

Biodiversity of man-made open habitats in an underused country: a class of multispecies abundance models for count data

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Abstract Since the 1960s, Japan has become highly dependent on foreign countries for natural resources, and the amount of managed lands (e.g. coppice, grassland, and agricultural field) has declined. Due to infrequent natural and human disturbance, early-successional species are now declining in Japan. Here we surveyed bees, birds, and plants in four human-disturbed open habitats (pasture, meadow, young planted forest, and abandoned clear-cut) and two forest habitats (mature planted forest and natural old-growth). We extended a recently developed multispecies abundance model to accommodate count data, and used the resulting models to estimate species-, functional group-, and community-level state variables (abundance and species richness) at each site, and compared them among the six habitats. Estimated individual-level detection probability was quite low for bee

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species (mean across species = 0.003; 0.16 for birds). Thirty-two (95% credible interval: 13–64) and one (0–4) bee and bird species, respectively, were suggested to be undetected by the field survey. Although habitats in which community-level abundance and species richness was highest differed among taxa, species richness and abundance of early-successional species were similar in the four disturbed open habitats across taxa except for plants in the pasture habitat which was a good habitat only for several exotic species. Our results suggest that human disturbance, especially the revival of plantation forestry, may contribute to the restoration of early-successional species in Japan.

Keywords Count data · Functional group · Hierarchical community model · Human disturbance · Plantation forestry · Species richness

Introduction

Biodiversity and its threats vary geographically, for example the tropics are an important biodiversity ‘hot spots’ (Myers et al. 2000). However biodiversity threats can also vary in time. For example, landuse is an important threat which varies in space and time (Ellis and Ramankutty 2008). For example, deforestation rates recently declined in Brazil and Indonesia, which had the highest loss of forest in the 1990s (FAO 2010). In many other countries, forests are expanding by afforestation (Kauppi et al. 2006; Meyfroidt et al. 2010). Forest regeneration in abandoned agricultural areas, which is called forest transition, has occurred during the 20th century in the temperate regions, and is now occurring in the tropics (Asner et al. 2009; Ellis et al. 2010).

Japanese people have used their land for millennia. The most drastic changes in land-use occurred after the 1950s. Intensification of agricultural areas progressed during the period 1960–1990. For example, the proportion of rice paddies equipped with assisting machinery increased from <5 in 1960 to >50% in 1990s (now >60%¹). Natural forests had been replaced by coniferous planted forests from 1950 to 1980s (Yamaura et al. 2009). River dams have been constructed in major rivers, river flows are now well regulated, and fewer flows occur (JBOSC 2010; Lehner et al. 2011). Many facilities have also been constructed to prevent landslides. Due to the historical uses of Japanese lands, until recently, intensification of land-use, called over-use, had been the prime threat of biodiversity (JBOSC 2010).

Although the period 1960–1980 was the key period when Japanese people strongly modified their lands, it was also the time when the self-sufficiency rate of food and wood products precipitously declined (food: >80–30%; wood products: >90–<40%). During and especially after that period (1990s–), many agricultural areas, grasslands, managed natural forests (coppice) and planted forests have been abandoned. Moreover, the Japanese human population has started to decline, and may be halved by 2100 (Department of Population Dynamics Research 2006; Appendix A as ESM). Vast areas of extensively managed lands or human-disturbed habitats, which have been maintained for millennia, harbor many species requiring natural disturbances (i.e. disturbance-dependent or early-successional species). Due to scarce natural disturbances (e.g. floods, landslides), human-disturbed open habitats such as meadow and cut-over area are now likely to be the major habitats for such species. Therefore, under the changes in land-use regime, a novel threat to biodiversity has just appeared in Japan: underuse. Indeed, early-successional species are now declining in

¹ http://www.maff.go.jp/j/nousin/sekkei/suido/s_suido/index.html.

Japan (Inoue 2005; Yamaura et al. 2009), and about 30% of the endangered plant species are threatened by underuse (JBOSC 2010). Threats of overuse and underuse are predicted to stagnate and increase, respectively, in Japan (JBOSC 2010).

In this context, it is now required to develop social systems by which Japanese people actively use their land and conserve early-successional species. Revival of plantation forestry is one possibility. This is because Japan now has the fifth-largest area of planted forests in the world, and the proportion of planted forest to total forested area (ca. 40%) is the second largest in the world (FAO 2006). Quite high proportions of planted forests are found in southwestern Japan, e.g., 65 and 66% of the forested area is planted forests in Kochi and Saga prefectures, respectively (Forestry Agency 2007). Plantation forestry entails site preparation and weeding after several years of tree planting. Several studies have suggested that young planted forests may harbor early-successional species across taxa (Bibby et al. 1989; Nagaike et al. 2006). However, these studies focused on single taxa, and only studied sites disturbed by plantation forestry. Therefore, the generality of the above studies to multiple taxa, and conservation performance of plantation forestry relative to other land uses remains unknown.

One useful way to evaluate habitats is to compare species richness among habitats (Lawton et al. 1998; Barlow et al. 2007). Although species richness is a common currency in this field, abundance is also important because it is related to species-level habitat selection and ecosystem function/service (Fretwell and Lucas 1969; Gaston and Fuller 2008). For mobile organisms, because individuals are not necessarily detected during the survey, it is a challenge to estimate these state variables at each site, and compare them among habitats (even for immobile organisms: Kéry et al. 2006). Until recently, species richness and abundance/occupancy of individual species have been estimated separately (Buckland et al. 2001; MacKenzie et al. 2006; Beck and Schwanghart 2010). Recent development of hierarchical community models allows us to integrate estimation of multi-level state variables (Royle and Dorazio 2008). Community models are an ensemble of species-level occupancy models from which community-level state variables (species richness) are derived (Dorazio et al. 2006). The use of these hierarchical models enables us to model rarely detected and undetected species (Sauer and Link 2002; Royle et al. 2007), which is especially useful for communities dominated by rare species (Ovaskainen and Soininen 2011). Recently, Yamaura et al. (2011) developed a multispecies abundance model, for binary observation data (detection/nondetection), by integrating the multispecies occupancy model with a species-level abundance model.

Here we extended this model to count data, and examined the role of young planted forests as habitats relative to other man-made open habitats for bees, birds, and plants. We chose birds and plants as focal taxa because previous research has indicated that early-successional species in these taxa are declining due to habitat loss (Yamaura et al. 2009; JBOSC 2010). Bees were selected as representative taxa which are closely related to open habitats (Steffan-Dewenter et al. 2002; Winfree et al. 2007). Our surveyed habitat types included four open habitats: pasture, meadow, young planted forest, and abandoned clear-cut. We also included two forest habitats (mature planted forest and natural old-growth) as reference habitats.

Functional group is defined as a group of species with similar ecological characteristics (e.g. Violle et al. 2007), and is a subset of the community. Our primary interest was to examine responses of early-successional species, which is a typical functional group designation. We used group-level hyper-parameters in our model, and examined responses of early-successional species as a group (cf. Sauer and Link 2002; Ruiz-Gutiérrez et al. 2010). That is, using a single model, we estimated species richness at functional group- and community-levels, and abundance at species-, functional group-, and community-levels in each site, and compared them among habitats.

Methods

Study area

We conducted this study in the northern part of Kitakami highland, Iwate prefecture (N39°50' E141°19'). This region is gently mountainous, and forests are dominated by deciduous natural and planted larch *Larix leptolepis*. Larch is a native deciduous coniferous species in Japan, and its natural distribution is limited to around the subalpine zone (Franklin et al. 1979). Larch as well as the other two major planted species in Japan (Japanese cedar *Cryptomeria japonica* and Hinoki cypress *Chamaecyparis obtusa*), are widely planted outside their natural distributions. The study area covered 15 × 15 km at an elevation ranging from 200 to 1,000 m (Appendix B as ESM). We surveyed six habitat types (four disturbed open habitats and two forest habitats), and selected five study stands at each habitat type (Appendix C–D as ESM). Because one survey stand of young planted forest for birds and bees was not used for plant survey (weeding was conducted before the plant survey), one stand was added, and 31 stands were surveyed in this study (Appendix B–C as ESM). All stands were larger than 4 ha. All the planted forests were composed of larch, that is, young planted forests (mean stand age = 4; range: 3–6) and abandoned clear-cuts (mean = 4; range: 3–5) were created by cutting larch planted forests. Abandoned clear-cuts (i.e., without replanting) were added into our surveyed habitats because this habitat has recently occurred in many parts of Japan including the study area (Yamagawa et al. 2010). Meadow stands were in the only remaining meadow (5 × 5 km; Hinoto grassland) in the study area. This meadow has been maintained for at least 100 years, and was traditionally managed (burned every year in the early spring) for the production of feed plants of war horses (e.g., *Miscanthus sinensis*, *Lespedeza bicolor*) until 20 years ago. The last burn was conducted 10 years ago. Due to the spatially biased land-use, we could not select stands in the spatially random manner. For example, old-growth only remained in the highest elevation. Forest cutting was conducted in the northern part because only private forests were cut in that time, and private forests dominated the northern area. We tried to make the stands spatially independent by spacing at least 600 m except for the meadow stands (separated at least 300 m).

Field sampling

We established one sample unit (transect) for each of 31 selected stands. We surveyed birds using line transect methods (Bibby et al. 2000). In each stand, we established a 400 × 100 m transect line in the center of the stand (Appendix E as ESM). We slowly walked the 300 m line down the center of the transect, and recorded the number of territories of each species (typically singing males) within the transect. Because understory layers (e.g. dwarf bamboos) could hamper hearing bird song/call, we complemented the line transect by point counts (Buckland et al. 2001). We stopped at the start, mid, and end points of the line for one and a half minutes, and recorded birds. Due to the difficulty of walking through old-growth where dwarf bamboo *Sasa kurilensis* (Appendix D as ESM) flourished, we placed our transects in areas surrounded by old growth. We did not record birds flying over except for swallows, and double counting of the same territories was avoided. We visited each site five times, at regular intervals (about one week) throughout the seasons. Low-elevation sites were visited first, and next visits commenced after the completion of the former visits for all the sites. We visited the sites in the morning (sunrise to 10:00 a.m.), and the survey was conducted from 19 May to 28 June 2009. This period

corresponds with the active season of birds and bees in which they are sampled (Ralph et al. 1993; Tschardt et al. 1998). Bias in the time of our visits was avoided by either reversing the order of visits, or changing the pairs of visits. No surveys were conducted when rain, fog, or high winds could potentially interfere with observations.

After the bird survey in the morning, we collected bees with sweep-nets (42 cm diameter) in the daytime (9:05 a.m. to 16:55 p.m.). We walked a 100 m-line at each site near the center of the bird line, swept understory layers 100 times. In the old-growth sites, we established the line in the forests apart from the paths at least 15 m. We visited the sites five times following the visiting order of bird sampling. We avoided bias in the time of the collection, and the survey was conducted only on sunny or cloudy days. The same observer (Y.Y.) conducted all bird surveys and bee collecting. Bees were pinned for identification, and voucher specimens were deposited with the Forestry and Forest Products Research Institute, Tsukuba, Japan.

After the bird and bee sampling, we surveyed plants from 7 July to 17 August. Separated from the bee sampling line by several meters, we established a 100 m plant survey line, which was parallel with the bee sampling line, at each site. Along the line, we established 20 1×1 m plots separated by 5 m, and recorded the plant species (<2 m height) occurring in each plot. Plant survey was conducted by two people (Y.Y. and one plant specialist: N.S., S.A., or T.S.). Some plant individuals were identified in the laboratory.

Statistical analysis

Data set

For bees and birds, we extended recently developed multi-species abundance models, which have previously been based on detection/nondetection data (Yamaura et al. 2011), for our multi-species count data. For plants, because observation data were occurrence frequency of each species (number of occurrence among 20 plots) rather than abundance, the model was based on a binomial distribution rather than Poisson distribution (see below). Further, for plants, we assumed perfect detection because we tried to identify all species in the plots irrespective of time (e.g. we took more than 20 min per species-rich plot).

We assigned bird species into early-successional and mature forest species according to the previous studies (Yamaura et al. 2009), while all bee species were assumed to be early-successional species due to their close relationships to open-habitats as a taxon (Steffan-Dewenter et al. 2002; Winfree et al. 2007). Plant species were first grouped into native and exotic species, and native species whose habitats were described as “grassland” in published literature (Miyawaki 1994; Okuda 1997) were assigned into early-successional species. Other native species were assigned into mature forest species. We estimated average responses of each group to six habitat types using group-level hyper-parameters (Sauer and Link 2002; Ruiz-Gutiérrez et al. 2010).

Model for bees and birds

For bees and birds, we accounted for imperfect detection, and assumed that each individual (territory for birds) was detected independently according to a binomial observation model: $y_{ijt} \sim \text{Binomial}(N_{ij}, p_i)$ where y_{ijt} is the number of detected individuals of

Table 1 An outline of the multi-species detection histories for birds

Common name	Species ^a	Group ^b	Site 1 (old growth)					–	Site 30 (young pl. for.)				
			1st	2nd	3rd	4th	5th		1st	2nd	3rd	4th	5th
Japanese bush warbler	6	2	3	2	3	6	4	–	1	2	2	2	1
Siberian meadow bunting	38	1	0	0	0	0	0	–	1	1	1	2	2
Coal tit	34	2	2	3	3	4	3	–	0	0	0	0	0
Siberian blue robin	23	2	2	4	2	5	3	–	0	0	0	0	0
Black-faced bunting	2	1	0	0	0	0	0	–	0	0	0	0	1
–	–	–	–	–	–	–	–	–	–	–	–	–	–
Horsfield's hawk-cuckoo	26	2	0	0	0	0	0	–	0	0	0	0	0
White's thrush	30	2	0	0	0	0	0	–	0	0	0	0	0
Blue-and-white flycatcher	11	2	0	0	1	0	0	–	0	0	0	0	0
Brown flycatcher	21	2	0	0	0	0	0	–	0	0	0	0	0
House swallow	29	1	0	0	0	0	0	–	0	0	0	0	0
Potential species 1	48	N/A	0	0	0	0	0	–	0	0	0	0	0
–	–	–	–	–	–	–	–	–	–	–	–	–	–
Potential species 30	77	N/A	0	0	0	0	0	–	0	0	0	0	0

Detection histories (cell values) are number of detected territories of each species in each visit (y_{ijt} in the text). Species were ordered by their total number of detected territories throughout this study. Data for only two sites (natural old growth and young planted forests) and five dominant and five rarest species are shown

^a Species id

^b Functional group id (only two groups for birds: early successional species = 1; mature forest species = 2). We added 30 potential (dummy) species which were always unobserved into our bird data to consider the existence of undetected species. Group membership of the potential species was allocated into one of the two groups in proportion to number of detected species among two groups

species i in site j and visit t (Table 1), N_{ij} is the abundance of species i in site j , and p_i is the individual-level detection probability of species i . The prior distribution for species-level detection probability on the logit-scale was assumed to be a normal distribution governed by community-level hyper-parameters (mean and variance: Fig. 1): $\text{logit}(p_i) \sim \text{Normal}(\mu_p, \sigma_p^2)$. We also assumed that N_{ij} and p_i were constant over the course of the $t = 1, \dots, T$ surveys, and that p_i did not vary among the sites. The former assumption could be unrealistic especially for bees, but sparseness of our bee data did not allow us to consider more complex models. For birds, the latter assumption was likely met because detectability within 50 m are comparable even among habitats with different vegetation structure (e.g. Schieck 1997).

Species-level abundance at each site is an unobserved variable, which was modeled by a Poisson distribution of the form $N_{ij} \sim \text{Poisson}(\lambda_{ij})$. Log-transformed expected abundance can be a linear combination of intercept α_{0i} , site-specific covariate(s) \mathbf{x}'_j and its coefficient(s) $\boldsymbol{\alpha}_i$:

$$\log(\lambda_{ij}) = \alpha_{0i} + \mathbf{x}'_j \boldsymbol{\alpha}_i$$

where λ_{ij} is the expected abundance of species i in site j . These estimates (α_{0i} and $\boldsymbol{\alpha}_i$) can be assumed to be normally distributed, e.g. $\alpha_{0i} \sim \text{Normal}(\mu_0, \sigma_0^2)$. In our case, however, we

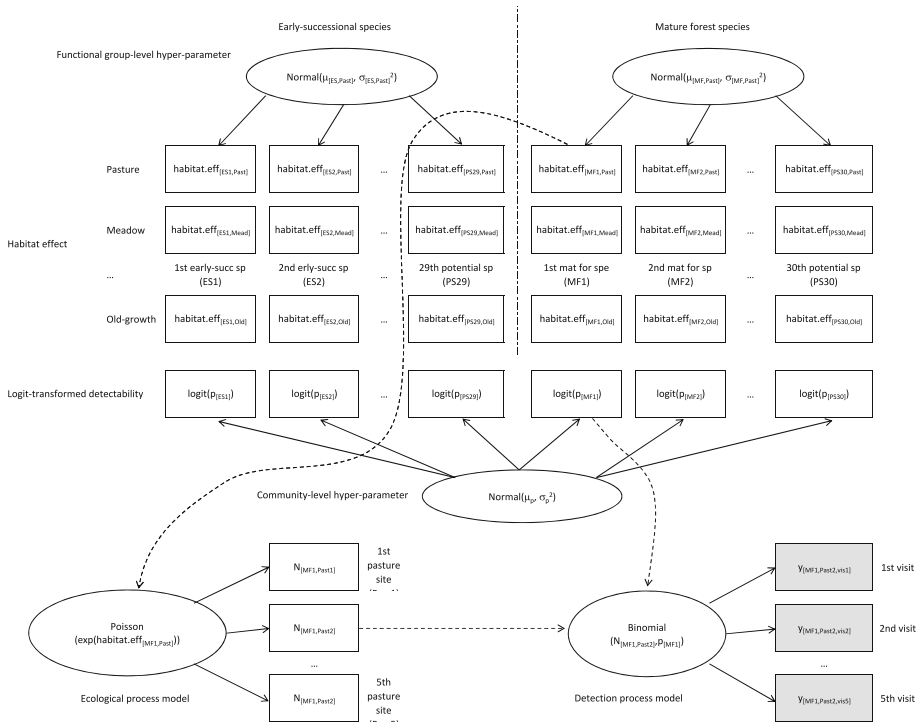


Fig. 1 Outline of the model structure for birds. Bird species were allocated into early-successional (*ES*) or mature forest species (*MF*). Species-level habitat effects (*habitat.eff*) were modeled by different normal distributions depending on their functional groups and habitats, and the normal distributions are depicted here only for pasture. Species-level logit-transformed detection probability ($\logit[p_i]$) was modeled by a normal distribution, but its mean and standard deviation (called community-level hyper-parameters) was shared by all species. Species-level parameters and group/community-level hyper-parameters are depicted by rectangular and ellipse, respectively. Thirty ‘potential’ species (*PS*) were added into the data to account for the existence of undetected species (see Table 1), and their group membership was modeled by a Dirichlet distribution (see text). Here the 29th and 30th potential species were allocated into early-successional and mature forest species, respectively. These parameters were used in ecological and detection process models (depicted by dotted lines). These two modeling processes are depicted for abundance of 1st mature forest species (*MS1*) in pasture (especially second pasture site). Finally, predicted counts were modeled by a binomial distribution (y_{ij} , grey boxes)

did not use intercepts, rather estimated expected abundance at each habitat at log scale, which is the “cell means” parameterization (Kéry 2010):

$$\log(\lambda_{ij}) = \text{habitat.eff}_{i, \text{habitat}[j]}$$

where $\text{habitat}[j]$ ($= 1, 2, \dots, 6$) is the habitat identity of site j . That is, our model has six distinct parameters (expected abundance) for each species. Log-transformed expected abundance was different among species, and governed by normal distribution with functional group-level hyper-parameters for each habitat: $\text{habitat.eff}_{i, \text{habitat}[j]} \sim \text{Normal}(\mu_{[i, \text{group}[i], \text{habitat}[j]]}, \sigma_{[i, \text{group}[i], \text{habitat}[j]]}^2)$ where $\text{group}[i]$ ($= 1$ for bees; 1, 2 for birds; 1, 2, 3 for plants) is a group identity of species i (Fig. 1). This model implies that all of the habitat effects have means that vary by functional groups and habitats (bees have six mean

parameters, 12 mean parameters for birds, and 18 for plants). This is the same for standard deviations.

Model for plants

For plants, we modeled occurrence frequency (number of occurrences among 20 plots) using a binomial distribution in the form $y_{ij} \sim \text{Binomial}(20, \psi_{ij})$ with

$$\text{logit}(\psi_{ij}) = \text{habitat.eff}_{i,\text{habitat}[j]} + \text{site.eff}_{ij}$$

where y_{ij} is the observed frequency of species i in site j . Logit-transformed species-level occurrence probability (ψ_{ij}) was function of habitat effects and random site effects (site.eff_{ij}), which is used to account for the variation of the frequency not captured by the binomial assumption (Kéry et al. 2009).

Habitat effects were modeled with a normal distribution as in bees and birds, and random site effects were also generated from species-level normal distribution in the form $\text{site.eff}_{ij} \sim \text{Normal}(0, \sigma_{s[i]}^2)$. We considered the differences in variance among species: $\log(\sigma_{s[i]}) \sim \text{Normal}(0, \sigma_s^2)$. We could not use random site effects for bees and birds due to data sparseness. We compared species richness and frequency of plants among habitats by predicting them in a new site at each habitat using habitat and random site effects.

Data augmentation and model fitting

Following Yamaura et al. (2011), we accounted for the existence of undetected species during the survey for bees and birds using the technique of data augmentation (Royle et al. 2007). In this technique, detection histories of certain amounts of undetected ‘potential’ species (i.e. all zero) are added to those of the detected species. Then, a set of latent variables is added to the model that partitions the data set into (i) species that are present but were not detected and (ii) species that are not present and therefore cannot be detected. That is, number of undetected species is estimated based on the given detection histories and model structure.

We augmented the data set 80 bee and 30 bird potential species (Table 1). Because the posterior distribution of inclusion rate (Ω), which indicates the proportion of undetected species in the augmented species, was concentrated well below 1 for both taxa (median <0.63), the number of augmented species was sufficiently large (Royle and Dorazio 2008). Because functional group membership is a latent variable (i.e., not observed for species that go undetected), we modeled functional group membership with a Dirichlet prior distribution (Yamaura et al. 2011). Under a model in which detection probability does not differ among groups (in this study), undetected species are allocated into functional groups based on the observed proportions of number of detected species among groups. Otherwise, under more complex models, we can assume different detection probability among groups (using group-level hyper-parameters), and group membership of undetected species is affected by group specific-detection probability (i.e. for groups with lower detection probability, estimated proportions would be larger than observed proportions; e.g. Gardner et al. 2010). We estimated responses of undetected species to the six habitat types using the above described group-level hyper-parameters. We used OpenBUGS Ver. 3.1.2 (Lunn et al. 2009) and R2OpenBUGS R package Ver. 3.1–2.1 (Sturtz et al. 2010) for the parameter estimation. We used conventional noninformative priors (e.g. $\mu_p \sim \text{Normal}[0, 100^2]$; $\sigma_p \sim \text{Uniform}[0, 10]$). We ran three chains of 20,000 iterations with different initial values, discarded the first 10,000 and thinned by 10 for bees and birds

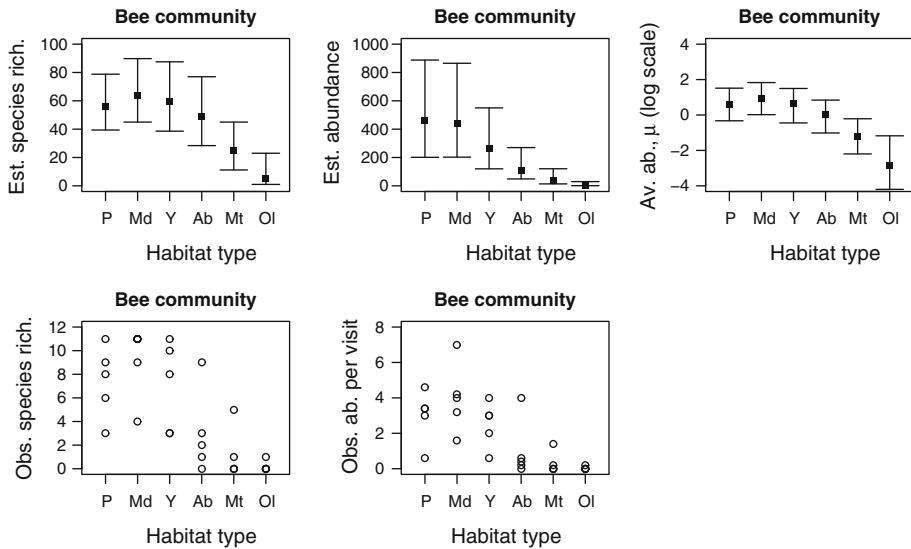


Fig. 2 Community-level responses of bees to six habitats. Six habitats were abbreviated as follows: pasture (P), meadow (Md), young planted forest (Y), abandoned clear-cut (Ab), mature planted forest (Mt), and old-growth (Ol). Median estimates and 95% CIs are shown by squares and vertical bars, respectively. Averaged values of observed species richness and abundance across five sites were shown by circles in the separate plots. Observed species richness and abundance were those recorded through five visits and for one visit, respectively

(for plants, 15,000 iterations, discarded the first 5,000). Markov chain convergence was examined by using the \hat{R} statistic (the Gelman-Rubin statistic), and \hat{R} all the above described parameters were less than 1.01, indicating that our model convergence was good (Gelman and Hill 2007). Posterior distributions were summarized by median and 95% credible intervals (CIs).

Results

We collected 274 individual bees, and excluded European honey bee *Apis mellifera* (managed non-native species; with one individual) because its distribution depends on the location of hives rather than land-use (Steffan-Dewenter et al. 2002; Winfree et al. 2007). We recorded 1,927 bird territories, and excluded common buzzard *Buteo buteo* (with one territory) because our transects were too small for effective sampling of this large-sized raptor species. We recorded 8,095 “occurrence” records for plants, 32 records were not identified for their species, and we excluded them. We applied our model to the remaining 47 native bee, 47 native bird, and 387 plant species. We divided 47 bird species into 10 early-successional and 37 mature forest species, and 387 plant species into 80 early-successional, 288 mature forest, and 19 exotic species.

We estimated that 32 (95% CI: 13–64) bee and one (0–4) bird species were undetected in our field survey (Appendix F–G as ESM). Averaged individual-level detectability (p_i) was 0.003 for bees ($\mu_p = -5.77$) and 0.16 for birds (-1.67). For bees, only *Ceratina japonica* had detectability higher than 10%. This species was the fourth dominant species

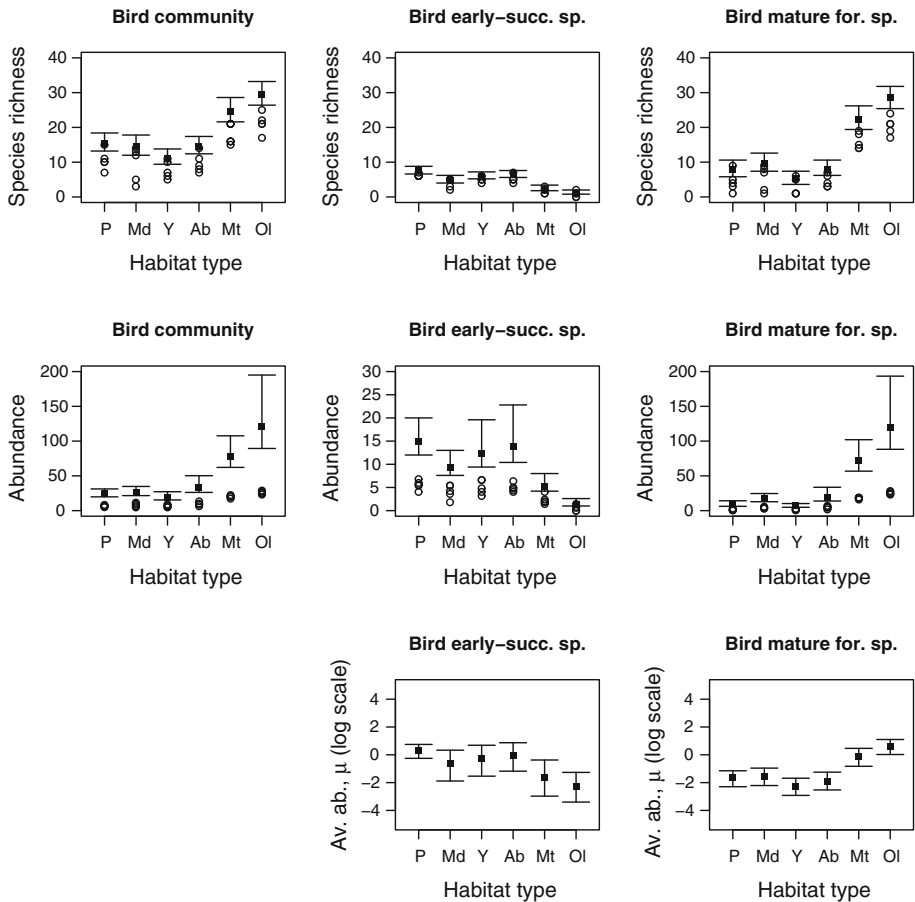


Fig. 3 Community- and functional group-level responses of birds. Observed species richness and abundance were depicted in the plots showing the estimates. See Fig. 2 for details

(Appendix I as ESM). Five species of birds had detection probability higher than 0.50: Three were early-successional species (common skylark *Alauda arvensis*, Siberian meadow bunting *Emberiza cioides*, and olive-backed pipit *Anthus hodgsoni*) while two were mature forest species (coal tit *Parus ater* and Japanese bush warbler *Cettia diphone*).

For the three taxa, differences in observed species richness and abundance/frequency among habitats were similar to differences in their estimates (Figs. 2, 3, 4). For bees, because estimates of detectability were quite low, estimates of species richness and abundance were larger than their measurements by two orders. Differences in estimates and measurements were smaller in birds. For birds and plants, differences in community-level state variables among habitats reflected those of mature forest species. Differences in species richness among habitats were similar with those in abundance/frequency and hyper-parameters for each functional group. Community-level state variables peaked in the three disturbed open habitats for bees (pasture, meadow, and young planted forest), in young forest habitats for plants (young planted forest and abandoned clear-cut), and in mature forest habitats for birds (mature planted forest and old growth). For

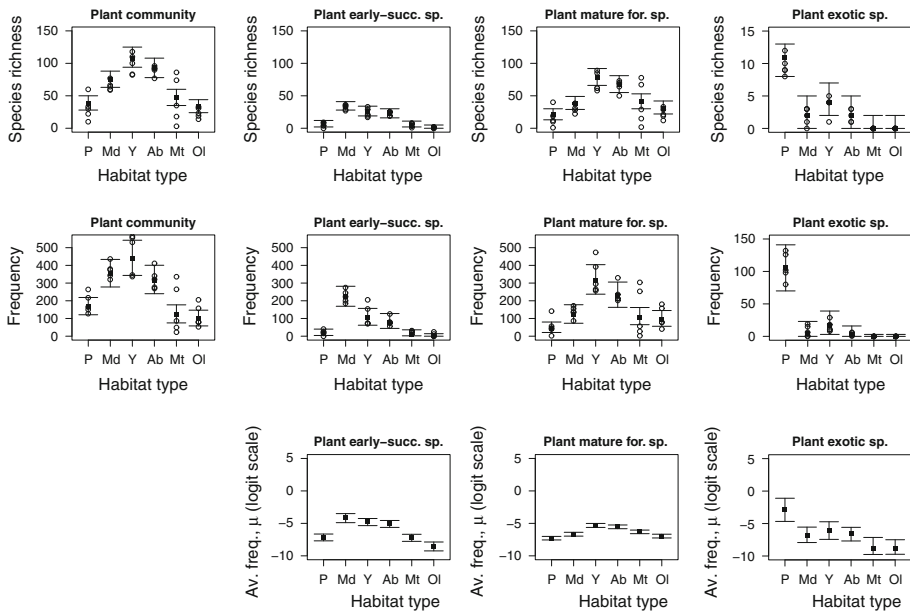


Fig. 4 Community- and functional group-level responses of plants. Species-level state variables were occurrence frequencies (number of occurrences out of 20 plots), and perfect detection was assumed. Species richness was number of detected species through 20 plots in each site

early-successional species, across the three taxa, four disturbed open habitats had roughly equal and higher values than two mature forest habitats except for pasture for plants. For plants, pasture was a good habitat only for exotic species. Meadow had the highest frequency of plant early-successional species, which contrasted with plant mature forest species whose species richness and frequency was higher in young planted forest and abandoned clear-cut than in meadow. There was large variance in measurements of plant community in mature planted forests, which is due that mature forest species were diverse and frequent in two sites with small amount of dwarf bamboo (frequency of *Sasa senanensis* was 12 and 2, while that of the other three sites was 20). Species richness and frequency was also low in old growth in which dwarf bamboo flourished (frequency of *Sasa kurilensis* was more than 18 in all the five sites).

Discussion

Estimates by multispecies abundance model

Hierarchical community models have been recently developed to integrate inferences about species-, functional group-, and community-level state variables. Such models have been developed for “detection/nondetection” data in which, typically, observed counts are reduced to a simple binary indicator of detection. Our model is based on the observed count data, which is one of the most widely collected types of data in field surveys (i.e., “point counts”). This is also important because “detection/nondetection” and the derived

estimates are not very informative summaries of bird populations, especially for more abundant species. The developed community model is an ensemble of multispecies abundance models. Functional groups are subsets of community, and composed of species with specific ecological traits. Their average responses are examined using group-specific hyper-parameters. We applied this model to bees and birds in four open and two forest habitats.

Results showed distinct differences in functional group- and community-level state variables among six habitats for bees and birds. Low detectability was estimated for bees, and the existence of many undetected bee species was suggested. This result was not unexpected because our sampling was not intensive (100 m line with 100 sweeping even with five visits). Conversely, for birds, the number of undetected species was estimated to be small, which is also reasonable because we adopted relatively intensive field survey: 4 ha survey area with 300 m line (complemented by point counts, and with five visits). However, there were clear differences in abundance between measurements and estimates, indicating the need of multiple visits to detect all existing individuals.

We inspected estimates related to species-level state variables (i.e. λ_{ij} and ψ_{ij} ; Appendix I–K as ESM), and the field experiences suggest that abundance of one bee and two bird species was likely overestimated. For example, although we collected 10 individuals of *Andrena sakagamii* (code 19) during the survey (Appendix I as ESM), expected abundance of *A. sakagamii* in pasture ($\lambda_{19, \text{habitat } [1]} = 41$ (95% CI: 8–134). This species was collected in only one of five visits in the three pasture sites. Number of collected individuals varied during the survey in many bee species (Appendix L as ESM). Captured individuals were also sequentially removed from the populations. Therefore, assumed constant abundance would be unrealistic, which have resulted in low detectability and high estimated abundance and species richness in bees. For birds, two bird species whose abundance was likely overestimated were large-bodied species, i.e., white-backed woodpecker *Dendrocopos leucotos* ($\lambda_{10, \text{habitat } [6]} = 7$: 1–43) and Eurasian jay *Garrulus glandarius* ($\lambda_{12, \text{habitat } [6]} = 5$: 1–20). They were sparsely detected (Appendix L as ESM), and our surveyed area (4 ha) likely only partially covered territories of these large-bodied species. Detectability of these two bird species was estimated to be lower than 10%. These estimates may be improved by considering the emigration of individuals from the surveyed area (e.g. Chandler et al. 2011).

Biodiversity in man-made open habitats

For early-successional bird species, four man-made open habitats had roughly equal species richness (hereafter diversity) and abundance, suggesting that birds did not discriminate among man-made open habitats. Of course, there were some exceptions, e.g. pasture was the only habitat of common skylark *Alauda arvensis* (Appendix J as ESM). Although diversity and abundance of mature forest species were higher in the forest habitats, especially in the old-growth, we found some individuals of mature forest species in the open habitats. Remaining trees were likely to be key resources (Appendix D as ESM), which is reported elsewhere (e.g. Fischer et al. 2010).

Bee diversity and abundance was high in the four open habitats. Plant diversity is reported to increase insect (and pollinator) diversity (Scherber et al. 2010). Meadow, young planted forest, and abandoned clear-cut had high diversity of plant early-successional species, which seems to explain high bee diversity. However, high bee diversity in pasture is noted irrespective of quite low plant diversity. The top nine dominant plant species in pasture were all exotic (estimates of occurrence >0.1; Appendix K as ESM), further, five of

the nine species were anemophilous species in the family *Poaceae*. However, the fourth species, dandelion *Taraxacum officinale*, had high occurrence (0.69), and is entomophilous species in the family *Asteraceae*. We collected many bees on this flower in the field, suggesting that dandelion may be the key species driving bee diversity. Schaffers et al. (2008) showed that plant composition determines insect assemblage, suggesting that some plant species could have a critical role. Our bee-dandelion relationship may be such a case.

For plants, diversity and frequency of early-successional species in meadow was comparable or higher than that in young planted forest and abandoned clear-cut. Mature forest species showed the opposite pattern. Periodic burning (and its legacy), which had annually been carried out for maintenance of meadow, would filter out many mature forest species and allow the dominance of early-successional species. High diversity and frequency of early-successional species in meadow suggests the important role of meadow for their conservation in Japan. However, meadow has been declining its area because meadow has lost its economic importance (Yamaura et al. 2009; JBOSC 2010). Young planted forests and abandoned clear-cuts were suitable habitats for both early-successional and mature forest species. Mature planted forests without dwarf bamboo were good habitats only for mature forest species. As described above, plant diversity in pasture was as low as in old growth in which dwarf bamboo flourished, but there was high diversity and frequency of exotic plants. It is natural because pasture is intensively managed for several exotic pasture species. We found some exotic plant species in the other open habitats.

Plantation forestry and conservation of early-successional species

High dependency of Japanese wood demands on foreign countries may not only result in abandonment of planted forests but also exporting ecological impacts into foreign countries with short land-use histories (cf. Ellis et al. 2010). It could be suggested that Japan has underused its own country, while overusing foreign countries. In Japan, matured wood resources are now being recognized. Revival of Japanese plantation forestry may contribute to the increase in self-sufficiency of wood products and conservation of early-successional species, i.e. a win-win outcome for resource use and biodiversity conservation. For example, roughly assume that standard cutting age is 40 year old for larch planted forests, and that planted forests that are less than 10 year old are suitable habitats for early-successional species. Further assume that early-successional species can find newly created young planted forests in the landscape after young planted forests grow up. In this case, ecological impacts of loss of meadow may be offset if we standardly manage four times the amount of planted forests as the amount of lost meadow.

Japan has characters of land-use, which are typical for developed countries. Lands have been maintained by human disturbances for millennia, and natural disturbances are now suppressed. If such countries/regions follow Japan, that is, depend on foreign countries for natural resources, and population starts to decline, the novel threat of biodiversity—underuse—may occur along with land abandonment. Although the value and status of early-successional species have been overlooked, they are now declining in many regions of the world and its importance are suggested (Askins 2001; Betts et al. 2010; Swanson et al. 2011). Human disturbances could entail introduction of exotic species, however, positive aspects of human disturbances should be revealed in such countries/regions.

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