Relationship Between Vegetation Structure and Avian Communities on Miyakejima Island, Japan, 13 years after a Major Volcanic Eruption

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Relationship Between Vegetation Structure and Avian Communities on Miyakejima Island, Japan, 13 years after a Major Volcanic Eruption[1]

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Abstract: Volcanic eruptions can have significant impacts on plant and animal communities. Thus, it is important to understand the recovery process following these eruptions, particularly on isolated islands, in order to assist with biodiversity management and conservation. We studied relationships between vegetation structure and avian species composition on Miyakejima Island, Japan, where a volcanic eruption in 2000 destroyed almost half of the vegetated land. Bird species and nine vegetation variables were surveyed at 24 sampling sites from 2011 to 2014. The results showed that avian species composition mainly varied along two vegetation variables, namely plant species richness and total basal area of all tree species. Bird species were classified into four groups, that is, grassland species, widely distributed species, developing-forest species, and developed-forest species. Developed-forest species were only recorded at the sites where vegetation height was more than 10 m. The relationship between developed-forest bird abundance and vegetation height was similar to that between total basal area of all tree species and vegetation height. The restoration of mature evergreen forest is essential to conserve avian diversity on the island, and natural seed dispersal by birds plays an important role in supporting forest restoration after a major disturbance.

Keywords: avian species composition, developed forest species, plant species richness, recovery from disturbance, restoration, volcanic island

Island volcanos are typical features of the Pacific region. In the Japanese islands, there are over a hundred volcanos, some of which are currently active. Miyakejima Island is an example; it is an active volcanic island of the Izu Islands in the western Pacific, close to Honshu, the main island of Japan (Figure 1). The volcano (Mt. Oyama) on Miyakejima Island has repeatedly erupted during recorded history. In particular, the eruption in 2000 was quite severe and destroyed a large part of the vegetation on the island. Of the vegetated area on the island, 46% became bare land (Takahashi et al. 2011). In other areas, vegetation and animal communities were damaged by volcanic ash, scoria, landslides, and volcanic gas (Katoh and Higuchi 2003, Kamijo et al. 2008).

As volcanic eruptions destroy ecological communities around the volcano, it is important to understand the recovery process of the

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FIGURE 1. Location of Miyakejima Island. The islands shown here are collectively called as the Izu Islands.

ecosystem on volcanic islands after eruption. The recovery process of vegetation has mainly been studied on various volcanos including insular and continental volcanos (del Moral and Grishin 1999). In contrast, fewer studies have been published on the recovery of animal communities. Among animals, birds are an important component of ecological communities on volcanoes because they arrive early after the eruption. They often play roles in seed dispersal (Howe and Smallwood 1982) and can accelerate native forest regeneration (Wunderle Jr. 1997).

Most studies concerning avian community recovery after volcanic eruptions revealed that damage and recovery of avian communities was related to the recovery of the vegetation. Manuwal et al. (1987) showed that vegetation destruction caused by the 1980 eruption of Mt. St. Helens in Washington, USA resulted in the loss of tree foliage, insectivores, and tree seed-eaters. These reported impacts could in turn influence avian communities. Although Manuwal et al. (1987) conducted their study on a continental volcano, the results can be applied to volcanic islands. Dalsgaard et al. (2007) focused on the effects of ash fall on forest birds on Montserrat Island and found that the terrestrial foragers were the most impacted community. Ortega-Álvarez et al. (2013) stated the importance of restoring understory vegetation for wildlife following volcanic damage after conducting surveys around Paricutín Volcano. These studies show the importance of restoring shrub and herb layers for maintaining avian habitats. On the Anak Krakatau Island of Indonesia, Zann (1992) showed the relationship between avian communities and vegetation, indicating that the immigration of new plant species was important for providing food resources to the birds. Thus, the importance of immigration of animals and plants should be emphasized for island ecosystems because of their isolation.

Avian communities on Miyakejima Island, Japan were studied after the eruption in 2000 by Katoh and Higuchi (2003, 2011, 2016). They reported that avian species richness was positively correlated with tree coverage. The importance of tree cover was revealed for some representative species on the island, such as the Varied Tit *Poecile varius* (on the island, subspecies *owstoni*) (Fujita et al. 2005) and Iijima's Leaf Warbler *Phylloscopus ijimae* (Takagi and Higuchi 2000), both of which are endemic and endangered species on the island. Physiognomy or dominant tree species also influenced avian species composition (Higuchi 1973) and breeding density (Higuchi 1978) on the island. These studies reported on the relationships between vegetation and avian communities by focusing on different properties of the vegetation, which suggests that only limited aspects of the vegetation were considered in each study.

Ecological processes on volcanic islands are important from the perspective of biodiversity conservation. Avian conservation on Miyakejima Island is also important because of the uniqueness of the island as an avian habitat. The island has often been called "Bird Island" (Moyer et al. 1985) because of the high density of songbirds such as Iijima's Leaf Warbler, Varied Tit, Izu Thrush *Turdus celaenops*, Japanese Robin *Luscinia akahige* (on the island, subspecies *tanensis*), and Eurasian Wren *Troglodytes troglodytes* (subsp. *mosukei*), which are representative avifaunal species of the Izu Islands. It should be noted that these five species (or subspecies) are all considered to be vulnerable or endangered by the IUCN (2019) and the Japanese Ministry of the Environment (2017) (Table 1). Furthermore, several endemic species or subspecies whose distribution is limited to the island and a few other islands are known; Japanese Wood Pigeon *Columba janthina*, Japanese Pigmy Woodpecker *Dendrocopos kizuki* (subsp. *matsudairai*), and Japanese White-eye *Zosterops japonicus* (subsp. *stejnegeri*) are examples. The main habitats of all these bird species are forests. Moreover, Miyakejima Island provides habitat for Styan's Grasshopper Warbler *Locustella pleskei*, which is recognized as an endangered (Japanese Ministry of the Environment 2017) or vulnerable species (IUCN 2019).

As mentioned above, variation in avian communities on Miyakejima Island is related to the vegetation. The vegetation successional sere on the island has been estimated based on a vegetation chronosequence created by

TABLE 1

List of Bird Species Observed in 24 Sampling Sites

English Name	Scientific Name[a]	Abbreviation	Conservation Status[d]	Recorded Seasons
Japanese Wood Pigeon	*Columba janthina* Temminck, 1830	COjan	Near threatened+o	Both
Oriental Turtle Dove	*Streptopelia orientalis* (Latham, 1790)	–[c]		Both
Lesser Cuckoo	*Cuculus poliocephalus* Latham, 1790	CUpol		Breeding
Pacific Swift	*Apus pacificus* (Latham, 1802)	–[c]		Breeding
Japanese Pygmy Woodpecker	*Dendrocopos kizuki matsudairai* (Kuroda, 1921)[b]	DEkiz	Endemic subspecies	Both
Bull-headed Shrike	*Lanius bucephalus* Temminck & Schlegel, 1845	–[c]		Both
Large-billed Crow	*Corvus macrorhynchos* Wagler, 1827	COmac		Both
Varied Tit	*Poecile varius owstoni* (Ijima, 1893)[b]	POvar	Endangered+o	Both
Japanese Tit	*Parus minor* Temminck & Schlegel, 1848	PAmin		Both
Brown-eared Bulbul	*Hypsipetes amaurotis* (Temminck, 1830)	HYama		Both
Japanese Bush Warbler	*Cettia diphone* (Kittlits, 1830)	CEdip		Both
Iijima's Leaf Warbler	*Phylloscopus ijimae* (Stejneger, 1892)	PHiij	Vulnerable+o	Breeding
Japanese White-eye	*Zosterops japonicus stejnegeri* Seebohm, 1891[b]	ZOjap	Endemic subspecies	Both
Eurasian Wren	*Troglodytes troglodytes mosukei* Momiyama, 1923[b]	TRtro	Endangered°o	Both[e]
Pale Thrush	*Turdus pallidus* Gmelin, 1789	TUpal		Wintering
Izu Thrush	*Turdus celaenops* Stejneger, 1887	TUcel	Vulnerable+, Endangered°o	Both
Naumann's Thrush	*Turdus naumanni* Temminck, 1820	TUnau		Wintering
Japanese Robin	*Luscinia akahige tanensis* (Kuroda, 1923)[b]	LUaka	Vulnerable+o	Both[f]
Brambling	*Fringilla montifringilla* Linnaeus, 1758	–[c]		Wintering
Oriental Greenfinch	*Chloris sinica* (Linnaeus, 1766)	CHsin		Both[g]
Eurasian Siskin	*Carduelis spinus* (Linnaeus, 1758)	–[c]		Wintering
Eurasian Bullfinch	*Pyrrhula pyrrhula* (Linnaeus, 1758)	–[c]		Wintering
Meadow Bunting	*Emberiza cioides* Brandt, 1843	EMcio		Both
Black-faced Bunting	*Emberiza spodocephala* Pallas, 1776	EMspo		Wintering

[a] English names, scientific names, and species authorities are according to the Ornithological Society of Japan (2012).
[b] Subspecies names are omitted in the text except when mentioning them for the first time.
[c] These abbreviations were not used because the species was omitted from the numerical analysis due to few sightings.
[d] Symbols "+" and "o" indicate designation by the IUCN (2019) and Japanese Ministry of the Environment (2017), respectively. Endemic subspecies means subspecies with limited distributions, mostly in Izu Islands (Ornithological Society of Japan 2012).
[e] Eurasian Wren was omitted from CCA of the wintering season data, because no individuals were recorded during the wintering season surveys. It should be noted that this species is known as a resident (Ornithological Society of Japan (2012).
[f] Japanese Robin was omitted from CCA of the wintering season data, because only three individuals were recorded during the wintering season surveys
[g] Oriental Greenfinch was omitted from CCA of the breeding season data, because only four individuals were recorded during the breeding season surveys

several volcanic eruptions occurring at different periods (Yoshioka 1942, Kamijo et al. 2002). These studies indicated that the major seral stages of primary succession on the island are: (1) perennial herbaceous vegetation mainly dominated by *Fallopia japonica* var. *hachidyoensis*, (2) deciduous shrub forest dominated by *Alnus sieboldiana*, (3) mixed broadleaved forest dominated by *A. sieboldiana* and *Cerasus speciosa*, and (4) evergreen forest dominated by *Castanopsis sieboldii* and/or *Machilus thunbergii* along the successional sere. A similar successional pattern was reported on Izu-Ooshima Island (Tezuka 1961), which also belongs to the Izu Islands.

It is reasonable to believe that the avian community changes along with the successional sere. Thus, the aim of the study was to explore the relationship between the vegetation and avian community on Miyakejima Island in order to understand the patterns of avian community changes following volcanic damage. Our objectives were to estimate the temporal changes from observed spatial variations in the vegetation and avian community at various successional stages using a chronosequence approach, and understand the relationships between different seral stages and avian species, especially threatened and/or endemic species. Our findings may assist with improving vegetation management for the conservation of avian communities on Miyakejima Island and other volcanically damaged areas.

MATERIALS AND METHODS

Study Site

Miyakejima Island, ca. 55 km^2 in area and 775 m high, is an active volcanic island and located about 180 km south of Tokyo (Figure 1). It is located in a humid warm-temperate climate zone. The annual mean monthly temperature is 17.7 °C and the annual total precipitation is 2,954 mm (Japan Meteorological Agency 2019). The climax of vegetation on Miyakejima Island is an evergreen broadleaved forest dominated by *C. sieboldii* and/or *M. thunbergii.*

Sampling Sites

We located 24 sampling sites on Miyakejima Island (Figure 2). These sites covered a wide range of different stages of vegetation degradation (i.e., from almost bare lands to mature evergreen forests) caused by volcanic activities since the eruption in 2000. Based on the vegetation features, sampling sites were categorized into three vegetation types, namely (1) grassland with no tree stems, which is 2.6 m or less in vegetation height and dominated by a grass species *Miscanthus condensatus* (almost bare land was included in this category); (2) shrubland with one or more tree stems, where vegetation height was more than 2.6 m and less than 8 m, except for one site where vegetation height was 2.6 m; and (3) forest, where vegetation height was more than 8 m. In all the forest sites, evergreen trees were dominant.

Bird Surveys

From December 2011 to January 2014, we conducted bird surveys at each sampling site. We considered the period from December to February as the wintering season and that from April to August as the breeding season. Each site was visited four times in each season during the survey period. We used the fixed radius point count method (Bibby et al. 2000) to record individual birds at each sampling site. All individuals observed within a 25 m radius from a point located within each site were recorded during a 20-minute period. Bird surveys were conducted between sunrise and noon and not conducted under rainy and/or windy conditions. Throughout the study period, the surveys were conducted by a single researcher (TY) to avoid any variations caused by multiple observers.

Vegetation Surveys

A 10 m × 10 m (100 m^2) quadrat was located in each sampling site. In July 2012, vegetation surveys were carried out within each quadrat using the Braun-Blanquet (1964) phytosociological method to determine plant species richness and composition for each sampling site. Species dominance was recorded in six dominance classes (5, 4, 3, 2, 1, and "+") using the total estimation method (Braun-Blanquet 1964). The number of plant species was counted in each quadrat using these data.

Detrended correspondence analysis (DCA) (Hill and Gauch 1980) was conducted to summarize species composition. When conducting the DCA, the recorded dominance class of each species was converted into median coverage, such that dominance classes 5, 4, 3, 2, 1 and "+" were converted into 87.5%, 62.5%, 37.5%, 17.5%, 5.5%, and 0.5% coverage, respectively. The sample scores of the first three axes were used in

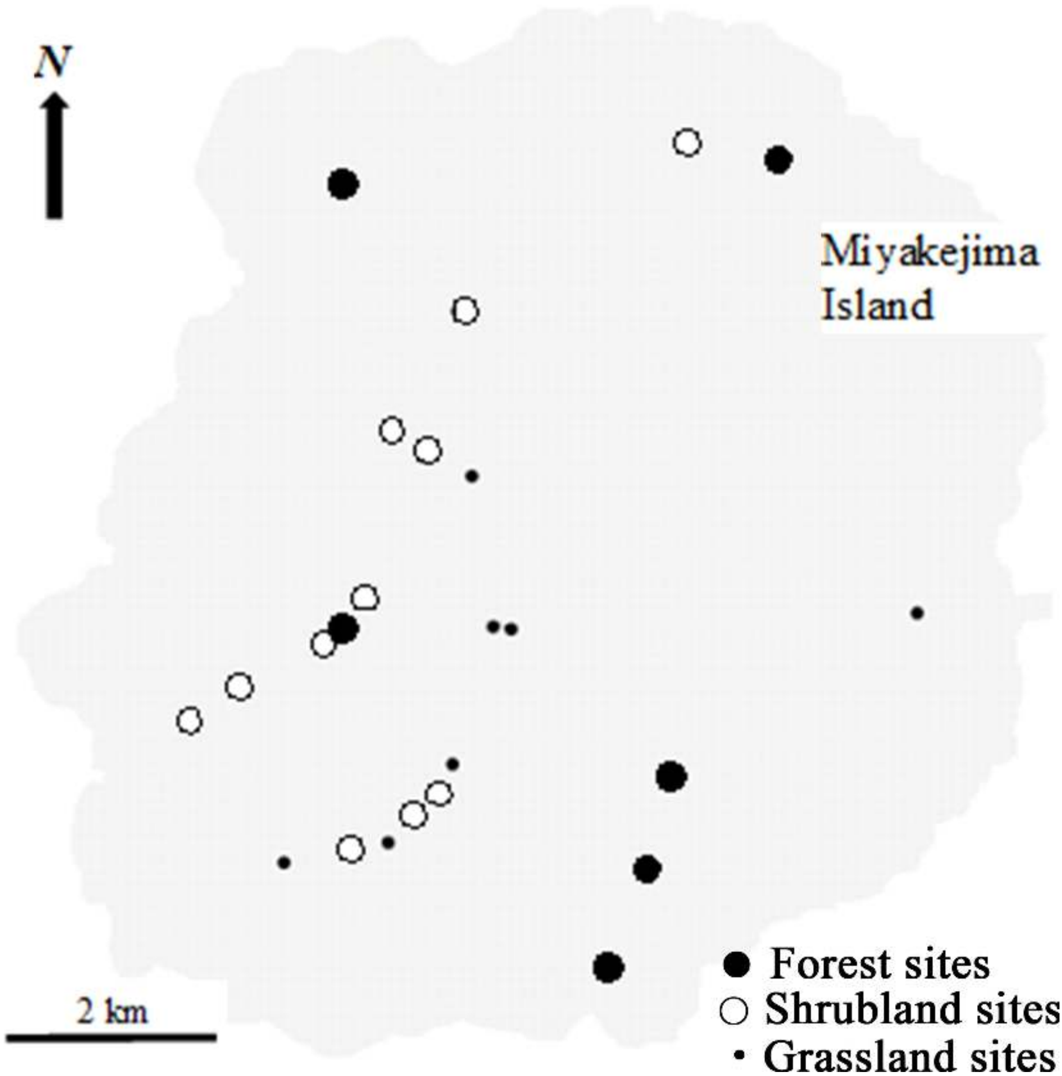

FIGURE 2. Location of the sampling sites on Miyakejima Island.

the following analysis: DCA was calculated by PC-ORD 6.0 (McCune and Mefford 2016), and species recorded in two or less sites (i.e., less than 10% of the sampling sites) were removed before the DCA was conducted to avoid the distorting effect of low frequency species (Gauch 1982).

Vegetative cover was stratified into four layers, namely tree layer, subtree layer, shrub layer, and herb layer (Braun-Blanquet 1964). Vegetation coverage of each layer (10% interval) and vegetation height (m) were visually estimated. The height of the tallest plant in the quadrat was regarded as vegetation height. Tree coverage was defined as the sum of the coverage of the tree and subtree layers. Similarly, shrub and herb coverage was defined as the sum of the coverage of the shrub and herb layers, which represented the understory cover in forest stands.

All living tree stems with a DBH (diameter at breast height, i.e., diameter at 1.3 m above the ground) of 5 cm or more were recorded for each species within each quadrat. DBH was measured by a tape measure. Basal area (BA) was calculated for each stem as the area of the circle with the diameter of the measured DBH. BA was summed for all stems to determine total BA of all tree species within a quadrat. Total BA of evergreen tree species was also calculated.

Statistical Analyses

A species compositional data table (sampling site × bird species) was constructed for each season (breeding and wintering) based on the bird survey records. Data collected from the four replications conducted in a season were pooled into one table.

To understand the species compositional changes among sampling sites and their constraining factors, a canonical correspondence analysis (CCA, Ter Braak 1986) was conducted. Vegetation measurements were used as the constraining variables. Based on the vegetation survey results, a vegetation variables table (sampling sites × vegetation variables) was prepared for CCA. The following nine vegetation variables were included in the table: (1–3) DCA scores of the first, second, and third axes; (4) vegetation height; (5) plant species richness; (6) tree coverage; (7) shrub and herb coverage; (8) total BA of all tree species; and (9) total BA of evergreen tree species. As these nine variables were correlated with one another, we removed some variables to avoid adverse effect of multicollinearity. As selecting variables correlated $|r| < 0.7$ is the most commonly applied method (Dormann et al. 2013), we used this threshold to find highly correlated variables.

We used the forward variable selection method to include the minimum number of constraining variables in the CCA model. CANOCO 5.0 (Ter Braak and Šmilauer 2012) was used for calculations. Based on the species plot obtained from the CCA, avian species were classified into groups following the process of ordination space partitioning (Gauch 1982). Originally, this process was applied to ordination plots produced by DCA, but we applied it to ordination plots produced by CCA because we considered vegetation variables as constraining variables. The number of individuals in each group was calculated and compared to vegetation height, which was considered as the vegetation development index because of its clarity in indicating vegetation development and simplicity in obtaining measurements. The other vegetation variables were also compared to vegetation height. Based on the results of the comparisons, the changes in vegetation and avian community were considered along a vegetation development gradient. Please note that we say "vegetation development" instead of "vegetation succession," because we did not survey succession itself.

RESULTS

Birds and Vegetation

During the study period, 18 and 20 bird species were recorded in the breeding and wintering seasons, respectively (Table 1). The results of the vegetation survey are shown in Table 2. Plant species richness was similar between the shrubland and forest sites while other variables such as the DCA Axis 1 score, total BA, and tree coverage were similar

TABLE 2

Median and Quartile Range (in Parentheses) of Vegetation Variables in Three Vegetation Types in the Study Site

Vegetation Type (Number of Sites)	Plant Species Richness	Tree Coverage	Shrub + Herb Coverage	Vegetation Height (m)	Total Basal Area (m^2/ha)	Total Basal Area of Evergreen Tree Species (m^2/ha)	DCA Axis 1	DCA Axis 2	DCA Axis 3
All sites (24)	21	0.23	1.03	6.0	7.3	2.5	276	80.5	28.5
(12–23)	(0–0.73)	(0.78–1.13)	(2.5–8.0)	(0–21.0)	(0–15.4)	(158–374)	(54.8–102)	(15.9–43.9)	
(a) Grassland (7)	7	0	0.60	1.2	0.0	0.0	383	79.7	18.8
(4.5–11)	(0–0)	(0.32–1.00)	(1.0–2.2)	(0–0)	(0–0)	(380–398)	(58.2–84.3)	(14.8–36.0)	
(b) Shrubland (11)	21	0.25	1.05	6.0	7.4	3.2	284	64.4	21
(19–22)	(0.18–0.45)	(1.00–1.20)	(4.75–7.0)	(4.9–11.2)	(0.77–6.0)	(253–323)	(42.0–95.2)	(14.5–41.7)	
(c) Forest (6)	25	1.1	0.98	13.5	62.2	46.9	56	110	30.3
(23.3–28.3)	(0.96–1.24)	(0.83–1.20)	(12.3–14.0)	(54.8–71.3)	(42.3–67.6)	(56.0–146)	(94.5–118)	(28.3–50.0)	

Tree coverage is the sum of the coverage of tree layer and that of subtree layer. Shrub + herb coverage is the sum of the coverage of shrub and herb layers. Therefore, the theoretical maximum value of them is 2.

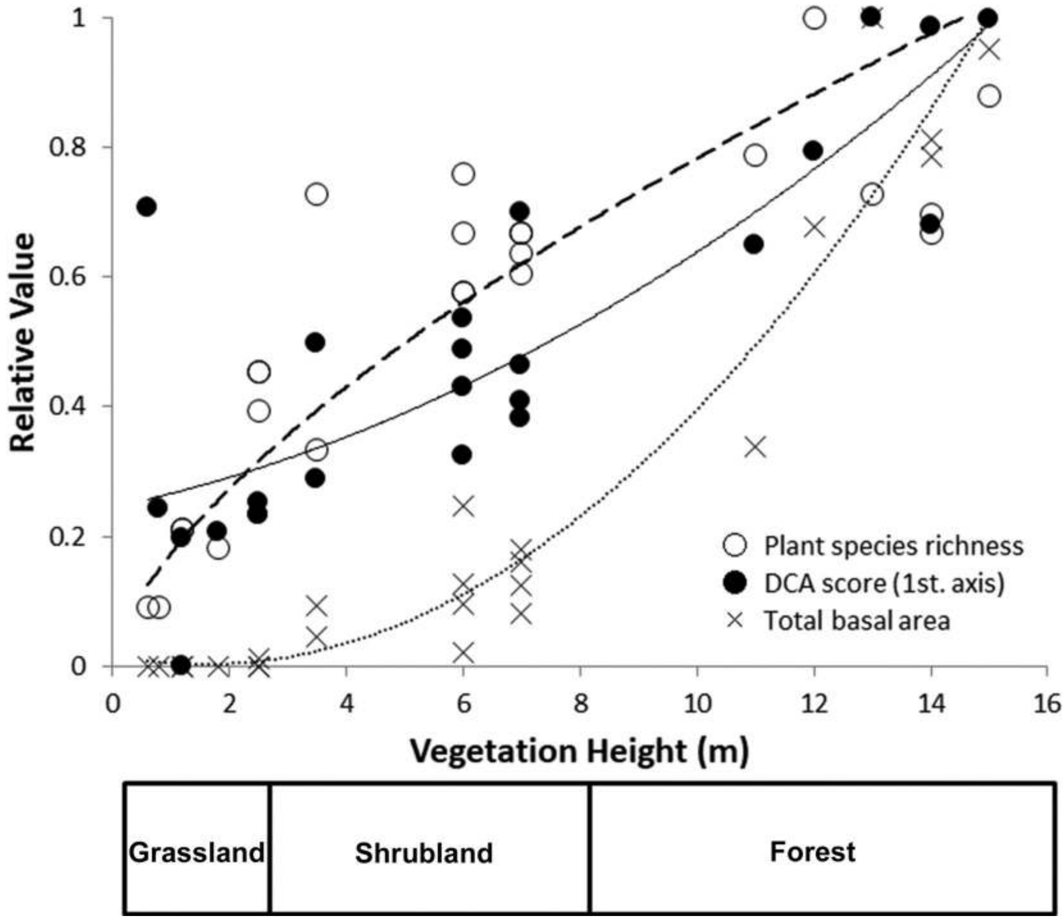

FIGURE 3. Relationship between vegetation height and other vegetation attributes (plant species richness, DCA 1st axis score, and total basal area) in three vegetation types, namely, grassland, shrubland, and forest. Plots were fitted to quadratic curves, where plant species richness: $y = -0.0056x^2 + 0.13x + 0.069$, $R^2 = 0.83$ (dashed line); DCA score (first axis): $y = 0.002x^2 + 0.019x + 0.25$, $R^2 = 0.71$ (solid line); and total basal area: $y = 0.0056x^2 - 0.018x + 0.018$, $R^2 = 0.94$ (dotted line).

between the grassland and shrubland sites. Vegetation height varied by vegetation type.

DCA results indicated variation in plant species composition among the sites. DCA Axis 1 (eigenvalue was 0.70) reflected compositional change along vegetation development: grassland sites showed larger values while forest sites showed smaller values. DCA axis 2 and Axis 3 reflected minor variations (eigenvalue was 0.18 and 0.079, respectively) and no apparent tendency was detected based on the sample scores and species scores.

Figures 3 and 4 show the relationship between vegetation height and other vegetation attributes, namely plant species richness, DCA 1st axis score, and total BA of all tree species (Figure 3), and tree coverage, shrub and herb coverage, and total BA of evergreen tree species (Figure 4). These variables were classified into three groups: (1) shrub and herb coverage and plant species richness, which increased with vegetation height when the vegetation was short and remained almost constant at a taller height; (2) the DCA 1st axis

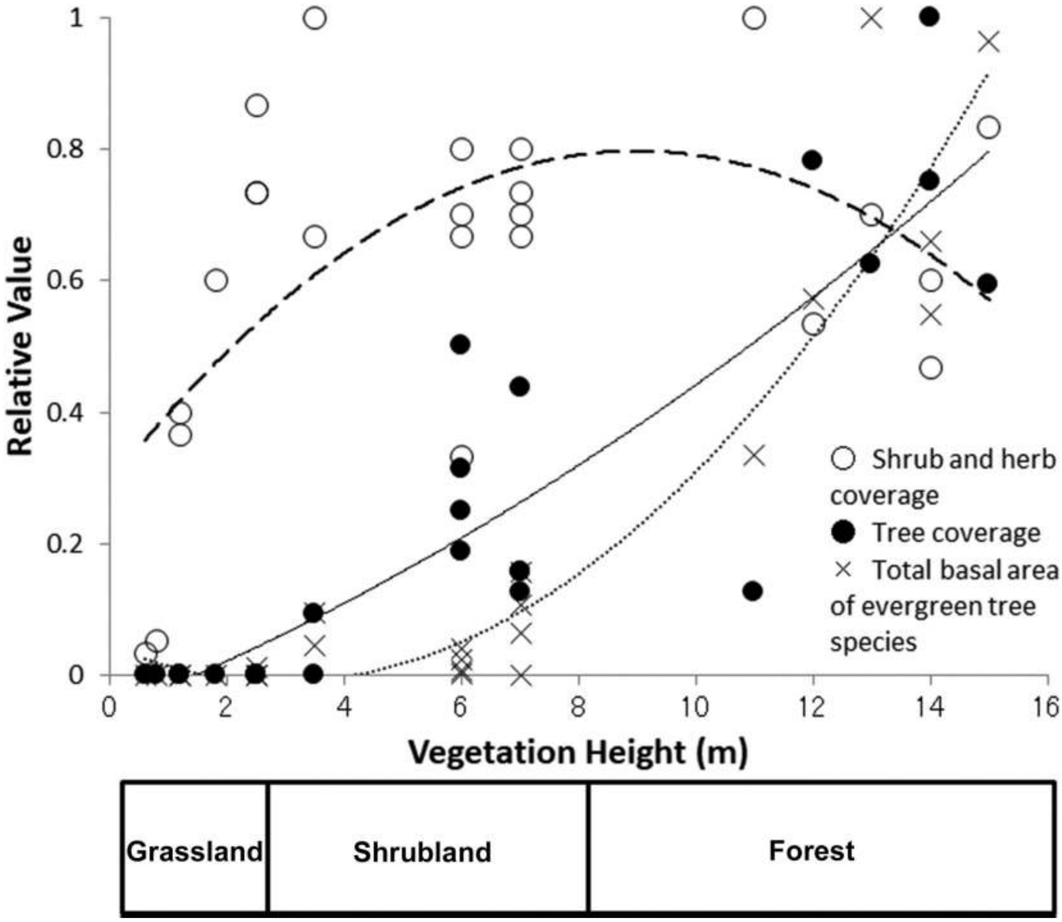

FIGURE 4. Relationship between vegetation height and other vegetation attributes (shrub and herb coverage, tree coverage, and total basal area of evergreen trees and shrubs) in three vegetation types, namely, grassland, shrubland, and forest. Plots were fitted to quadratic curves, where shrub and herb coverage: $y = -0.0062x^2 + 0.11x + 0.29$, $R^2 = 0.32$ (dashed line); tree coverage: $y = 0.0014x^2 + 0.036x - 0.054$, $R^2 = 0.76$ (solid line); and total basal area of evergreen tree species: $y = 0.0063x^2 - 0.037x + 0.045$, $R^2 = 0.89$ (dotted line).

score and tree coverage, which increased almost linearly with vegetation height; and (3) total BA of all tree species and that of evergreen tree species, which tended to be low when vegetation height was less than 8 m, but increased rapidly when the vegetation was taller than 8 m, and the curve was even steeper when only evergreen tree species were included. Vegetation height was classified in the second group based on the linear relationship with the variables included in the group. The results showed that the seven vegetation variables were positively correlated with each other, though these variables increased with vegetation height in three different patterns.

Canonical Correspondence Analysis

Based on the correlation matrix among the vegetation variables, the following variables were removed from the constraining variables in the CCA: the DCA score of the first axis, vegetation height, tree coverage, and total BA of evergreen tree species. These variables

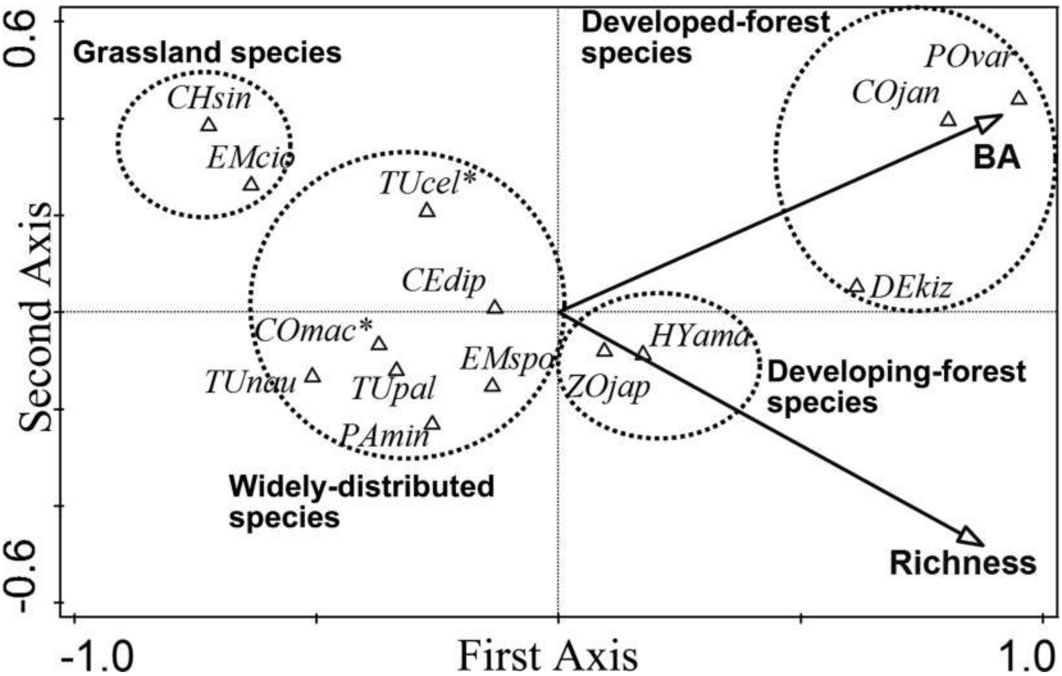

FIGURE 5. Biplot showing the species and selected environmental variables based on the canonical correspondence analysis (CCA) results using breeding season data. Species groupings are shown by dotted circles. Because Black-faced Bunting (EMspo), Naumann's Thrush (TUnau), Pale Thrush (TUpal), and Oriental Greenfinch (CHsin) are wintering birds, these species were not recorded in the breeding season. "BA" and "Richness" indicate total basal area of all tree species and plant species richness, respectively.

TABLE 3

Canonical Correspondence Analysis (CCA) using Breeding Season Data

(a) Basic Statistics of the First Four Axes

Statistic	Axis1	Axis2	Axis3	Axis4
Eigenvalues	0.367	0.09	0.307	0.175
Explained variation (cumulative %)	26.5	33.0	55.2	67.9
Pseudo-canonical correlation	0.935	0.599	0	0
Explained fitted variation (cumulative %)	80.29	100		

Axis 1 and Axis 2 are constrained by the vegetation variables. The other axes are unconstrained.

(b) Contribution of the Vegetation Variables Included

Variable Name	Explained %	*p*	*p*(adj)
Plant species richness	22.6	.002	.006
Total BA of all tree species	10.4	.004	.012

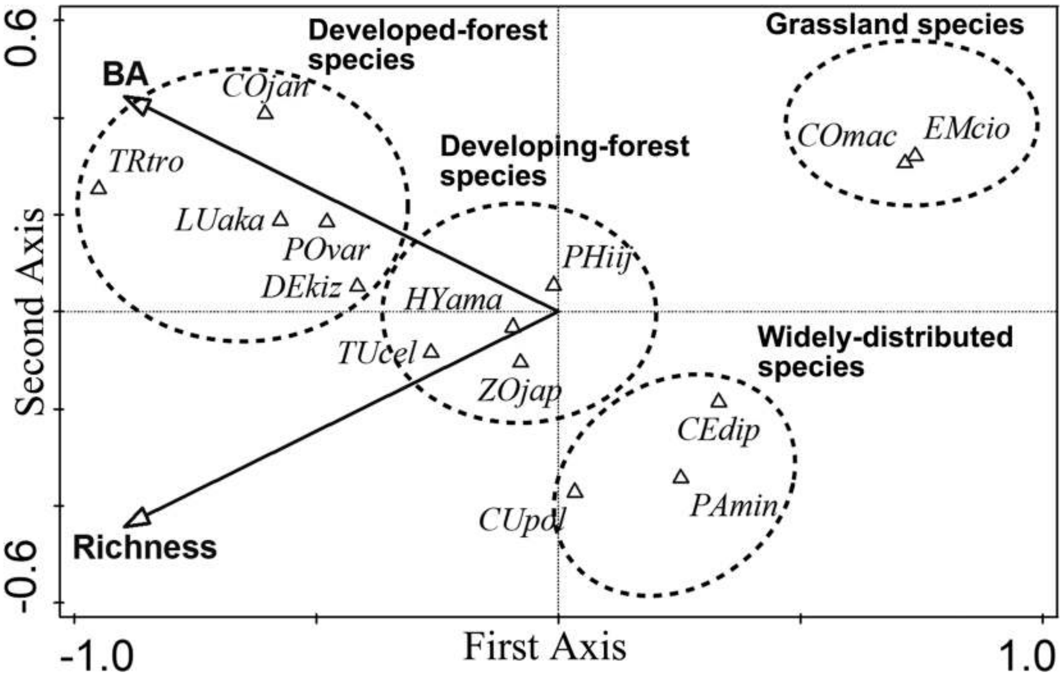

FIGURE 6. Biplot showing the species and selected environmental variables based on the canonical correspondence analysis (CCA) results using wintering season data. Species groupings are shown by dotted circles. Eurasian Wren (TRtro), Japanese Robin (LUaka), Iijima's Leaf Warbler (PHiij), and Lesser Cuckoo (CUpol) were not recorded in the wintering season. * Izu Thrush (TUcel) and Large-billed Crow (COmac) were classified to the different group from the breeding season. "BA" and "Richness" indicate total basal area of all tree species and plant species richness, respectively.

TABLE 4

Canonical Correspondence Analysis (CCA) using Wintering Season Data

(a) Basic Statistics of the First Four Axes

Statistic	Axis1	Axis2	Axis3	Axis4
Eigenvalues	0.312	0.068	0.241	0.202
Explained variation (cumulative %)	21.9	26.7	43.6	57.7
Pseudo-canonical correlation	0.901	0.609	0	0
Explained fitted variation (cumulative %)	82.1	100		

Axis 1 and Axis 2 are constrained by the vegetation variables. The other axes are unconstrained.

(b) Contribution of the Vegetation Variables Included

Variable Name	Explained %	*p*	*p*(adj)
Plant species richness	19.1	.002	.006
Total BA of all tree species	7.6	.046	.138

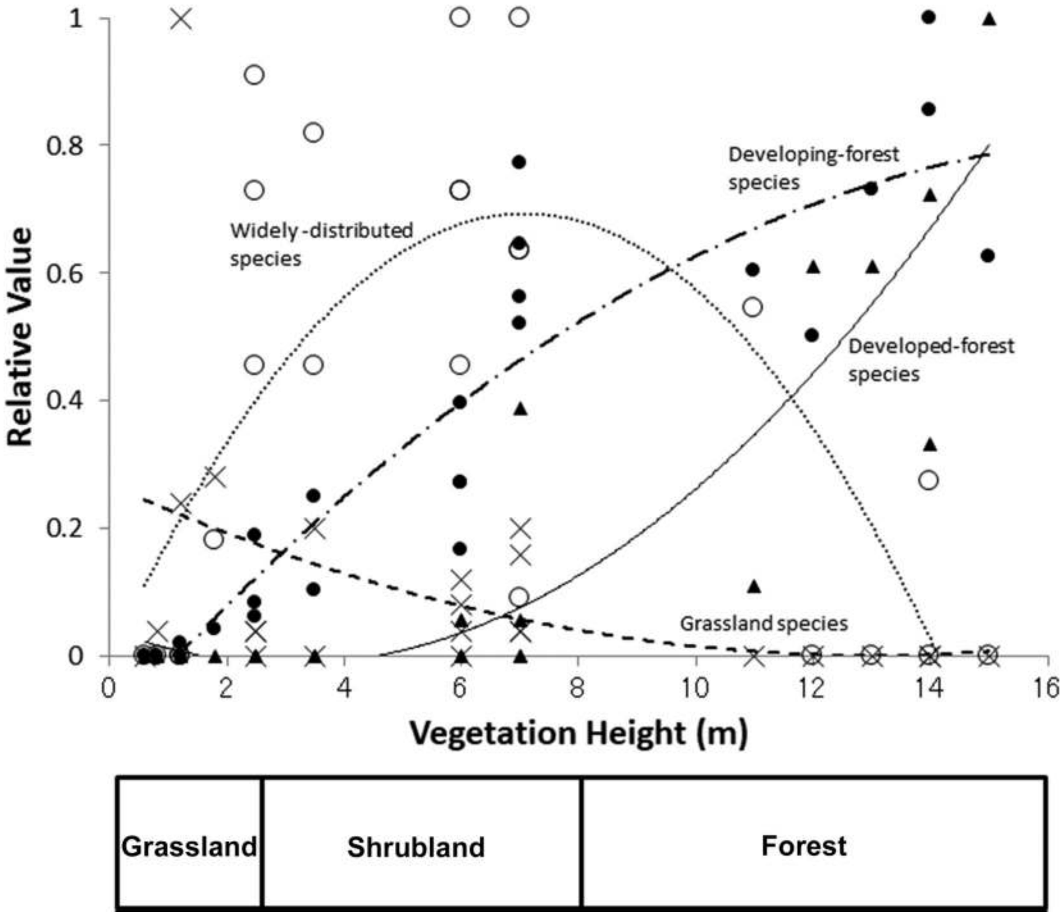

FIGURE 7. Relationship between vegetation height and four avian groups in the breeding season. Total number of recorded individuals belonging to each group was calculated and relativized by the maximum. ▲ "Developed-forest species" include Japanese Wood Pigeon, Japanese Pygmy Woodpecker, Varied Tit, Eurasian Wren, and Japanese Robin. ● "Developing-forest species" include Brown-eared Bulbul, Japanese White-eye, Iijima's Leaf Warbler, and Izu Thrush. ○ "Widely distributed" species include Lesser Cuckoo, Japanese Tit, and Japanese Bush Warbler. × "Grassland species" represent Meadow Bunting and Large-billed Crow. Plots were fitted to quadratic curves, where developed-forest species: $y = 0.0057x^2 - 0.035x + 0.042$, $R^2 = 0.82$ (solid line); developing-forest species: $y = -0.0028x^2 + 0.10x - 0.11$, $R^2 = 0.82$ (long dashed dotted line); widely distributed species: $y = -0.014x^2 + 0.20x - 0.0013$, $R^2 = 0.51$ (dotted line); grassland species: $y = 0.0016x^2 - 0.041x + 0.27$, $R^2 = 0.16$ (dashed line).

showed strong correlations with total BA of all tree species ($0.85 < r < 0.96$) and each other ($0.71 < r < 0.93$). Among them, total BA of all tree species was selected as the representative variable. Absolute values of correlation coefficients calculated between any two of the remaining variables were less than 0.7. One grassland site was removed from the CCA because no birds were counted there.

Avian species composition could be explained by total BA of all tree species and plant species richness, both in the breeding (Figure 5, Table 3) and wintering seasons (Figure 6, Table 4). The first axis was considered to represent the change in avian species composition with vegetation recovery (or development). The direction of both vegetation variables indicated that in the breeding season species such as the Japanese Wood Pigeon, Japanese Robin, Varied Tit, Japanese Pigmy Woodpecker, and Eurasian Wren tended to occur more frequently in

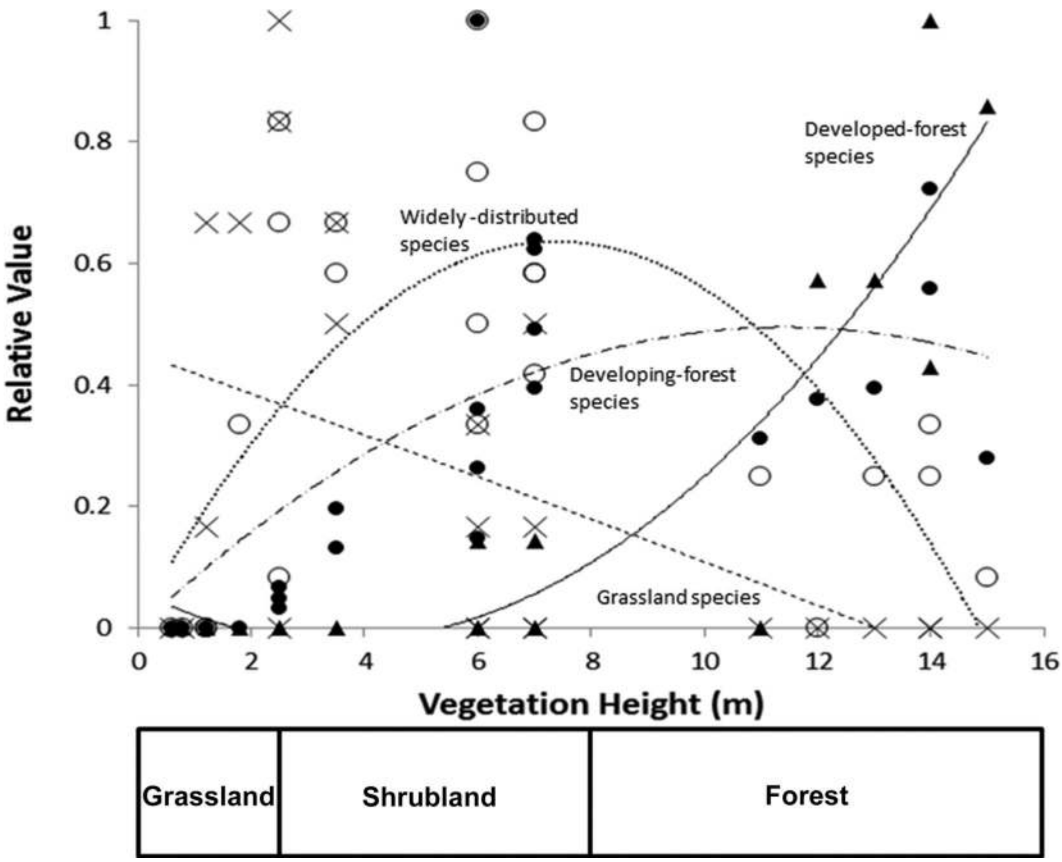

FIGURE 8. Relationship between vegetation height and four avian groups in the wintering season. Total number of recorded individuals belonging to each group was calculated and relativized by the maximum. ▲ "Developed-forest species" include Japanese Wood Pigeon, Japanese Pygmy Woodpecker, and Varied Tit (solid line). ● "Developing-forest species" include Brown-eared Bulbul and Japanese White-eye (long dashed dotted line). ○ "Widely distributed" species include Japanese Tit, Pale Thrush, Naumann's Thrush, Izu Thrush, Black-faced Bunting, Large-billed Crow, and Japanese Bush Warbler (dotted line). × "Grassland species" represents Meadow Bunting and Oriental Greenfinch (dashed line). Plots were fitted to quadratic curves, where developed-forest species: $y = 0.0065x^2 - 0.046x + 0.061$, $R^2 = 0.83$ (solid line); developing-forest species: $y = -0.0038x^2 + 0.087x$, $R^2 = 0.52$ (dash and dot line); widely distributed species: $y = -0.011x^2 + 0.17x + 0.011$, $R^2 = 0.46$ (dotted line); and grassland species: $y = -0.0001x^2 - 0.033x + 0.45$, $R^2 = 0.25$ (dashed line).

vegetation with greater plant species richness and a larger BA (Figure 5). These species were classified into the same group, namely developed-forest species, by ordination space partitioning. The other species were classified into three groups, namely grassland species, widely distributed species, and developing-forest species. In the wintering season, similar bird species groups were obtained and similar relationships were observed between changes in avian species composition along the first CCA axis and vegetation variables (Figure 6). Japanese Robin and Eurasian Wren are not shown in Figure 6 because of the limited observations of these species in the wintering season. The two vegetation variables showed different correlations with the second axis of the CCA, whereas total BA of all tree species showed a positive correlation with the second axis in both seasons while plant species richness showed a negative correlation.

Figure 7 shows the relationship between vegetation height and the number of individuals in the four avian groups in the breeding season. The grassland species decreased with vegetation height while the developing-forest species and developed-forest species showed the opposite tendency. The developed-forest species were only observed abundantly at sites with vegetation taller than 10 m. The developing-forest species were more frequently observed at sites with shorter vegetation. Widely distributed species were observed at almost all sites. They were the most abundant at sites with vegetation of intermediate height (2–10 m). The same relationships were observed in the wintering season (Figure 8). This result and the resemblance of the CCA results obtained in both the seasons (Figures 5 and 6) indicate that the relationship between avian species composition and vegetation attributes did not vary seasonally in the present study, regardless of the seasonal change of avian species composition caused by some migratory species.

DISCUSSION

After the eruption on Miyakejima Island in 2000, a large part of the spatial heterogeneity in the avian community was explained by vegetation development indicated by tree coverage (Katoh and Higuchi 2003, 2011, 2016). For example, Katoh and Higuchi (2011) reported that almost half or more of spatial variation in avian species richness or population density observed on the island showed strong correlation ($r^2 > 0.48$) with tree coverage in any breeding season, although other vegetation variables were not considered. In our study, plant species richness increased with vegetation height when the vegetation was short and remained almost constant at a taller height. Total BA of all tree species tended to be low when vegetation height was less than 8 m, but increased rapidly when the vegetation was taller than 8 m. Tree coverage showed the intermediate tendency and increased almost linearly with vegetation height (Figures 3 and 4). The former two variables explained the spatial variation of avian communities on the island (Figures 5 and 6) better than tree coverage only. Some studies reported that avian communities had similar responses to different tree vegetation variables (e.g., Thinh 2006). The results of the present study were not the same; at least, total BA of all tree species and plant species richness showed different relationships with avian communities. It appears that vegetation variables may affect avian communities differently depending on the situation, such as the vegetation developmental stage.

Relationships between avian communities and vegetation have been studied in areas other than volcanic islands. Such studies have considered the various properties of vegetation. Tree BA and canopy cover (Thinh 2006), vegetation cover at specific heights (Katoh et al. 2003), foliage height diversity (Erdelen 1984), plant species composition (Rotenberry 1985), and presence of certain species (Douglas et al. 1992) have been used to analyze the relationship between vegetation and avian communities. Except for the role of specific plant species, previous studies have not revealed a framework to summarize the relationships among the different vegetation variables and avian community attributes. The present study has attempted to understand these complex relationships (Figures 3, 4, 7 and 8).

Conservation Implications

The restoration of mature evergreen forests is needed to conserve developed-forest bird species including the five endemic and endangered (sub)species, Japanese Wood Pigeon (near threatened species), Japanese Pygmy Woodpecker (endemic subspecies *D. kizuki matsudairai*), Varied Tit (endangered subspecies *P. varius owstoni*), Eurasian Wren (endangered subspecies *T. troglodytes mosukei*), and Japanese Robin (vulnerable subspecies *L. akahige tanensis*) (Table 1). To accomplish this, seed dispersal during earlier seral stages is essential. Fortunately, developing-forest species such as the Japanese White-eye and Brown-eared Bulbul are seed dispersers of various plant species (Fukui 1995, Yoshikawa et al. 2009). Large-billed Crows *Corvus macrorhynchos* also disperse seeds (Nishi and Tsuyuzaki 2004, Yoshikawa and Higuchi 2018). They are known as a “dual habitat user” using both open habitat and tall vegetation (Kurosawa 2009) and were common throughout the island, including on the bare land near the top of the island (Higuchi, Katoh, and Yoshikawa, personal observations). In fact, the seedlings of *M. thunbergii* were observed near the highest points on the island (unpublished data). These birds cannot spread seed if there are no seed sources. Thus, the conservation of mature evergreen trees as seed sources, and the movement of seed dispersers between seed sources and vegetation in earlier seral stages are essential.

Large seeds like those of *C. sieboldii* and *Styrax japonica* are dispersed by few animal species, such as the Varied Tit (Higuchi 1975, Hashimoto et al. 2002). As Varied Tits tended to be observed in evergreen forests (Figures 5 and 6), this vegetation should be considered as corridors or stepping-stones thereby encouraging the movements of Varied Tits (Hashimoto 2008) for increasing the seed dispersal range. Though shrublands and deciduous forests were not suitable habitats for developed-forest species, they may be used by these species for moving between habitats. Such shrublands and deciduous forests are habitats to the developing-forest species and widely distributed species, which include threatened species such as Izu Thrush and Iijima's Leaf Warbler.

Conserving the remaining populations of developed-forest bird species is important. del Moral and Grishin (1999) found that the populations of insects, birds, and mammals followed vegetation recovery because of their mobility. However, this is premised on the existing species source nearby. In the case of islands, species sources should be on the same island, as the immigration of individuals is difficult. Thus, maintaining developed-forest bird populations and their habitats, that is, the remaining evergreen forests are important on Miyakejima Island.

Since 2017, spurts of volcanic gas have almost stopped and vegetation recovery has occurred throughout the island. However, the recovery of mature forest with forest birds and other organisms are yet to be achieved. We propose promoting the establishment/protection of the forests and other seral stages while monitoring the state of ecological communities using suitable measures. Our findings can advise on the most suitable vegetation variables to be monitored.

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