Chapter 4
Biogeographic Pattern of Japanese Birds: A Cluster Analysis of Faunal Similarity and a Review of Phylogenetic Evidence

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Abstract The Japanese islands accommodate 102 native breeding species/subspecies of water birds (comprising 99 species belonging to 58 genera and 22 families) and 246 native breeding species/subspecies of land birds (comprising 156 species belonging to 101 genera and 40 families). The degree of endemism at the species/subspecies level is low in the former (11.8 %) and high in the latter (47.2 %). In this chapter, I investigated the geographic patterns of the community composition of land birds in detail. Using hierarchical and nonhierarchical methods, the cluster analysis of faunal similarity revealed that, despite high vagility, land birds on continental islands exhibited the same biogeographic patterns as other terrestrial vertebrates. This result suggests that the land birds and non-volant terrestrial vertebrates have evolved under the strong influence of the island geohistory, including the appearance and disappearance of land bridges. The cluster analysis also revealed that, in contrast to the non-volant terrestrial vertebrates, the Japanese land birds formed comparatively rich and distinct faunas on these oceanic islands.

Keywords Japanese birds • Species diversity • Endemism • Biogeography • Continental islands • Oceanic islands • Cluster analysis • Faunal similarity

4.1 Introduction

4.1.1 History of Studies on Japanese Avifauna

Japan is a long chain of islands located off the eastern coast of continental China (Fig. 4.1). It comprises four main islands, Hokkaido, Honshu, Shikoku, and Kyushu, with more than 6800 adjacent islands (Statistics Bureau, Ministry of Internal Affairs and Communications 2015). These islands differ greatly in geological and

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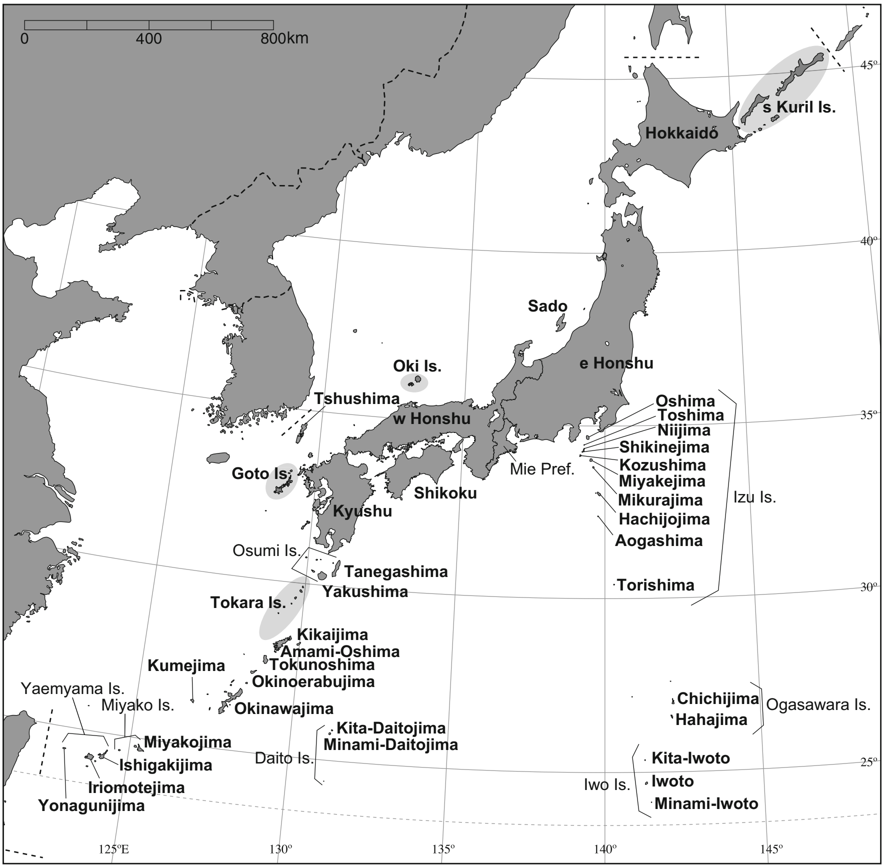

Fig. 4.1 Map of Japan showing location of the 40 study sites (in *bold letters*)

environmental traits (e.g., area, altitude, geological origin, climate, and vegetation) and thus support a rich avifauna.

Although scientific research on Japanese birds had already begun in the late eighteenth century, at that time, Japan was officially closed to all Western nations, except The Netherlands. Thus, because of the paucity of collection material, research activity was low (Dekker et al. 2001; Morioka et al. 2005). Since then, studies on the diversity of Japanese birds have gone through three major periods of high activity (Fig. 4.2).

The first peak was in the 1830s to the 1840s. During this period, the famous series *Fauna Japonica* was published, in which Coenraad Jacob Temminck, the director of the National Museum of Natural History in Leiden, and Hermann Schlegel, a curator of vertebrates, described about 50 new species or subspecies. They examined the large collection of Franz Philipp Balthasar von Siebold, a German naturalist who resided in Japan in the 1820s as a medical officer of the Dutch trading post (Mearns and Mearns 1988; Morioka et al. 2005). Additionally,

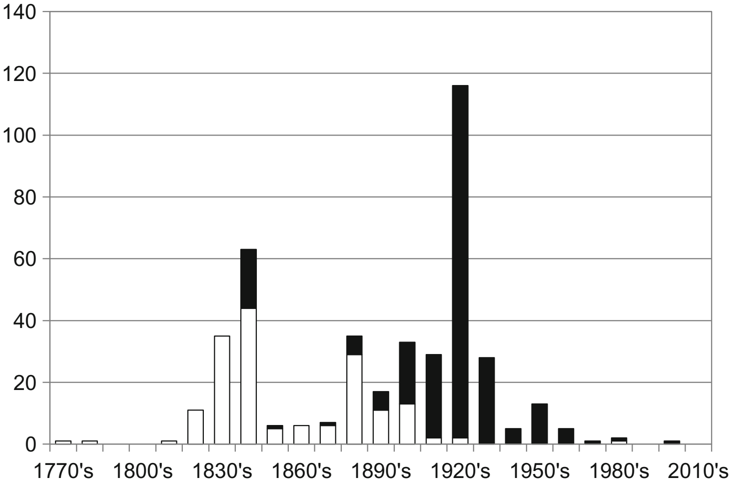

Fig. 4.2 Temporal trends in the number of newly described species/subspecies of Japanese birds. Taxa now in synonymy are included, but those based on fossils or subfossils are excluded. (Data are derived from Morioka et al. 2005). A subspecies described in 2009 (Nishiumi and Morioka 2009) is also included. *White bars* indicate species. *Black bars* indicate subspecies

during this period, Nicholas Aylward Vigor, an Irish naturalist, and Friedrich Heinrich von Kittlitz, a German naturalist, described about 10 new species or subspecies from the Ogasawara Islands, which were then claimed as a British territory (Mearns and Mearns 1988; Morioka et al. 2005).

In the 1860s, Japan was opened to the Western world. However, research activity did not increase, likely because of a sharp decline in public safety (Fig. 4.2). The second peak of new bird descriptions appeared in the 1880s, when public order was restored. During this period, Leonhard Hess Stejneger, a curator of the U.S. National Museum, and Henry Seebohm, an English ornithologist, described 30 or so new species/subspecies using many of the specimens gathered by Thomas Wright Blakiston, Henry James Stovin Pryer, Motoyoshi Namiye, and others (see the American Ornithologists' Union 1919; Mearns and Mearns 1988; Morioka et al. 2005).

In the decades after the second peak, species-level descriptions declined substantially, whereas reports of new subspecies increased considerably. The third major period of new bird descriptions took place in the 1920s. This, the most prominent peak, was mainly attributable to works by two Japanese ornithologists, Nagamichi Kuroda and Tokutaro Momiyama. However, most of the scientific names proposed by the latter (91.1 %) are now regarded as junior synonyms of other bird names, whereas many of the birds described by the former are considered valid (Kuroda 1932; Vaurie 1959, 1965; Morioka 1979; Morioka et al. 2005).

Since the third peak period, the rate of new bird descriptions has declined. In the past 70 years, despite the gross increase of ornithological studies in Japan (Fig. 4.3), only 24 new species or subspecies have been reported from Japan (in contrast to

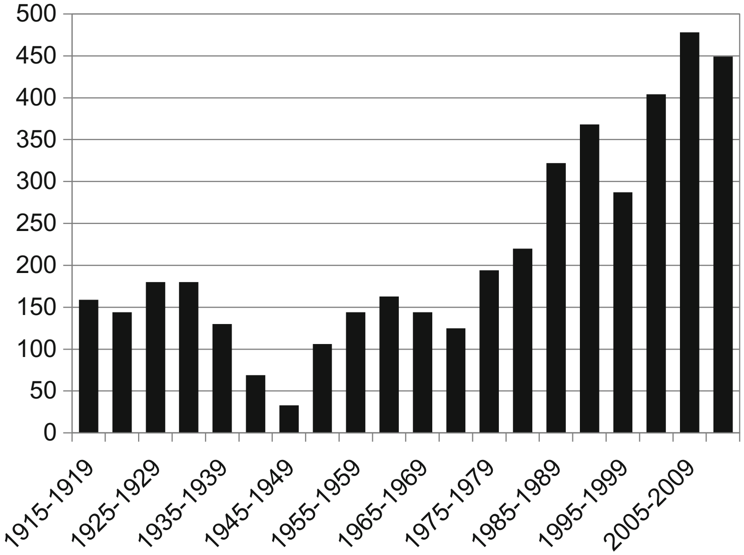

Fig. 4.3 Temporal trends in the number of articles published in Japanese ornithological journals. Total numbers of articles in the following seven journals are shown every 5 years: Tori, Japanese Journal of Ornithology, Ornithological Science, Journal of the Yamashina Institute for Ornithology, Strix, the Bulletin of the Japanese Bird Banding Association and Bird Research. Data were gathered from the J-STAGE database (https://www.jstage.jst.go.jp/browse) and three journals' home pages (http://www.wbsj.org/activity/conservation/publications/strix/, http://birdbanding-assn.jp/J03_bulletin/archive.html, http://www.bird-research.jp/1_kenkyu/index.html)

265 in the preceding seven decades), no fewer than 18 of which are now regarded as invalid (Morioka et al. 2005; Nishiumi and Morioka 2009). This situation clearly means that the possibility of finding new species and subspecies of Japanese birds has become vanishingly small. Instead, during the past seven decades, research on Japanese avifauna has mainly focused on taxonomic revisions of subspecies previously proposed based on insufficient evidence (e.g., Vaurie 1959, 1965; Morioka 1994; Yamasaki 2006). In particular, many subspecies based on arbitrary division of clinal variation have been invalidated. As a result, our understanding of geographic patterns of phenotypic variations of Japanese birds has become considerably more robust. In addition, during this period, details of the geographic distributions, including records of rare vagrants, have also been studied vigorously. Therefore, despite a few new bird descriptions, the number of species recorded in Japan has increased steadily (for example, 489, 542, and 633 native species reported by the Ornithological Society of Japan 1974, 2000, and 2012, respectively).

Now that considerable relevant information has been gathered, it is an appropriate time to discuss the characteristics and formation processes of the Japanese avifauna.

4.1.2 Comparison of the Avifaunas of Japan and the British Isles

Japan and the British Isles are similar island groups of comparable sizes (see Table 4.1), equally situated on the periphery of the Eurasian continent. Based on this information, Hachisuka (1925) attempted to compare the avifaunas of Japan and the British Isles to illustrate the characteristics of each fauna. However, he eventually only gathered relevant information and avoided deriving conclusions, because he believed that the information available to him was still very incomplete. Ninety years have passed, and I conducted a similar comparison using materials accumulated since Hachisuka's work.

The results of the comparison are summarised in Tables 4.1 and 4.2, which show that Japan has 255 native breeding species belonging to 159 genera, 62 families, and 20 orders, whereas the British Isles have 205 species belonging to 131 genera, 58 families, and 20 orders. It is noteworthy that the number of species per unit area (species density) is larger in Japan than in the British Isles: this is also true for both the water bird subgroup (defined here as birds belonging to Anseriformes, Podicipediformes, Phaethontiformes, Gaviiformes, Procellariiformes, Ciconiiformes, Suliformes, Pelecaniformes, Gruiformes, and Charadriiformes) and the land bird subgroup (defined here as birds belonging to Galliformes, Columbiformes, Cuculiformes, Caprimulgiformes, Apodiformes, Accipitriformes, Strigiformes, Coraciiformes, Piciformes, Falconiformes, and Passeriformes). Moreover, the results also reveal that the Japanese land birds encompass more pronounced intraspecific geographic variation than those of the British Isles, although the degree of geographic variation is almost the same in water birds, which include most highly vagile species (e.g., pelagic birds). These patterns seem to reflect the more heterogeneous climates of Japan resulting from the elongated shape of the land from north to south (Fig. 4.1) and mountainous terrain (Table 4.1). However, Table 4.2 also shows that, in contrast to the general patterns, the British Isles have more breeding species than Japan in three orders (Anseriformes, Gaviiformes, and Charadriiformes). This pattern seems to be present mainly

Table 4.1 Comparisons of geographic traits of Japan and the British Isles

	Japan	The British Isles
Area (km^2)[a]	364,560	311,580
Forest cover (%)[a]	68.6	11.7
The latitude of the northernmost point[b]	45.55°N	60.86°N
The latitude of the southernmost point[b]	20.42°N	48.95°N
The highest peak (m)[c]	3,776	1,343

[a] Values for 2012 are shown. Water bodies are excluded. Data were extracted from The World Bank (2015)

[b] Data were gathered using Google Maps (https://maps.google.com)

[c] Data were extracted from Statistics Bureau, Ministry of Internal Affairs and Communications (2015) (for Japan) and Merriam-Webster (1997) (for the British Isles)

Table 4.2 Comparisons of native breeding avifaunas of Japan and the British Isles

	Japan					The British Isles				
Order	Family	Genus	Species[a]	Species/ subspecies	Sub-speciation[b]	Family	Genus	Species[a]	Species/ subspecies	Sub-speciation[b]
Water birds										
Anseriformes	1	8	14(0.38)	14	1.00	1	9	17(0.55)	17	1.00
Podicipediformes	1	2	3(0.08)	4	1.33	1	2	4(0.13)	4	1.00
Phaethontiformes	1	1	1(0.03)	1	1.00	0	0	0(0.00)	0	
Gaviiformes	0	0	0(0.00)	0		1	1	2(0.06)	2	1.00
Procellariiformes	3	6	14(0.38)	14	1.00	2	4	4(0.13)	4	1.00
Ciconiiformes	1	1	1(0.03)	1	1.00	1	1	1(0.03)	1	1.00
Suliformes	3	3	7(0.19)	7	1.00	2	2	3(0.10)	4	1.33
Pelecaniformes	2	9	17(0.47)	17	1.00	2	4	4(0.13)	4	1.00
Gruiformes	2	8	10(0.27)	11	1.10	3	7	8(0.26)	8	1.00
Charadriiformes	8	20	32(0.88)	33	1.03	8	26	40(1.28)	43	1.08
Subtotal	22	58	99(2.72)	102	1.03	21	56	83(2.66)	87	1.05
Land birds										
Galliformes	1	5	5(0.14)	12	2.40	1	4	6(0.19)	6	1.00
Columbiformes	1	4	7(0.19)	11	1.57	1	2	5(0.16)	5	1.00
Cuculiformes	1	2	4(0.11)	4	1.00	1	1	1(0.03)	1	1.00
Caprimulgiformes	1	1	1(0.03)	1	1.00	1	1	1(0.03)	1	1.00
Apodiformes	1	2	3(0.08)	4	1.33	1	1	1(0.03)	1	1.00
Accipitriformes	2	11	13(0.36)	16	1.23	2	8	11(0.35)	11	1.00
Strigiformes	1	7	9(0.25)	15	1.67	2	4	5(0.16)	5	1.00
Coraciiformes	2	4	4(0.11)	6	1.50	1	1	1(0.03)	1	1.00
Piciformes	1	6	11(0.30)	25	2.27	1	3	4(0.13)	4	1.00
Falconiformes	1	1	3(0.08)	4	1.33	1	1	4(0.13)	4	1.00
Passeriformes	28	58	96(2.63)	148	1.54	25	49	83(2.66)	100	1.20

Subtotal	40	101	156(4.28)	246	1.58	37	75	122(3.92)	139	1.14
Total	62	159	255(6.99)	348	1.36	58	131	205(6.58)	226	1.10

Ordinal and familiar taxonomy follows The Ornithological Society of Japan (2012). Generic, specific and subspecific taxonomy and distributional data were based on The Ornithological Society of Japan (2012) (for Japan) and Parkin and Knox (2010) (for the British Isles)

[a] Values in parentheses represent species density (the number of species per 10^4 km^2)

[b] The total number of species/subspecies is divided by the total number of species to reflect the intensity of intraspecific geographic variation

because these orders of the British Isles include many migratory species preferring water bodies at high latitudes (Gooders 1982). The British Isles, which are located at a more northern latitude than the Japanese islands (Table 4.1), abound in such environments.

Additionally, compared with the British Isles, Japan also has more forest-dwelling birds and fewer open-habitat birds. For example, 72.9 % (113/155) of Japanese breeding land bird species are observed in some sort of woodland in the breeding season, whereas only 49.2 % (60/122) exploit woodlands in the British Isles [calculated based on habitat information provided by the Ornithological Society of Japan (2012) and Nakamura and Nakamura (1995) for Japanese birds, and by Gooders (1982) and del Hoyo et al. (2010) for those of the British Isles]. This pattern may reflect the fact that much higher forest cover is observed in the Japanese islands (Table 4.1).

4.1.3 A Comparison of Fauna of Japanese Birds and Other Terrestrial Vertebrates

As well as birds, the other terrestrial vertebrate faunas of Japan are also characterised by the high species richness (Sengoku et al. 1996; Abe et al. 2005); interestingly, detailed inspection reveals a markedly different pattern of diversity among them. In particular, although the Japanese native avifauna (633 species including 255 regularly breeding birds) is much richer than that of mammals, reptiles, and amphibians (110, 66, and 59 species, respectively, excluding marine species), their degree of endemism is much lower. Only 7.1 % of the breeding birds (14 resident and 4 migratory species; Table 4.3) are endemic to Japan, whereas no less than 40.0 % of mammals, 56.1 % of reptiles, and 78.0 % of amphibians are endemic (Sengoku et al. 1996; Abe et al. 2005; The Ornithological Society of Japan 2012).

In a series of biogeographic studies, Morioka argued that the paucity of endemism in Japanese birds is attributable to recent colonisation by continental birds across sea barriers and subsequent replacement of native species (Morioka 1971, 1974; Morioka and Sakane 1980). He considered that geohistorical factors, for example, sea level changes during the glacial periods, had little influence on the distribution of Japanese birds, although they are often considered the most significant factors for the evolution of Japan's mammalian fauna and herpetofauna (Ota 1998, 2000; Millien-Parra and Jaeger 1999).

Morioka's studies, similar to those of other contemporary researchers (e.g., Short 1973), did not use numerical and objective comparative methods. Furthermore, since his studies were published, substantial taxonomic changes have taken place (e.g., Yamasaki 2006; Saitoh et al. 2010) and new information on distribution has been published (see Sect. 4.1.1). In the following sections, I conduct a numerical cluster analysis of local assemblages of Japanese breeding birds using recently

Table 4.3 Bird species endemic to Japan

Species	Common name	Resident/ migratory	Family
Water birds[a]			
Gorsachius goisagi[b]	Japanese Night Heron	Migratory	Ardeidae
Gallirallus okinawae	Okinawa Rail	Resident	Rallidae
Scolopax mira	Amami Woodcock	Resident	Scolopacidae
Land birds[c]			
Syrmaticus soemmerringii	Copper Pheasant	Resident	Phasianidae
Columba versicolor	Bonin Wood Pigeon	Resident	Columbidae
Columba jouyi	Ryukyu Wood Pigeon	Resident	Columbidae
Picus awokera	Japanese Green Woodpecker	Resident	Picidae
Sapheopipo noguchii	Okinawa Woodpecker	Resident	Picidae
Garrulus lidthi	Lidth's Jay	Resident	Corvidae
Phylloscopus xanthodryas	Japanese Leaf Warbler	Migratory	Phylloscopidae
Phylloscopus ijimae	Ijima's Leaf Warbler	Migratory	Phylloscopidae
Apalopteron familiare	Bonin White-eye	Resident	Zosteropidae
Cichlopasser terrestris	Bonin Thrush	Resident	Muscicapidae
Turdus celaenops	Izu Thrush	Resident	Muscicapidae
Luscinia komadori	Ryukyu Robin	Resident	Muscicapidae
Prunella rubida	Japanese Accentor	Resident	Prunellidae
Chaunoproctus ferreorostris	Bonin Grosbeak	Resident	Fringillidae
Emberiza sulphurata	Yellow Bunting	Migratory	Emberizidae

This table includes species whose breeding distributions are confined to (but winter outside of) Japanese territory. Data were obtained from The Ornithological Society of Japan (2012)

[a] Breeding ranges of Bryan's Shearwater *Puffinus bryani* Pyle, Welch and Fleischer, 2011 are not well known. Future studies might show that it is a breeding bird endemic to Japan

[b] There are a few records of casual breeding of this species in Taiwan and Korea (BirdLife International 2015)

[c] OSJ (2012) considered the Japanese Wagtail, *Motacilla grandis*, to be a casual breeder in Korea, where this species may actually be a rare but locally abundant resident bird (Choi and Nam 2008)

published material. The purpose of this study is to elucidate the geographic patterns of faunal similarities among local assemblages and to identify factors that significantly influenced the Japanese avifauna formation.

4.2 Materials and Methods

I selected 35 islands and four island groups that have been comparatively well surveyed and cover almost the entire range of Japan as independent units for the analysis (Fig. 4.1). Morioka and Sakane (1980) pointed out that the largest island, Honshu, has two considerably different avifaunas in its northeastern and southwestern regions. Thus, I treated these two regions as separate units for the following analyses. The northeastern avifauna includes birds from Niigata, Nagano, Gifu, and Aichi Prefectures and eastward. The southwestern avifauna includes Toyama, Ishikawa, Fukui, Shiga, Kyoto, Nara, and Wakayama Prefectures and westward. Birds from Mie Prefecture were ignored, because this area has a mixture of the two aforementioned faunas. As for the four island groups (southern Kuril, Oki, Goto, and Tokara Islands), it was difficult to treat each island as an independent unit because of the lack of detailed distribution information. For each of the 40 localities examined, I compiled a list of native species/subspecies that breed there regularly. I also recorded whether each taxon is endemic to the Japanese territory. Taxonomic and distributional data were obtained from The Ornithological Society of Japan (2012).

To describe the geographic pattern of faunal similarity within Japan, I computed the Simpson's similarity indices (S) for all pairwise comparisons among the 40 local communities at both the species and species/subspecies levels. The formula $S = C/N$ was used, where C is the number of shared species or species/subspecies, and N the number of species or species/subspecies in the smaller community. The calculations were done using data on land birds only. The values were then converted into distances (D) by the formula: $D = 1 - S$. The resulting distance matrices were subjected to cluster analysis using the unweighted pair-group means algorithm (UPGMA). For computation and visualisation of results, I used two computer programs, PHYLIP version 3.695 (Felsenstein 1989) and MEGA version 6.06 (Tamura et al. 2013). To assess the degree of support for each of the UPGMA clusters, I also conducted bootstrap analysis using the macro language VBA with the RANDBETWEEN and INDEX functions in Excel® 2010 (Microsoft, Redmond, WA, USA). Random selection of species or species/subspecies was carried out 1000 times. Bootstrap replicates, including zero-sized communities, made it impossible to calculate D; they were therefore discarded and a recalculation was done.

To evaluate possible biases arising from the lack of phylogenetic information (Holt et al. 2013), I conducted a preliminary UPGMA cluster analysis incorporating available, albeit incomplete, phylogenetic information. For this purpose, I used the method recently developed by Holt et al. (2013). This preliminary analysis was only done for the species/subspecies level. I assumed that each order, family, genus, and species in the classification of The Ornithological Society of Japan (2012) represented a monophyletic group. I also postulated polytomies at the ordinal, familiar, generic, specific, and subspecific levels. Using the resulting phylogenetic relationship, I calculated the modified Simpson's indices following the formula $S' = C'/N'$, where C' is the number of shared phylogenetic branches, and N' the number of branches in the smaller community. These data were then analysed as already described.

As a complementary nonhierarchical description of the geographic pattern of faunal similarity, I also plotted the 40 local communities in three-dimensional space based on the multidimensional scaling (MDS) procedure with the ordinal level option in SAS version 9.3 (SAS, Cary, NC, USA). For this analysis, I used the aforementioned D distance matrix calculated at the species/subspecies level without incorporating phylogenetic information.

4.3 Results

The native fauna of regularly breeding birds in Japan includes 99 species (38.8 %) of water birds and 156 species (61.2 %) of land birds (Table 4.4). Compared with the mammalian fauna and herpetofauna, the percentages of endemic species are much smaller in both water birds (3.0 %) and land birds (9.6 %). The degree of endemism in the water birds is low even at the species/subspecies level (11.8 %). However, as with the land birds, a considerably large fraction of species/subspecies are confined to the Japanese territory (47.2 %) (Table 4.4).

At the species level, the UPGMA dendrogram of land bird faunal similarity yielded only two small clusters with high bootstrap supports (>70 %): one combining Hokkaido and the southern Kuril Islands (bootstrap value = 76 %) and the other combining Yakushima and Tanegashima (bootstrap value = 87 %). In contrast, the UPGMA dendrogram based on data at the species/subspecies level detected no less than 15 distinct clusters with high bootstrap support (Fig. 4.4). The preliminary UPGMA dendrogram incorporating phylogenetic information also supported, or at least did not refute, the presence of these 15 clusters (Fig. 4.5). There were 5 main clusters: (1) the four main islands of Japan together with some adjacent islands, or the Japanese Archipelago, and the Izu Islands, (2) Yakushima and Tanegashima, (3) the Daito Islands, (4) the central and southern Ryukyus, and (5) the Ogasawara and Iwo Islands. The Tokara Islands are not included in any of these clusters at the top level. In the first cluster (1), the first node isolates (6) Hokkaido and the southern Kuril Islands from (7) the other localities. The second node separates (9) the Izu Islands and (8) the others. Cluster 8 contains a well-supported subcluster, (10) eastern Honshu and Sado. Cluster 4 is divided into the (11) central and (12) southern Ryukyus. The latter is further divided into the Miyako and (13) Yaeyama Islands. The highest level cluster 5 consists of two well-supported subclusters, (14) Ogasawara and (15) the Iwo Islands.

The multidimensional scaling analysis scatterplot (Fig. 4.6) supported the presence of 14 of the 15 clusters described. However, it did not confirm the close relationship between eastern Honshu and Sado.

Table 4.4 Summary of the native breeding avifauna of Japan

	Species		Species/subspecies	
	Total	Endemic[a]	Total	Endemic[a]
Water birds	99	3 (3.0 %)	102	12 (11.8 %)
Land birds	156	15 (9.6 %)	246	116 (47.2 %)
Total	255	18 (7.1 %)	348	128 (36.8 %)

[a] Birds whose breeding distributions are confined to Japanese territory

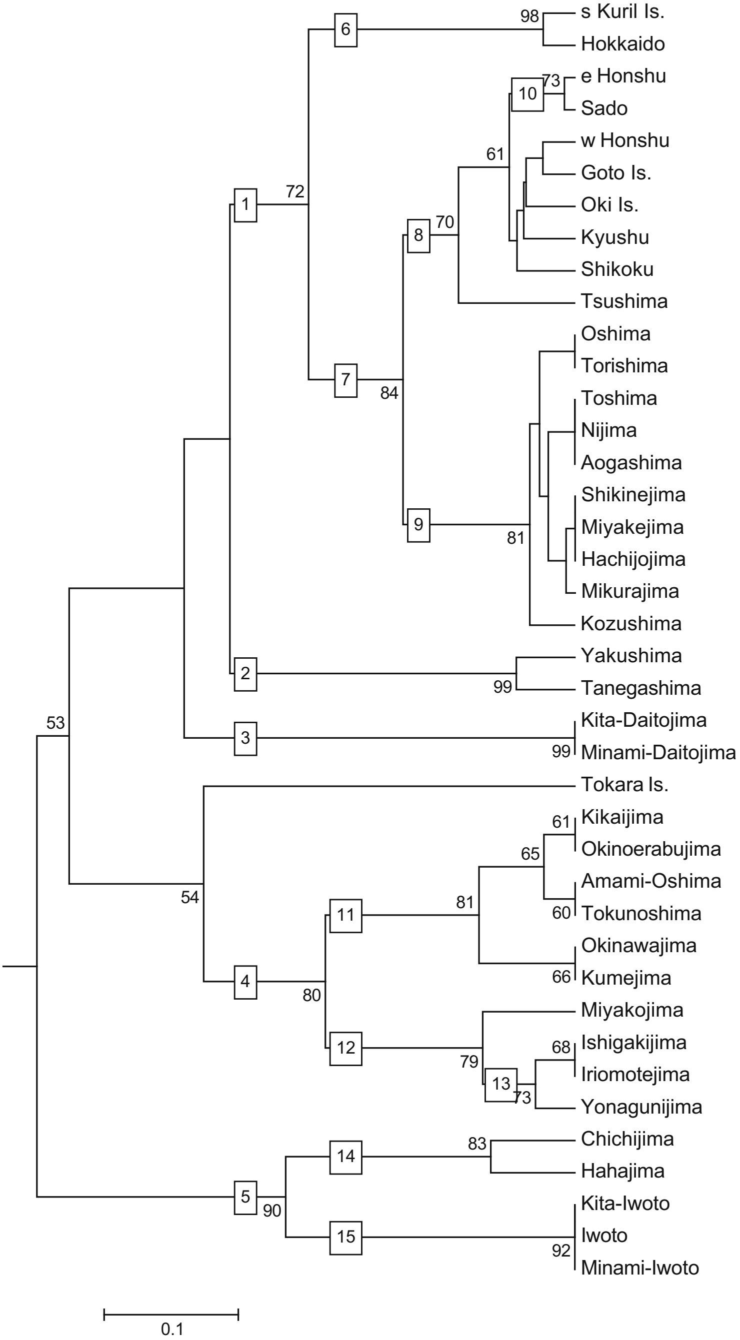

Fig. 4.4 Unweighted pair-group means algorithm dendrogram of faunal similarity for the native breeding land birds of Japan based on Simpson's similarity indices calculated at the species/subspecies level. Bootstrap values >50 % are shown at the nodes. Highly supported clusters (>70 %) are numbered serially

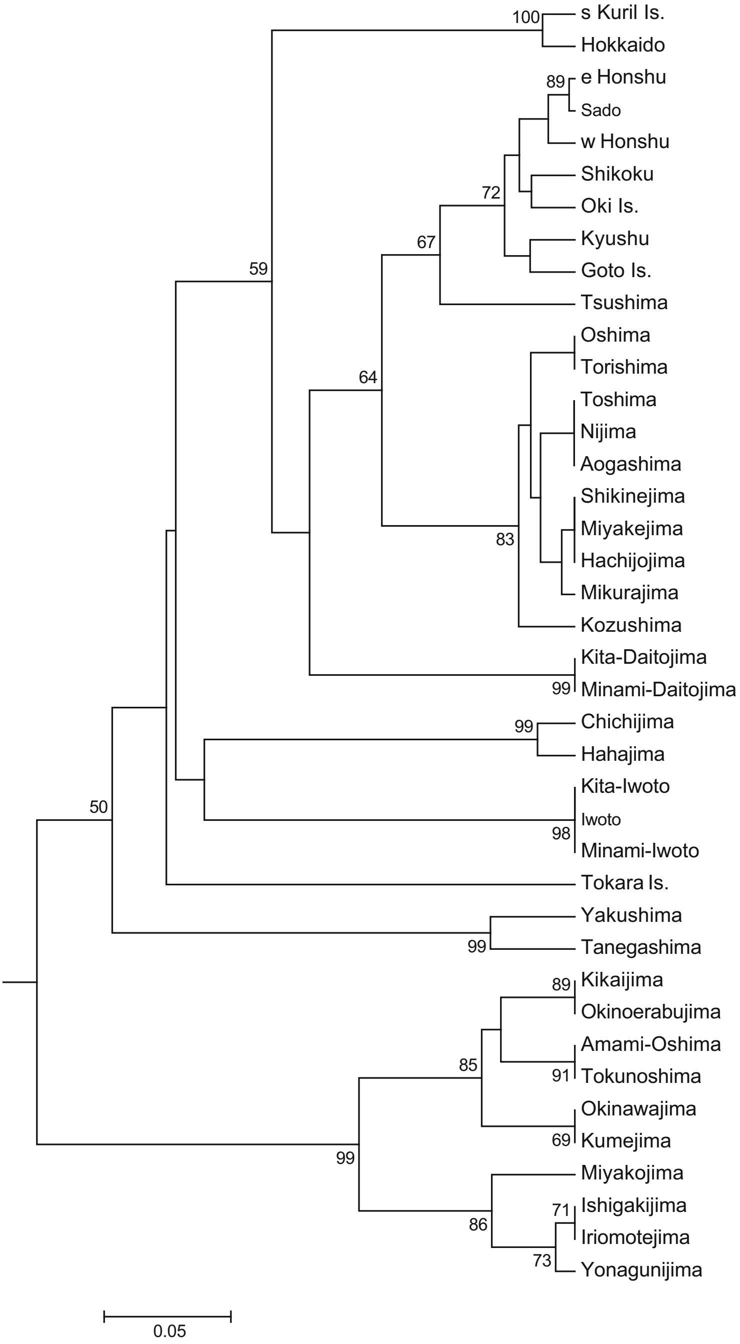

Fig. 4.5 Unweighted pair-group means algorithm dendrogram of faunal similarity for the native breeding land birds of Japan based on corrected Simpson's similarity indices calculated at the species/subspecies level incorporating phylogenetic information. Bootstrap values >50 % are shown at the nodes

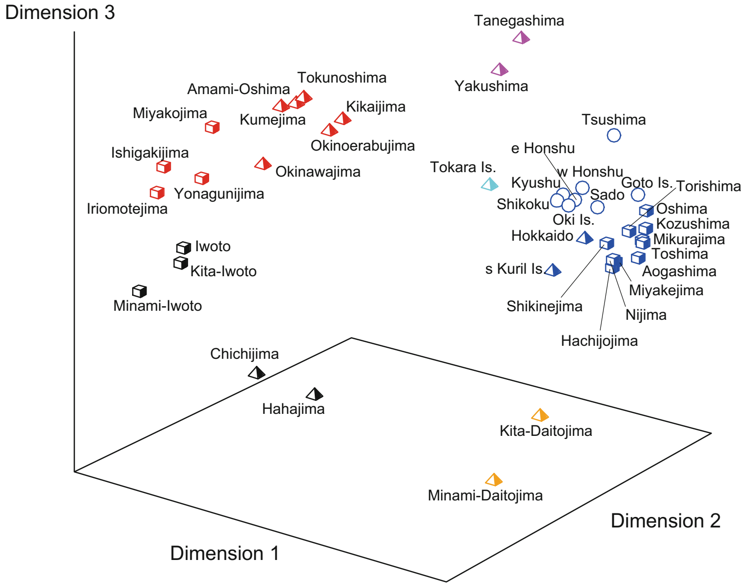

Fig. 4.6 Scatterplot of the multidimensional scaling analysis for faunal similarity of the native breeding land birds based on Simpson's similarity indices calculated at the species/subspecies level. Different colours show different major clusters of the UPGMA analysis (see Fig. 4.4). Tokara Islands, which do not belong to any of the top-level clusters, are represented by *cyan*. Different *marks* indicate different subclusters

4.4 Discussion

The Japanese avifauna does not exhibit either high endemism or any strong biogeographic structure at the species level (see Table 4.4 and Sect. 4.3). These results appear to support Morioka's hypothesis that the Japanese avifauna would have been formed through recent colonisation by continental birds across sea barriers and the subsequent rapid replacement of native species (Morioka 1971, 1974; Morioka and Sakane 1980). He also postulated that geohistorical factors, such as sea level changes during the glacial periods, had little influence on the distribution of Japanese birds.

However, the present study also revealed that, aside from water birds, which include birds that have a very wide distribution range (e.g., pelagic birds), the Japanese birds exhibit a considerably high degree of endemism at the specific/subspecific level (see Table 4.4). Morioka considered these subspecies as only slightly different from their continental counterparts in terms of phenotypic characteristics, and thus concluded that they have not been geographically isolated for long (Morioka and Sakane 1980). He argued that biogeographic analyses of Japanese birds should not be carried out on subspecific-level data (Morioka 1971). However, diagnostic traits possessed by Japanese endemic subspecies, even if they seem trivial, are potential evidence that these subspecies have a biogeographic history independent from continental birds (Cracraft 1983). Moreover, in contrast to Morioka's view of close affinity, a recently published analysis of DNA barcode data reported that several of these subspecies are actually highly genetically divergent from other conspecifics; of 156 land birds breeding in Japan, at least 24 species have intraspecific variation greater than 1.6 % Kimura two-parameter distance (Saitoh et al. 2015), which is a distance threshold proposed for delimiting bird species of the Eurasian continent (Kerr et al. 2009). To date, only a fraction of the 24 species have been studied in detail, but the presence of many cryptic endemic species has already been confirmed (Saitoh et al. 2010; McKay et al. 2014; Dong et al. 2015). Thus, it seems likely that the frequency of bird species endemic to Japan will increase with further research.

The high degree of endemism of the Japanese land birds at the specific/subspecific level seems to suggest that sea straits separating the Japanese islands and continental China have served as important biogeographic barriers, even for these highly vagile animals. The faunal similarity analysis conducted at the species/subspecies level also indicated the possibility that, as with terrestrial vertebrates, the Japanese land bird fauna has evolved under the strong influence of geohistory. The analysis revealed the presence of the same biogeographic regions as those found in surveys on non-volant terrestrial vertebrates (Fig. 4.4) (Ota 1998, 2000; Millien-Parra and Jaeger 1999).

Excluding the oceanic islands, the Japanese islands are grouped into two main regions, the Japanese Archipelago and the Ryukyu Archipelago; in the Japanese Archipelago, the Tsugaru Strait separating Hokkaido and Honshu serves as a biogeographic border; despite low bootstrap support, the Tsushima Strait, located between Tsushima and Kyushu, might also be another biogeographic border (see also Figs. 4.5 and 4.6). The Ryukyu Archipelago is further divided into two subregions, the central and southern Ryukyus. It is noteworthy that each of these regions and subregions has many endemic species/subspecies (Table 4.5). These species/subspecies have either evolved in situ or only survived in one place, suggesting that each of the regions/subregions has a distinct evolutionary history.

The multidimensional scaling analysis of faunal similarity (Fig. 4.6) revealed that the avifaunas of Yakushima, Tanegashima, and the Tokara Islands have characteristics intermediate of those in the Japanese and Ryukyu archipelagos. However, the Yakushima and Tanegashima avifauna is not a simple mix but is characterised as having comparatively many endemic species/subspecies (Table 4.5). The Osumi Islands, which comprise Yakushima and Tanegashima together with adjacent islets, exhibit very high environmental heterogeneity, such as high mountain ranges (~2000 m) and plains, which might promote strong divergent natural selection, the driving force of the ecological speciation process. In contrast to this, no endemic birds are known from the Tokara Islands, although some authors suggest the possibility of undescribed forms (Morioka 1990; Seki et al. 2011). A study on the herpetofauna of this area revealed the presence of a biogeographic border at the strait within the islands (Ota 1998, 2000). For birds, it is

Table 4.5 Summary of native land birds breeding in each of Japan's 17 biogeographic regions

	Species/subspecies	
Region	Total	Endemic[a]
1. The Japanese archipelago (including the Izu Islands)	182	49 (26.9 %)
2. Yakushima and Tanegashima	32	5 (15.6 %)
3. Daito Islands	13	6 (46.2 %)
Tokara Islands	25	0 (0.0 %)
4. Central and southern Ryukyus	51	25 (49.0 %)
5. Ogasawara and Iwo Islands	17	13 (76.5 %)
6. Hokkaido and the southern Kuril Islands	120	6 (5.0 %)
7. Honshu, Shikoku, and Kyushu with adjacent islands and Izu Islands	149	35 (23.5 %)
8. Honshu, Shikoku, and Kyushu with adjacent islands	141	28 (19.9 %)
9. Izu Islands	39	4 (10.3 %)
10. Eastern Honshu and Sado	123	9 (7.3 %)
11. Central Ryukyus	38	9 (23.7 %)
12. Southern Ryukyus	29	11 (37.9 %)
Miyako Islands	17	0 (0.0 %)[b]
13. Yaeyama Islands	27	8 (29.6 %)
14. Ogasawara Islands	14	7 (50.0 %)
15. Iwo Islands	8	3 (37.5 %)

The numbers before the region names refer to the cluster number in the unweighted pair-group means algorithm dendrogram (see Fig. 4.4)

[a] Birds whose breeding distributions are confined to the biogeographic region

[b] Miyako Island Kingfisher, *Todiramphus miyakoensis*, which is known by a single specimen from Miyakojima Island, was excluded from the analysis because it is possible that it does not breed there (Morioka 1974)

difficult to perform analysis using each island as a unit of comparison because of the paucity of information on the distribution of birds breeding within the islands.

The only obvious difference in biogeographic patterns between the land birds and other terrestrial vertebrates is that biogeographic regions comprising oceanic islands are only seen in the former. The oceanic islands Izu, Daito, Ogasawara, and Iwo have comparatively rich and distinct avifaunas (Fig. 4.4, Table 4.5), but they have poor non-volant terrestrial vertebrate faunas. Highly vagile land birds seem to have been able to colonise these isolated islands and experienced rapid evolution in the face of strong natural selection attributable to the poor biotas.

4.5 Conclusion

In summary, the land birds breeding in Japan exhibit a high degree of endemism at the specific or subspecific level. On continental islands, they exhibit the same biogeographic patterns as other terrestrial vertebrates. The strong marine barriers within and around the Japanese islands have effectively restricted range expansion in these highly vagile animals. However, colonisation into oceanic islands with poor biotas seems to have led to the rapid generation of distinct but evolutionarily short-lived forms. To understand the biogeography of the Japanese birds in depth, more precise descriptions of phenotypic and genetic diversity and distribution ranges, particularly near the biogeographic borders, are necessary.

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