeric grassland	0	8174974	17009564	29489655	278477501
Mesic grassland	0	18999	376489	1776416	128649373
Urban (URBAN)	0	1892255	7906908	23627709	325391878
(d) 40 × 40 km (n = 234)					
Species richness					
Forest species	10	26	33	37	50
Foliage gleaner	6	15	16	18	24
Frugivore	9	16	19	21	28
Transect length covered by forest (Effort) (km)	1.5	9.3	12.1	15.5	24.6
Climate and topography					
Annual temperature (ATP) (°C)	1.9	7.2	10.5	13.1	16.2
Temperature in breeding season (°C)	11.0	14.7	17.4	19.8	22.0
Temperature in wintering season (°C)	-11.1	-3.7	0.2	3.2	7.8
Annual precipitation (APP) (mm)	756	1324	1667	2151	3285
Precipitation in breeding season (mm)	200	374	502	688	1301
Precipitation in wintering season (mm)	77	160	235	325	997
Mean elevation (ELV) (m)	15	178	308	477	1438
Range of elevation (m)	44	766	1086	1430	3342
NDVI					
Average through twelve months	0.27	0.45	0.50	0.59	0.77
Average in breeding season (or spring)	0.32	0.59	0.68	0.74	0.81
Average in wintering season (or winter)	0.04	0.18	0.34	0.49	0.77
Land-use (area: m ²)					
Natural forest (NATL)	13886909	326356076	558481332	807560570	1369968959
Conifer plantation (PLANT)	1739587	208983070	321660047	485074155	1239121432
Arable field (ARABL)	109756	28684999	68005531	140849245	781897675
Paddy field (PADDY)	0	45454169	137196721	240489741	673156995
Xeric grassland	487054	36804013	73365477	113370026	777585597
Mesic grassland	0	844077	3155411	8035005	150888174
Urban (URBAN)	0	13452333	44296721	85911396	908230770
(e) 80 × 80 km (n = 59)					
Species richness					
Forest species	22	37	45	49	57
Foliage gleaner	13	18	20	22	25
Frugivore	13	21	23	26	32
Transect length covered by forest (Effort) (km)	21.4	35.7	44.3	52.5	66.8
Climate and topography					
Annual temperature (ATP) (°C)	3.2	7.5	9.7	13.0	15.6
Temperature in breeding season (°C)	12.0	15.0	17.0	19.8	21.6
Temperature in wintering season (°C)	-9.9	-3.2	-0.6	3.3	6.7
Annual precipitation (APP) (mm)	942	1327	1594	2165	2721
Precipitation in breeding season (mm)	225	361	474	683	1144
Precipitation in wintering season (mm)	91	177	230	314	797
Mean elevation (ELV) (m)	21	229	347	455	1189
Range of elevation (m)	134	1172	1500	1795	3388

(Continued)

Appendix 4. (Continued)

	Min	25%	50%	75%	Max
NDVI					
Average through twelve months	0.36	0.45	0.49	0.57	0.68
Average in breeding season (or spring)	0.45	0.60	0.65	0.71	0.78
Average in wintering season (or winter)	0.06	0.19	0.34	0.49	0.66
Land-use (area: m ²)					
Natural forest (NATL)	224869069	1237013674	2084132785	2919326591	4196784240
Conifer plantation (PLANT)	69817273	846216622	1146650471	1877909412	2901207696
Arable field (ARABL)	27446749	143855165	293166186	500854486	1596460356
Paddy field (PADDY)	0	290800066	587687415	850845942	1667634313
Xeric grassland	15344030	189819720	287919481	424744634	1159375193
Mesic grassland	900595	5086951	16425527	27703768	291561697
Urban (URBAN)	14114073	83094530	187904634	356979177	2269057747

Minimum value, 25%, 50%, 75% percentiles, and the maximum value of each variable are shown. *Range of elevation = maximum elevation–minimum elevation.

Appendix 5. Details of seven land-use types.

Habitat type	Details and composite sub-habitat classes
Natural forest	Naturally regenerated forests including secondary forests, e.g. evergreen and deciduous broad-leaved forest, mixed forest
Conifer plantation	Artificially regenerated coniferous forests, e.g. Japanese cedar <i>Cryptomeria japonica</i> plantation, hinoki cypress <i>Chamaecyparis obtusa</i> plantation, Japanese larch <i>Larix leptolepis</i> plantation
Arable field	Cropland excluding paddy field, and orchard
Paddy field	Flooded cropland, mainly for rice <i>Oryza sativa</i>
Xeric grassland	Semi-natural grassland, pasture, meadow, clear-cut, golf course
Mesic grassland	Marsh vegetation, fen vegetation, abandoned paddy field
Urban	Road, building

Appendix 6. Correlation matrix for explanatory variables.

	Effort	ATP	BTP	WTP	APP	BPP	WPP	ELV	RngELV	ANDVI	BNDVI	WNDVI	NATL	PLANT	ARABL	PADDY	XLCGRS	MSCGRS	URBAN
(a) 5 × 5 km																			
Effort	1.00																		
ATP	-0.24	1.00																	
BTP	-0.22	0.98	1.00																
WTP	-0.22	0.99	0.95	1.00															
APP	0.22	0.31	0.29	0.35	1.00														
BPP	0.16	0.50	0.48	0.52	0.84	1.00													
WPP	0.13	-0.06	-0.04	-0.05	0.56	0.12	1.00												
ELV	0.42	-0.42	-0.40	-0.39	0.35	0.30	0.14	1.00											
RngELV	0.47	-0.25	-0.24	-0.21	0.45	0.37	0.23	0.78	1.00										
ANDVI	0.43	0.19	0.21	0.21	0.48	0.60	-0.03	0.38	0.47	1.00									
BNDVI	0.51	-0.33	-0.28	-0.33	0.25	0.17	0.21	0.45	0.49	0.76	1.00								
WNDVI	0.24	0.57	0.55	0.59	0.50	0.74	-0.20	0.20	0.30	0.86	0.33	1.00							
NATL	0.45	-0.42	-0.38	-0.40	0.12	-0.04	0.26	0.47	0.48	0.30	0.57	0.00	1.00						
PLANT	0.34	0.04	0.05	0.06	0.36	0.41	-0.01	0.28	0.34	0.65	0.50	0.56	-0.18	1.00					
ARABL	-0.31	0.18	0.19	0.15	-0.25	-0.13	-0.25	-0.28	-0.30	-0.18	-0.25	-0.08	-0.41	-0.15	1.00				
PADDY	-0.39	0.45	0.49	0.42	-0.06	0.01	0.00	-0.38	-0.39	-0.19	-0.35	0.00	-0.41	-0.27	0.17	1.00			
XLCGRS	-0.08	-0.34	-0.35	-0.33	-0.18	-0.18	-0.07	0.00	-0.07	-0.11	0.10	-0.26	-0.06	-0.15	-0.12	-0.21	1.00		
MSCGRS	-0.21	-0.04	-0.07	-0.03	-0.13	-0.11	-0.08	-0.12	-0.18	-0.21	-0.20	-0.16	-0.16	-0.18	0.01	0.09	0.06	1.00	
URBAN	-0.35	0.40	0.41	0.37	-0.12	-0.04	-0.13	-0.33	-0.36	-0.45	-0.64	-0.14	-0.42	-0.33	0.15	0.31	-0.12	0.12	1.00
(b) 10 × 10 km																			
Effort	1.00																		
ATP	-0.21	1.00																	
BTP	-0.21	0.98	1.00																
WTP	-0.19	0.99	0.96	1.00															
APP	0.18	0.33	0.31	0.37	1.00														
BPP	0.12	0.53	0.51	0.55	0.83	1.00													
WPP	0.11	-0.07	-0.06	-0.06	0.55	0.10	1.00												
ELV	0.37	-0.43	-0.41	-0.40	0.31	0.24	0.14	1.00											
RngELV	0.39	-0.28	-0.28	-0.24	0.43	0.31	0.25	0.81	1.00										
ANDVI	0.36	0.16	0.17	0.18	0.47	0.58	-0.04	0.38	0.43	1.00									
BNDVI	0.43	-0.40	-0.36	-0.39	0.22	0.12	0.20	0.49	0.50	0.75	1.00								
WNDVI	0.18	0.58	0.56	0.59	0.51	0.75	-0.22	0.17	0.24	0.85	0.30	1.00							
NATL	0.36	-0.48	-0.46	-0.47	0.08	-0.10	0.28	0.51	0.47	0.28	0.58	-0.07	1.00						
PLANT	0.28	0.06	0.06	0.08	0.40	0.45	-0.04	0.27	0.33	0.69	0.51	0.60	-0.17	1.00					
ARABL	-0.26	0.18	0.19	0.15	-0.26	-0.11	-0.28	-0.28	-0.26	-0.18	-0.26	-0.07	-0.45	-0.14	1.00				
PADDY	-0.31	0.45	0.50	0.42	-0.09	-0.01	0.00	-0.40	-0.40	-0.20	-0.35	0.01	-0.42	-0.28	0.20	1.00			
XLCGRS	-0.02	-0.37	-0.39	-0.37	-0.19	-0.20	-0.07	0.01	-0.07	-0.08	0.16	-0.27	0.01	-0.13	-0.12	-0.24	1.00		
MSCGRS	-0.18	-0.02	-0.05	-0.02	-0.15	-0.13	-0.09	-0.14	-0.20	-0.22	-0.21	-0.16	-0.16	-0.18	0.04	0.12	0.07	1.00	
URBAN	-0.32	0.44	0.45	0.41	-0.13	-0.03	-0.15	-0.35	-0.35	-0.44	-0.65	-0.11	-0.44	-0.33	0.19	0.33	-0.15	0.15	1.00
(c) 20 × 20 km																			
Effort	1.00																		
ATP	-0.09	1.00																	
BTP	-0.09	0.98	1.00																

(Continued)

Appendix 6. (Continued)

	Effort	ATP	BTP	WTP	APP	BPP	WPP	ELV	RngELV	ANDVI	BNDVI	WNDVI	NATL	PLANT	ARABL	PADDY	XLGGRS	MSCGRS	URBAN
WTP	-0.08	0.99	0.96	1.00															
APP	0.14	0.38	0.36	0.41	1.00														
BPP	0.12	0.59	0.57	0.60	0.82	1.00													
WPP	0.04	-0.05	-0.03	-0.04	0.57	0.09	1.00												
ELV	0.29	-0.42	-0.40	-0.39	0.27	0.19	0.14	1.00											
RngELV	0.30	-0.28	-0.27	-0.25	0.40	0.26	0.26	0.83	1.00										
ANDVI	0.30	0.21	0.22	0.21	0.46	0.59	-0.08	0.38	0.38	1.00									
BNDVI	0.30	-0.40	-0.35	-0.40	0.20	0.08	0.19	0.51	0.47	0.71	1.00								
WNDVI	0.19	0.62	0.60	0.63	0.49	0.76	-0.24	0.15	0.18	0.85	0.25	1.00							
NATL	0.19	-0.53	-0.50	-0.52	0.06	-0.16	0.32	0.55	0.47	0.22	0.59	-0.14	1.00						
PLANT	0.24	0.14	0.13	0.15	0.41	0.48	-0.08	0.23	0.27	0.72	0.48	0.63	-0.21	1.00					
ARABL	-0.16	0.16	0.18	0.13	-0.27	-0.09	-0.32	-0.25	-0.21	-0.17	-0.25	-0.05	-0.47	-0.08	1.00				
PADDY	-0.15	0.48	0.52	0.44	-0.05	0.03	0.02	-0.41	-0.36	-0.15	-0.33	0.06	-0.42	-0.21	0.21	1.00			
XLGGRS	0.00	-0.41	-0.42	-0.41	-0.25	-0.24	-0.11	0.01	-0.08	-0.07	0.22	-0.27	0.05	-0.12	-0.11	-0.25	1.00		
MSCGRS	-0.12	-0.05	-0.09	-0.05	-0.14	-0.11	-0.08	-0.12	-0.18	-0.18	-0.16	-0.14	-0.11	-0.17	0.03	0.06	0.12	1.00	
URBAN	-0.20	0.46	0.47	0.43	-0.09	0.02	-0.15	-0.34	-0.32	-0.37	-0.61	-0.04	-0.45	-0.28	0.23	0.38	-0.17	0.13	1.00
(d) 40 × 40 km																			
Effort	1.00																		
ATP	-0.07	1.00																	
BTP	-0.05	0.99	1.00																
WTP	-0.07	1.00	0.97	1.00															
APP	0.14	0.48	0.46	0.50	1.00														
BPP	0.16	0.67	0.65	0.68	0.83	1.00													
WPP	-0.02	-0.02	0.01	-0.01	0.55	0.07	1.00												
ELV	0.43	-0.34	-0.32	-0.32	0.23	0.15	0.12	1.00											
RngELV	0.41	-0.24	-0.22	-0.21	0.34	0.20	0.23	0.85	1.00										
ANDVI	0.43	0.27	0.29	0.28	0.44	0.60	-0.12	0.43	0.37	1.00									
BNDVI	0.40	-0.44	-0.38	-0.44	0.10	-0.01	0.18	0.57	0.50	0.63	1.00								
WNDVI	0.27	0.68	0.67	0.69	0.50	0.78	-0.26	0.16	0.15	0.84	0.14	1.00							
NATL	0.28	-0.52	-0.47	-0.52	-0.01	-0.23	0.32	0.58	0.46	0.18	0.63	-0.20	1.00						
PLANT	0.37	0.17	0.17	0.18	0.37	0.48	-0.14	0.27	0.31	0.74	0.45	0.63	-0.21	1.00					
ARABL	-0.14	0.09	0.10	0.06	-0.30	-0.09	-0.37	-0.17	-0.11	-0.13	-0.21	-0.04	-0.40	0.00	1.00				
PADDY	-0.17	0.49	0.55	0.46	0.00	0.08	0.05	-0.33	-0.24	-0.04	-0.25	0.15	-0.32	-0.10	0.18	1.00			
XLGGRS	0.06	-0.50	-0.51	-0.49	-0.33	-0.32	-0.14	0.02	-0.06	-0.09	0.27	-0.32	0.12	-0.14	-0.09	-0.30	1.00		
MSCGRS	-0.17	-0.10	-0.15	-0.10	-0.21	-0.18	-0.12	-0.17	-0.22	-0.24	-0.17	-0.20	-0.10	-0.21	0.02	0.03	0.26	1.00	
URBAN	-0.16	0.47	0.48	0.44	-0.06	0.06	-0.16	-0.30	-0.24	-0.25	-0.55	0.07	-0.41	-0.19	0.26	0.46	-0.22	0.20	1.00
(e) 80 × 80 km																			
Effort	1.00																		
ATP	-0.02	1.00																	
BTP	0.04	0.99	1.00																
WTP	-0.04	1.00	0.98	1.00															
APP	0.09	0.53	0.54	0.55	1.00														

(Continued)

Appendix 6. (Continued)

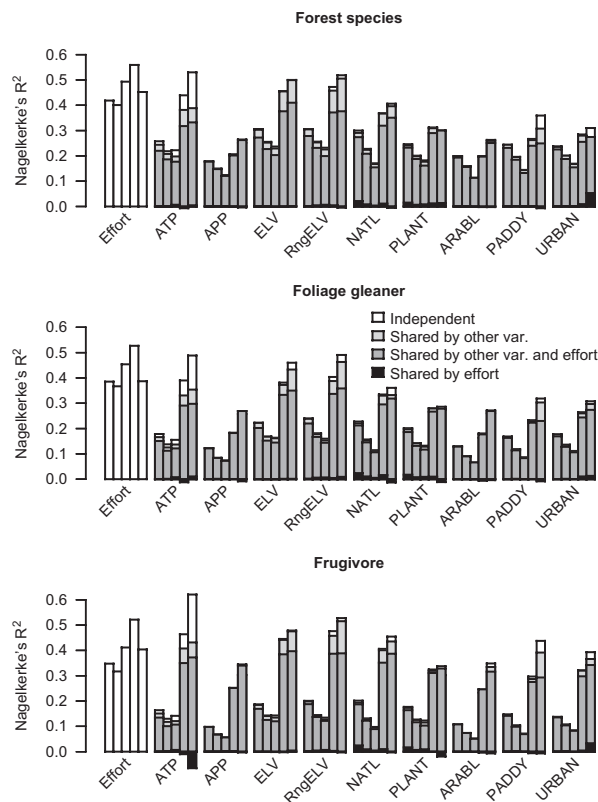
	Effort	ATP	BTP	WTP	APP	BPP	WPP	ELV	RngELV	ANDVI	BNDVI	WNDVI	NATL	PLANT	ARABL	PADDY	XLGGRS	MSCGRS	URBAN
BPP	0.14	0.75	0.75	0.75	0.83	1.00													
WPP	-0.02	-0.09	-0.06	-0.07	0.54	0.06	1.00												
ELV	0.59	-0.23	-0.20	-0.22	0.24	0.13	0.20	1.00											
RngELV	0.47	-0.20	-0.17	-0.19	0.31	0.13	0.28	0.87	1.00										
ANDVI	0.46	0.43	0.45	0.43	0.49	0.68	-0.17	0.43	0.30	1.00									
BNDVI	0.46	-0.46	-0.40	-0.46	0.09	-0.06	0.25	0.62	0.49	0.47	1.00								
WNDVI	0.25	0.78	0.78	0.78	0.52	0.81	-0.32	0.15	0.07	0.86	-0.03	1.00							
NATL	0.49	-0.54	-0.47	-0.54	-0.09	-0.29	0.36	0.61	0.47	0.12	0.74	-0.29	1.00						
PLANT	0.42	0.31	0.31	0.32	0.39	0.54	-0.23	0.31	0.31	0.71	0.28	0.64	-0.18	1.00					
ARABL	-0.13	0.07	0.06	0.05	-0.35	-0.10	-0.48	-0.17	-0.05	-0.10	-0.21	0.00	-0.36	0.07	1.00				
PADDY	0.05	0.55	0.59	0.53	0.11	0.20	0.05	-0.18	-0.07	0.09	-0.21	0.26	-0.16	0.06	0.18	1.00			
XLGGRS	0.24	-0.60	-0.59	-0.62	-0.43	-0.41	-0.14	0.11	0.02	-0.08	0.46	-0.37	0.39	-0.19	0.05	-0.34	1.00		
MSCGRS	-0.24	-0.09	-0.12	-0.08	-0.21	-0.17	-0.14	-0.20	-0.16	-0.23	-0.14	-0.16	-0.12	-0.22	0.02	0.05	0.11	1.00	
URBAN	0.04	0.50	0.51	0.47	0.01	0.14	-0.19	-0.22	-0.07	-0.09	-0.50	0.21	-0.34	-0.03	0.29	0.47	-0.26	0.26	1.00

See Appendix 4 for variable abbreviations

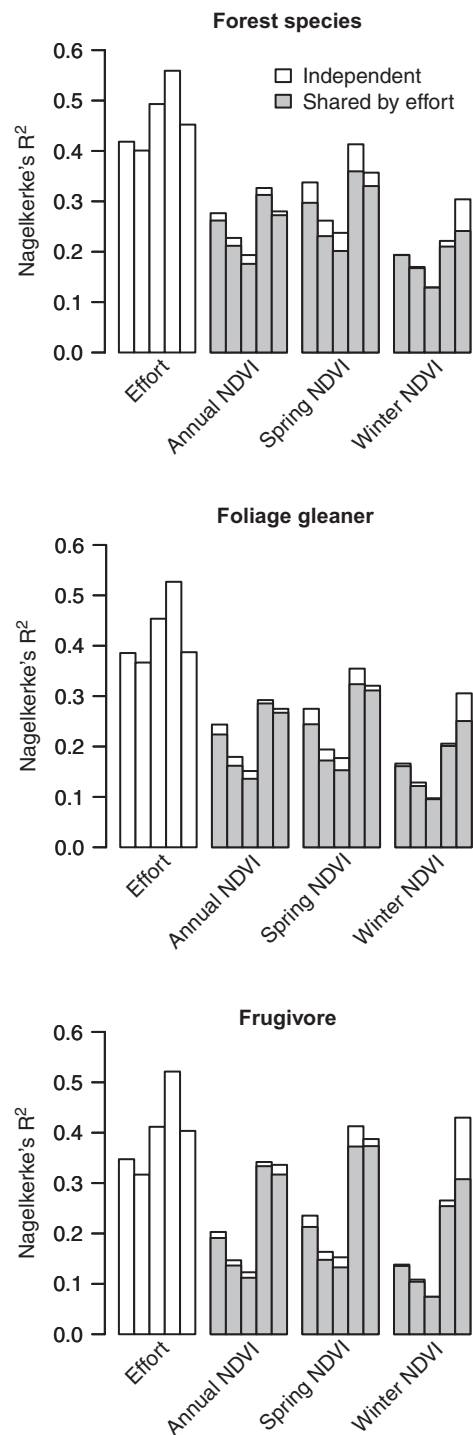
Appendix 7. Results of regression analysis. We examined the support of each model by Nagelkerke pseudo- R^2 and w_i (Akaike weight). Akaike's information criterion (AIC) and Δ_i were required for the calculation of w_i (Burnham and Anderson 2002).

Response variable	Explanatory variable	SAR model type	Nagelkerke's R^2	AIC	Δ_i	exp $(-\Delta_i/2)$	w_i (%)	Estimate ($\hat{\psi}$)
Forest species richness	annual temperature	linear	0.66	1386	14	0	0	8.1
		quadratic	0.68	1372	0	1	55	
		piecewise	0.68	1372	0	1	45	
Natural forest	annual temperature	linear	0.52	9626	12	0	0	5.3
		quadratic	0.53	9620	7	0	3	
		piecewise	0.55	9613	0	1	97	
		OLS linear*	0.28	9720	15	0	0	12.6
		OLS quadratic*	0.30	9713	8	0	1	
		OLS piecewise*	0.33	9705	0	1	98	
NDVI in spring	annual temperature	linear	0.41	-513	50	0	0	11.3
		quadratic	0.49	-545	19	0	0	
		piecewise	0.53	-563	0	1	100	
Forest species richness	elevation	linear	0.62	1412	26	0	0	267
		quadratic	0.64	1401	15	0	0	
		piecewise	0.66	1386	0	1	100	
Natural forest	elevation	linear	0.50	9633	19	0	0	197
		quadratic	0.53	9623	9	0	1	
		piecewise	0.55	9614	0	1	99	
NDVI in spring	elevation	linear	0.41	-515	75	0	0	453
		quadratic	0.56	-582	7	0	3	
		piecewise	0.58	-589	0	1	97	
Forest species richness	natural forest	linear	0.59	1431	12	0	0	662094129
		quadratic	0.61	1420	1	1	35	
		piecewise	0.61	1419	0	1	65	
Forest species richness	NDVI in spring	linear	0.61	1416	0	1	50	0.50
		quadratic	0.61	1417	2	0	23	
		piecewise	0.61	1417	1	1	26	
Forest species richness	conifer plantation	linear	0.57	1438	6	0	5	223230937
		quadratic	0.58	1435	3	0	14	
		piecewise	0.59	1432	0	1	81	

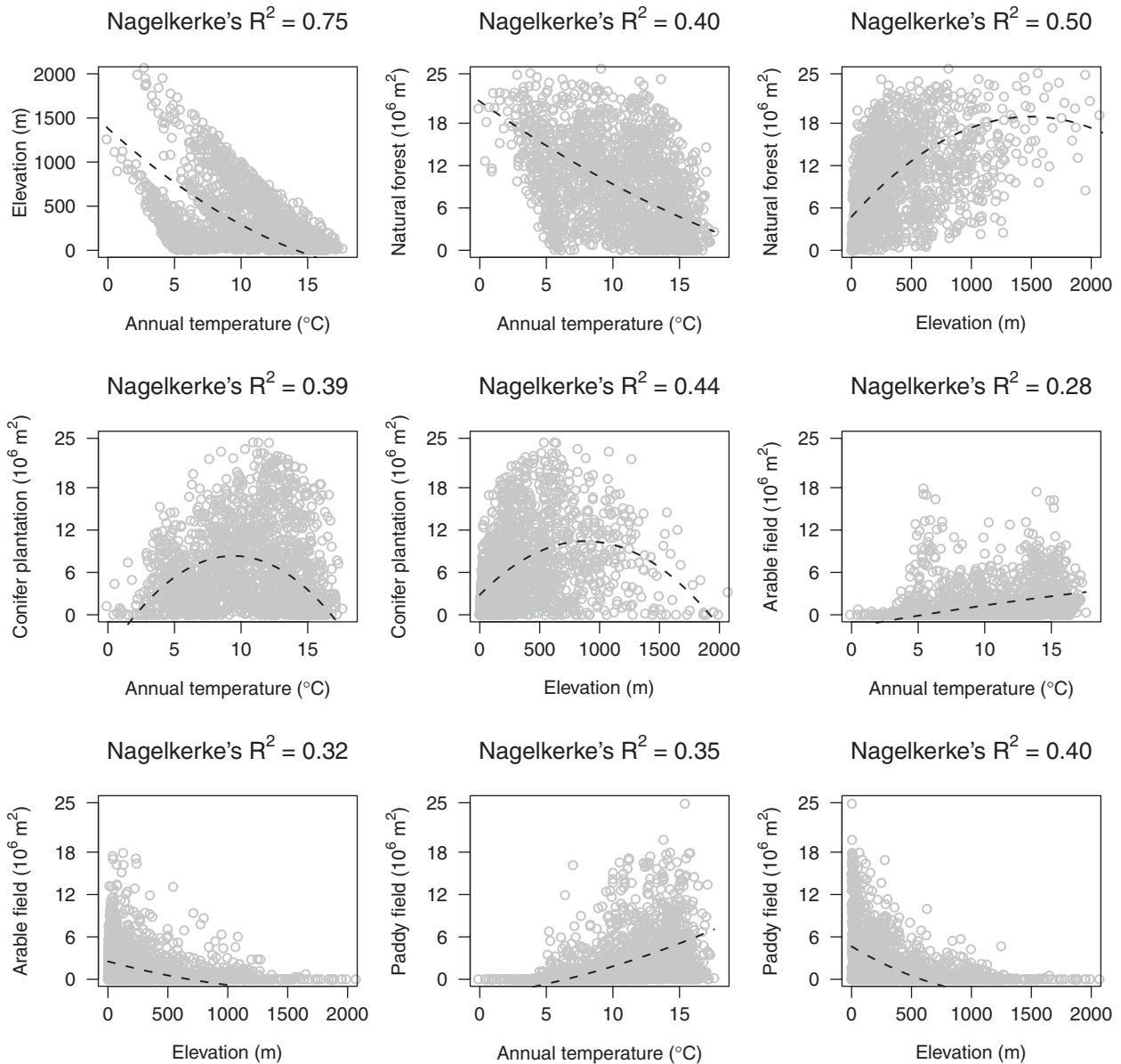
*These three regression models are ordinary least squared (OLS) regressions rather than simultaneously autoregressions (SARs). R^2 is not Nagelkerke's pseudo- R^2 but normal R^2



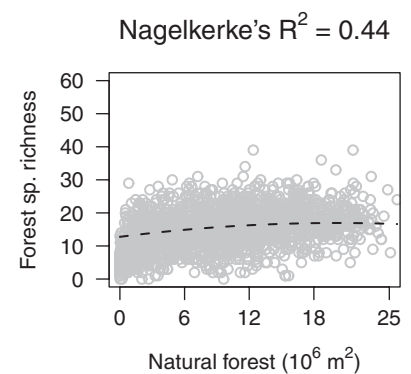
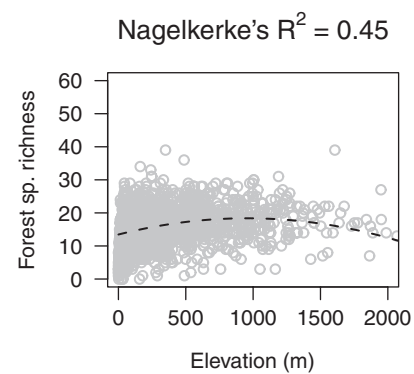
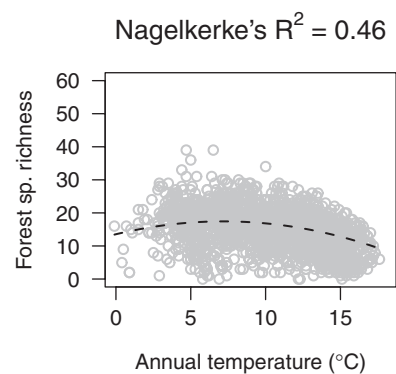
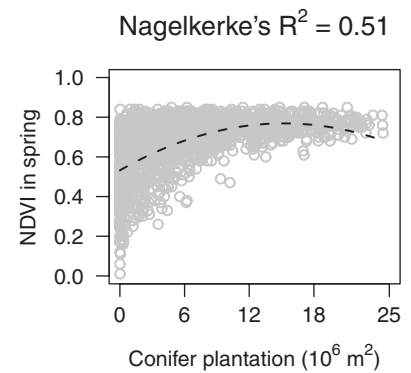
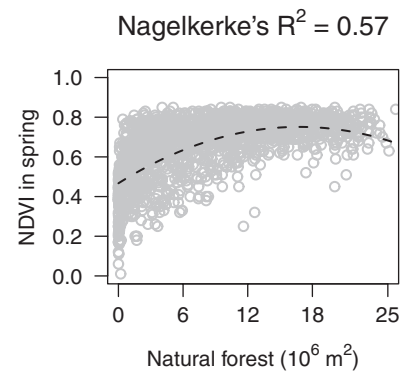
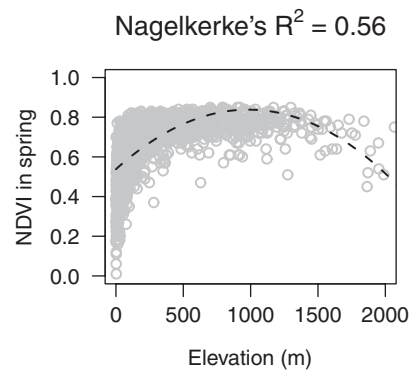
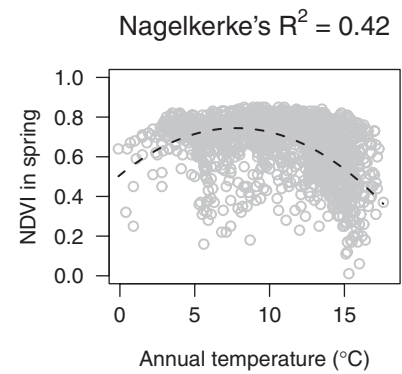
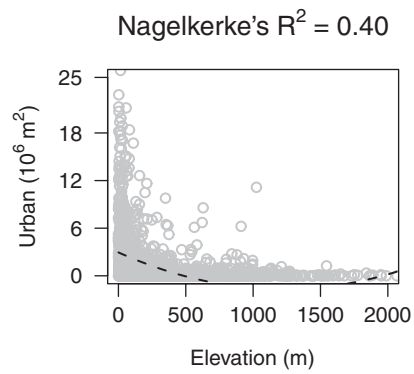
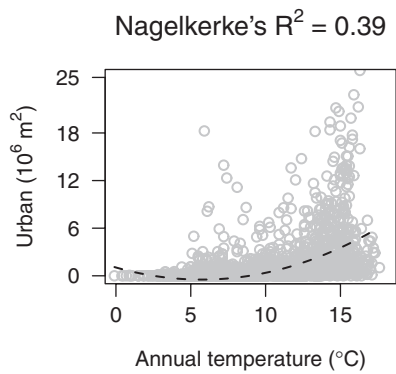
Appendix 8. Results of partial regression analysis for nine explanatory variables. Effects of each variable at 5-, 10-, 20-, 40- and 80-km resolutions are shown in groups arranged from left to right, respectively. Abbreviations: Effort (census effort); ATP (annual temperature); APP (annual precipitation); ELV (mean elevation); RngELV (range of elevation); NATL (natural forest area); PLANT (conifer plantation area); ARABL (arable field area); PADDY (paddy field area); URBAN (urban area). The explained variation in each response variable (Nagelkerke pseudo- R^2) includes not only the effects of explanatory variables but also the effects of spatial error terms. Total effect of census effort was not decomposed.



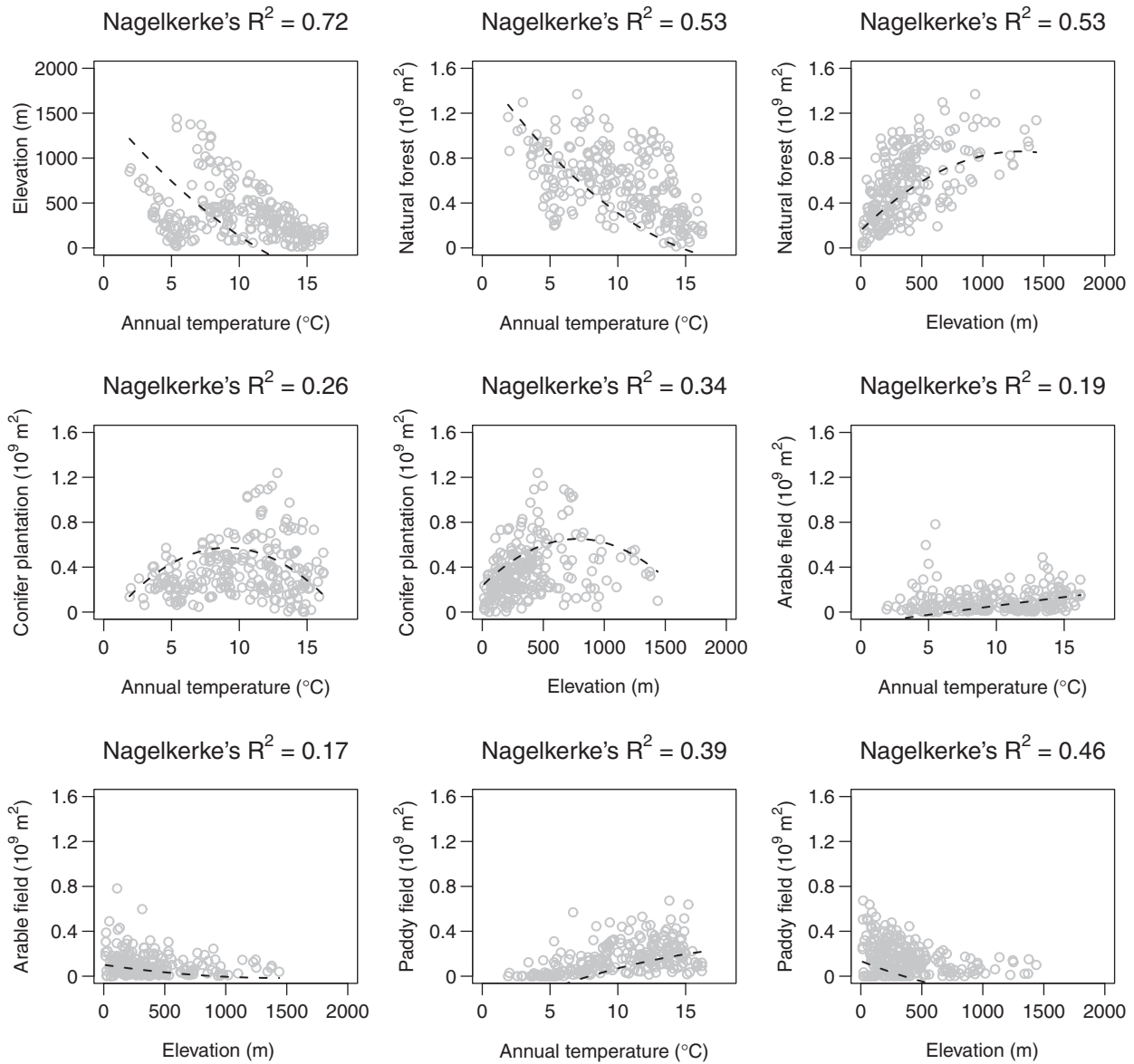
Appendix 9. Results of partial regression analysis for three NDVI variables. Figures are depicted the same as in Appendix 8.



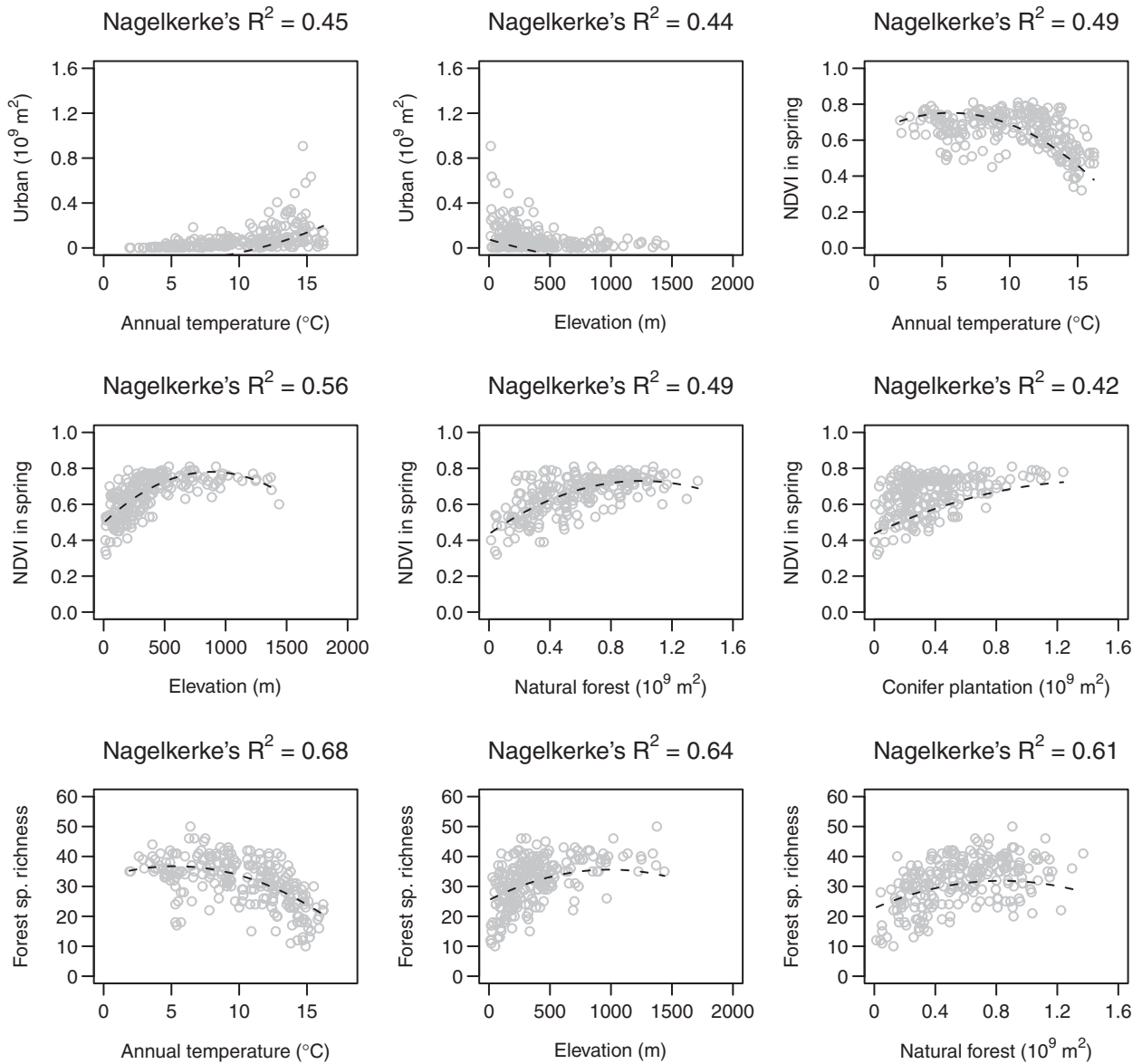
Appendix 10. Relationships among climate/topography, land use, NDVI, and forest species richness at 5-km resolution. Broken lines represent fitted quadratic lines of simultaneous autoregression, SAR. When species richness was treated as a response variable, simple and quadratic terms of census effort were also used as explanatory variables (covariates). In the regression, census effort was held to the average value, and spatial error terms were set to zero.



Appendix 10. (Continued)



Appendix 11. Relationships among climate/topography, land use, NDVI, and forest species richness at 40-km resolution. Figures are depicted in the same way as in Appendix 10.



Appendix 11. (Continued)