Ongoing collapse of avifauna in temperate oceanic islands close to the mainland in the Anthropocene

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Abstract

1. Oceanic island ecosystems are highly vulnerable to human activity. Furthermore, oceanic islands close to the mainland provide distinct perspectives on natural processes, including overseas dispersal from the mainland. However, the effects of overseas dispersal and human activity on insular community changes have not been empirically demonstrated.

2. To clarify the mechanisms driving changes in insular communities due to overseas dispersal and human activity, we investigated bird assemblages on ten islands from 2016 to 2021 and compared them to bird assemblages from 1970 to 1973 on the Izu Islands, Japan.

3. The effects of changes in mainland distribution and species traits on the colonisation and disappearance of bird species on the islands were examined using phylogenetic generalised least squares (PGLS) models. Bird community structures on each island were examined based on species richness and functional and phylogenetic structures. A null modelling approach was used to examine functional and phylogenetic cluster/overdispersion structures; clustering implies species elimination by environmental filters and overdispersion implies a limiting similarity. The effects of geographical and topographical characteristics of the islands, weasel introduction, and landscape transformation were examined using generalised linear models (GLMs).

4. Species that expanded their mainland distribution and have large clutches colonised more islands. Raptors disappeared from many islands. Species richness decreased, and functional and phylogenetic structures clustered on almost all islands, which were only statistically associated with geographical and topographical characteristics of the islands. The lack of an association between changes in community structures and landscape transformation or weasel introduction might be due to the spillover effects of weasels introduced on several islands in the archipelago.

5. The mirroring of the distribution changes in species between the mainland and islands indicates that changes in communities on the mainland affect insular communities via overseas dispersal. Furthermore, introduced predators on an island would have spillover impacts on avian communities across the archipelago through competition for food resources and direct predation, which suggests the need for comprehensive conservation strategies across the archipelago to effectively conserve insular biodiversity.

Keywords

bird assemblage, functional structure, human disturbance, overseas dispersal, island biogeography, phylogenetic structure

1. Introduction

Oceanic island ecosystems are unique and biologically irreplaceable because they have never been connected to continental mainlands (Delgado et al., 2017; Sobral et al., 2016). Natural processes that shape insular communities are highly stochastic and rare immigration events on oceanic islands (MacArthur & Wilson, 1967). Human activities have increasingly affected biodiversity and communities, even in insular ecosystems. The major threats to insular communities in the Anthropocene (Lewis & Maslin, 2015) are invasive exotic species and human-induced landscape transformations (Russell & Kueffer, 2019). However, no study has empirically demonstrated the effects of human activities and natural processes, including overseas dispersal from the mainland, on insular community changes.

Humans have deliberately or accidentally introduced thousands of exotic species to oceanic islands (Blackburn et al., 2008; Sax & Brown, 2000), which can pose high risks to native insular species through predation or competition (Wood et al., 2017). This impact is particularly severe when the introduced species are predators (Blackburn et al., 2004; Doherty et al., 2016; Kawakami & Horikoshi, 2022), as insular species frequently lack defence mechanisms against predators (Russell & Kueffer, 2019). Additionally, chronic transformations of landscape composition by humans cause the permanent and irreversible erasing of the uniqueness of insular communities (Russell & Kueffer, 2019; Sugimura et al., 2014).

As the distribution ranges of mobile species on islands are maintained by overseas dispersal from the mainland (Walter, 2000), changes in mainland communities also affect nearby insular communities (Haila et al., 1979). Although several studies conducted on oceanic (Diamond, 1971; Paxton et al., 2016) and continental islands (Azeria et al., 2006; Diamond, 1969; Foufopoulos & Mayer, 2007; Haila et al., 1979) have empirically captured changes in community structures through immigration and extinction, no study has examined the combined effects of changes in mainland communities, introduced predators, and human-induced landscape transformation on changes in insular community structures.

The traditional equilibrium theory of island biogeography (ETIB) focused on the taxonomic richness of each assemblage (MacArthur & Wilson, 1967). However, the characterisation of community structure based on functional and phylogenetic attributes of species (McGill et al., 2006; Mouquet et al., 2012) could provide deep insights into ecosystem health and stability (Mouillot et al., 2013; Schrader et al., 2023). Quantifying functional and phylogenetic clustering/overdispersion structures of an assemblage has enhanced our understanding of the key ecological processes that structure assemblages (Cadotte et al., 2013). Functional or phylogenetic clustering occurs under strong environmental filtering (Boyce et al., 2019; Si et al., 2017). However, overdispersion implies a limiting similarity corollary for the competitive exclusion of species (Boyce et al., 2019; Si et al., 2017). Studies on plant (Carvajal-Endara et al., 2017) and bird (Sato et al., 2020) assemblages on oceanic islands and bird assemblages on islands created by dams (Si et al., 2017) have shown that functional or phylogenetic structures clustered on smaller and more isolated islands than on larger and less isolated ones, which suggests predominant influences of filtering by dispersal and environmental limitations on these islands. The association between the functional and phylogenetic structures and the geography of the islands is mediated by human activities. Functional structures of bird assemblages are overdispersed in agricultural areas and clustered in forests on isolated islands (Zhao et al., 2024). However, to the best of our knowledge, no studies have quantified changes in functional or phylogenetic clustering/overdispersion structures of insular assemblages over the past few decades. Changes in the cluster/overdispersion structure in relation to human activities and natural processes can explain the mechanisms driving changes in insular communities.

In the present study, we examined the mechanisms driving changes in taxonomic, functional, and phylogenetic structures of insular bird assemblages based on well-developed ecological and evolutionary information on birds. Here, bird community structures on ten islands in the Izu Islands (Figure 1) were investigated from 2016 to 2021 and compared with data from comprehensive surveys conducted from 1970 to 1973 (Higuchi, 1973). The following questions were addressed: 1) What functional traits or how the changes in mainland distribution of species are related to the disappearance from or colonisation on these islands over the past half century? 2) What factors contributed to changes in species richness and functional and phylogenetic clustering/overdispersion structures on the islands? We focused on the geographical and topographical characteristics of the islands, the introductions of Japanese weasel *Mustela itatsi*, and human-induced landscape transformations. As the ETIB posits that islands close to source areas have high colonisation rates, we hypothesised that i) species that have expanded their mainland distribution have increased the number of recorded islands (Figure 2b). ii) Human-induced landscape transformations have decreased species richness on heavily disturbed islands by eliminating bird species that inhabit intact habitats, resulting in increased functional and phylogenetic clustering (Figure 2c). iii) Introduced mammalian predators consume various food resources that birds rely on and directly prey on the birds themselves (Hamao et al., 2009; Hasegawa, 1999). This reduction of food availability by the introduced mammals has eliminated food competitors such as large carnivorous birds (Figure 2d), resulting in decreased species richness and increased functional and phylogenetic clustering on the islands where they have been introduced.

2. Materials & Methods

2.1 Study areas

The bird assemblages were investigated on ten islands in the Izu Islands: Oshima, Toshima, Niijima, Shikine, Kozu, Miyake, Mikura, Hachijo, Hachijo-kojima, and Aogashima (Figure 1). The largest island, Oshima, is 90.7 km^2 and the smallest, Hachijo-kojima, is 3.0 km^2. These islands are located approximately 25 km (Oshima) to 250 km (Aogashima) from the mainland and were formed by volcanic activity that occurred less than one million years ago (Tani et al., 2011). The most recent eruptions since 1970 occurred in Oshima in 1986 and Miyake in 2000. Natural vegetation was not extensively damaged except in the summit areas and pathways of mudflow and volcanic gas (Kamijo & Hashiba, 2003). The islands are located in a warm-temperate zone and are largely covered by broad-leaved evergreen forests and secondary broad-leaved deciduous forests. Nine of the ten islands are inhabited, except for Hachijo-kojima, which has been uninhabited since 1969.

We focused on the introduction of Japanese weasels because they disrupt food webs on the introduced islands (Hasegawa, 1999). Although weasels are native to Oshima, they were introduced to the other four islands for biological control of rats, resulting in the establishment of breeding populations after their release on Toshima in 1934 or 1935, Hachijo between 1960 and 1962, Miyake in 1982, and Aogashima between 1979 and 1981 (Hasegawa, 1999). In Miyake, Okada's five-lined skinks *Plestiodon latiscutatus* and Izu thrush *Turdus celaenops* have declined by 99.9% and 50% due to predation by these introduced weasels, respectively (Hasegawa, 1999; Takagi & Higuchi, 1992).

2.2 Historic and current bird assemblages on islands

The bird species composition on each island was examined during the 1970s (hereafter, historic) and 2010s–2020s (hereafter, current). Historic bird assemblages on ten islands were surveyed from 1970 to 1973 (Higuchi, 1973) by walking over as wide an area as possible within

2–5 days on each island each year. For the current bird assemblages, Sato et al. (2019) conducted field surveys on these ten islands between 2016 and 2018 using the line-transect census (Section S1). The census was conducted by 51 well-trained citizen researchers from May to June in 2017 and 2018. Transects (mean = 1.19 km) were established according to an approximately 1 km^2 mesh (267 meshes) placed over the map of the Izu Islands (Figure S1). Additionally, we used the citizen science database from 2016 to 2021 by directly interviewing citizen bird watchers using two entry forms, and by gathering records obtained from the citizen researchers outside the line-transect survey time (Section S1). Records were obtained between May and June (n = 1,243). We examined terrestrial and freshwater bird species that potentially breed on the islands because Higuchi (1973) focused only on these bird species (Section S2).

2.3 Geography, topography, and landscape compositions

The geographic and topographical characteristics of the islands were obtained from publicly available databases. The area of each island was examined using a government report on land area (Geospatial Information Authority of Japan, 2023). The degree of isolation of each island was evaluated as the minimum distance between the outer edges of each island and the Izu Peninsula, the nearest mainland shore. We calculated the highest elevation of each island based on a 1 km resolution digital elevation map (Geospatial Information Authority of Japan, 2011).

The landscape transformations of each island were investigated by comparing two vegetation maps created by the Biodiversity Center of Japan, Ministry of the Environment (https://www.biodic.go.jp/index_e.html). Vegetation maps from the surveys conducted between 1979 and 1986 were developed at a scale of 1:50,000, while those conducted between 1999 and 2023 were developed at a scale of 1:25,000. As the vegetation categories between these maps were different, they were re-categorised into 13 categories (Section S3). Three variables related to landscape transformation were investigated based on changes in the ratio of afforested, cultivated, and human-settlement areas to the total focal vegetation areas. Habitat heterogeneity was also considered as it can support a large number of species by increasing the availability of ecological niches (Ding et al., 2021; MacArthur & MacArthur, 1961). The change in habitat heterogeneity was estimated by comparing the Shannon diversity indices of the vegetation categories between the two maps, computed as Iijima et al. (2023).

2.4 Bird Traits

We examined 27 bird traits related to morphology, diet, habitat preference, cold tolerance, and life history (Table S1) that affect the distribution of bird species on the islands (Appendix 1, Section S4). All traits were divided into seven categories: beak-related morphology, morphology related to dispersal ability, cold tolerance, foraging strata, diet, nesting microhabitat, and life history.

2.5 Bird phylogeny

The phylogeny of extant birds based on the Ericson backbone was used in the analysis (Jetz et al., 2012). One hundred trees were randomly chosen from 10,000 possible tree topologies. We constructed a maximum clade credibility tree from these trees by sampling 5,000 pseudo-posterior distributions and using the common ancestor height option in TreeAnnotator v2.6.4 of BEAST 2 (Bouckaert et al., 2019). This tree was used for the subsequent phylogenetic analyses.

2.6 Functional and phylogenetic structures

Functional and phylogenetic structures of bird assemblages on each island were examined based on metrics commonly used in island biogeography (Si et al., 2017; Sobral et al., 2016). We calculated the mean pairwise distance in the multivariate functional space (MFD, Gower's distance) and phylogenetic tree (MPD, branch length). Gower's distance can handle quantitative and qualitative variables simultaneously (Gower, 1966). MFD was calculated using the gowdis function in the FD package (Laliberté et al., 2014) and the ses.mpd function in the picante package (Kembel et al., 2010). All continuous trait values were standardised before calculating MFD. Equal weights were assigned to and within each trait category (Table S1). MPD was computed using the cophenetic.phylo function in the ape package (Paradis & Schliep, 2019) and the ses.mpd function. To ensure that the choice of the mean pairwise functional distance did not alter the inference, we further quantified functional richness (FRic), dispersion (FDis), and divergence (FDiv) based on the pairwise distance in the multidimensional functional space (Laliberté & Legendre, 2010; Villéger et al., 2008) using the dbFD function in the FD package.

The standardised effect size (SES) of the MFD (SES.MFD), MPD (SES.MPD), FRic (SES.FRic), FDis (SES.FDis), and FDiv (SES.FDiv) in each assemblage was calculated based on 9,999 random assemblages by shuffling the species composition with equal probability from the recorded regional species pool and holding the species richness in each assemblage as the recorded ones but did not prune the phylogenetic tree. The regional species pool was obtained from all recorded focal species of the historic and current bird assemblages on the Izu Islands. A positive SES value indicates overdispersion, and a negative value indicates clustering of the observed assemblage.

2.7 Data analyses

All statistical analyses were performed using R version 4.3.2 (R Core Team, 2023). The species accumulation curve was computed for the current bird assemblage using individual-based interpolation with the rarefy function in the vegan package (Oksanen et al., 2019) to evaluate whether species richness was adequately sampled in this study.

The association of species traits or changes in mainland distribution with changes in bird species distribution on the Izu Islands from the historic to current times through colonisation or disappearance on each island was examined. As our focal species come from ecologically and morphologically distinct clades, phylogenetic generalised least squares (PGLS) models were used to account for phylogenetic effects among species (Garamszegi, 2014) using the Brownian motion correlation matrix (corBrownian) in the ape package (Paradis & Schliep, 2019) and the gls function in the nlme package (Pinheiro et al., 2021). The changes in the number of recorded islands of each bird species from the historic to current times were utilised as the objective variable; the value ranges from -10 to 10. To conservatively examine the relative importance of each trait, principal component analysis (PCA) was used to achieve dimension reduction for the traits of each of the three binary categories (foraging strata, nesting microhabitat, and diet). The PCA was run using the prcomp function in the stats package (R Core Team, 2023) with standardisation (scale and centre options). The first principal component (PC1) represented the variation in the foraging microhabitat from trees to the ground for the foraging strata (PC1_FOR_STRATA), inverse vertical nesting height for the nesting microhabitat (PC1_NEST), and carnivores to herbivores for diet (PC1_FOOD) (Figure S2). Furthermore, the change in the mainland distribution of each species was quantified by analysing data from the Breeding Bird Atlas of Tokyo (Ueta & Sato, 2021; Section S5)—the most systematic survey on the mainland near the Izu Islands. The recorded number of meshes in mainland Tokyo was regressed by the first survey year of the three survey periods in the atlas (1973, 1993, and 2017) using simple linear models (LMs) for each species (Table S2). The coefficient of the first survey year (hereafter, the coefficient of mainland distribution change) was used as an explanatory variable in the PGLS model to account the effects of changes in mainland distribution. This coefficient for the four insular species was set to zero, and seven species with no records in the bird atlas on mainland Tokyo were excluded from the analysis (Table S2). Finally, eight species traits and the coefficient of mainland distribution change were used as explanatory variables, which were standardised before the analysis. There was no serious multicollinearity in these nine variables, as checked by computing variance inflation factors (VIFs <2.07) according to the general rule of thumb (Albright & Winston, 2010). Model selection was performed by ranking and evaluating all combinations of explanatory variables based on the Akaike Information Criterion corrected for a small sample size (AICc). The model with the lowest AICc value was considered the best model, and models where the difference in AICc relative to that of the best model (ΔAICc) was <2 were also considered to be substantially supported (Burnham & Anderson, 2004). We interpreted point estimates and 95% confidence intervals (CIs) of each explanatory variable based on the nuanced approach (Amrhein et al., 2019) in the models with ΔAICc <2. Additionally, differences in the changes in the number of recorded islands among the orders were visualised. Nonetheless, statistical tests were not performed because of the low number of species recorded per order.

The change in the species composition of each island from the historic to current times was examined by non-metric multidimensional scaling (NMDS) using the metaMDS function in the vegan package. The Jaccard index was used as the distance measure. The effects of pairwise geographic distance and survey decade (historic and current) on the inter-island pairwise distance on ordination were examined using LMs. The survey decade was included as a factor. Pairwise geographic distance was standardised before analysis. We included an interaction term for the pairwise geographic distance and survey decade to investigate the pattern by which the species composition of the islands became more homogeneous or heterogeneous from the historic to current times. No serious multicollinearity (VIFs <3) was observed. The models were compared based on AIC and interpreted in the same way as the PGLS model.

The effects of the geographical and topographical characteristics of islands, weasel introduction, and landscape transformation on changes in species richness, and functional and phylogenetic clustering/overdispersion structures were analysed using generalised linear models (GLMs). All models were constructed using a Gaussian error distribution and an identity link function. Changes in species richness (species richness and colonised or extinct species richness) or each SES value (SES.MPD, SES.MFD, SES.FRic, SES.FDis, and SES.FDiv) were used as the objective variables, calculated by subtracting the values of the historic assemblages from those of the current assemblages. Thus, a negative SES value indicates clustering, while a positive value indicates overdispersion. Variables related to geographical and topographical characteristics, including island area, isolation, elevation, and volcanic activity after 1970 (1, erupted; 0, not erupted), were summarised into two dimensions using PCA. PC1 (PC1-GEO) represented island volume and volcanic activity, and PC2 represented isolation (PC2-GEO; Figure S3). Landscape transformations, including changes in the ratio of afforestation, cultivated, and human-settlement areas, and habitat heterogeneity, on each island were also summarised. PC1 for landscape transformation (PC1-LAND-TF) negatively represented habitat simplification due to increasing human-settlement and afforestation areas (Figure S3). PC2 for landscape transformation was not used in the analysis because it was highly correlated with PC1-GEO (Pearson's $r = 0.77$, $p = 0.008$). Weasel introduction was treated as a factor (1, introduced; 0, not introduced). Final GLMs were constructed using four explanatory variables: PC1-GEO, PC2-GEO, PC1-LAND-TF, and weasel introduction. Multicollinearity was not an issue (VIFs <1.81). Models were compared with AICc and interpreted in the same way as PGLS models. The association between colonised and extinct species richness was examined by Pearson's *r* using the cor.test function in the stats package.

3. Results

3.1 Species composition

In total, 48 species from ten orders were recorded (Figure S4). Several arboreal species, including White-bellied green-pigeon *Treron sieboldii*, Japanese tit *Parus minor*, and Narcissus flycatcher *Ficedula narcissina*, and large fish-eating species, including Intermediate egret *Mesophoyx intermedia* and Great egret *Casmerodius albus* expanded their distributions on the Izu Islands. However, large carnivorous species, including Gray-faced buzzard eagle *Butastur indicus* and Eastern buzzard *Buteo buteo*, and farmland birds, including Bull-headed shrike *Lanius bucephalus* and Oriental greenfinch *Chloris sinica* disappeared from several islands. The species accumulation curve almost reached the asymptote on all islands, which indicates that species richness on each island was well sampled (Figure S5).

3.2 Distribution change of species

The results of the PGLS analysis showed that all models with ΔAICc <2 selected clutch size and the coefficient of the mainland distribution change, which was positively associated with the change in the number of recorded islands (Figure 3, Table S3). The other three traits selected in the ΔAICc <2 models with the 95% CIs that overlapped with zero. Regarding phylogeny, only Accipitriformes showed a decline in the number of islands recorded for all species among the orders with multiple species recorded (Figure 4). Conversely, the largest increase in the median number of recorded islands was observed for Pelecaniformes.

3.3 Changes in community structures

The NMDS ordination (stress = 0.18) based on species composition and LMs demonstrated that the species composition of the islands became more heterogeneous from the historic to the current times (Figures 5 and S6, Table S4). The interaction term in the LMs demonstrated that the greater the pairwise geographical distance between islands, the greater the distance in the ordination, which was more pronounced in the current bird assemblages (Figure 5, Table S4). Among the ten islands, species richness decreased on eight islands (Figure 6). There was a negative correlation between colonised and extinct species richness (r = -0.74, p = 0.012; Figure S7). SES.MFD and SES.MPD values became smaller on nine and eight islands, respectively (Figure 6). A predominant tendency towards smaller values was also observed for SES.FRic and SES.FDis (Figure S8). The clustering tendency was stronger on five islands for SES.FDiv. Although colonised species richness and the changes in species richness were positively associated with PC1-GEO, a proxy for island volume and volcanic activity, the null model was selected in the ΔAICc <2 models (Figures 7 and S9, Table S5). Changes in SES.MFD and SES.FDis values were positively associated with PC2-GEO, a proxy for island isolation. Changes in SES.FRic were negatively associated with PC1-GEO and weasel introduction. The null model was the best for extinct species richness, SES.MPD, and SES.FDiv.

4. Discussion

As predicted by the ETIB, we empirically demonstrated that species distribution changes on the islands and mainland were mirrored (Figure 2b). According to our hypotheses, functional and phylogenetic structures in the current bird assemblage clustered compared to those in the historic ones. Unexpectedly, we did not find statistical associations between these changes and predator introduction or landscape transformation, except for SES.FRic.

4.1 Species traits and the mainland distribution

The PGLS analysis indicates an association between the species distribution change on islands from the historic to current times and clutch size or changes in mainland distribution. The effects of other traits were negligible. Our findings support that clutch size is negatively correlated with extinction risk in birds due to less recovery potential during disturbance (Bennett & Owens, 1997), despite reduced clutch size being favoured on islands with milder or less-seasonal climates than on the mainland (Covas, 2012). Therefore, bird assemblages on the Izu Islands are considered threatened by various forms of disturbance.

Our findings indicate that species distributions on the mainland and islands are mirrored, which supports the findings of a previous study in the northern region (Haila et al., 1979). Furthermore, we revealed that the dominant effect of changes in mainland distribution surpassed those of several traits. Arboreal bird species expanded their distribution on the Izu Islands, which have expanded their distribution in Japan because of the increase and maturity of forest vegetation (Ueta & Sato, 2021; Ueta & Uemura, 2021). Moreover, several Ardeidae species have colonised the Izu Islands, which is consistent with the increase of large fish-eating bird species in the mainland following the improvement of water pollution, pesticide use, and development after the reductions in the 1970s (Ueta & Sato, 2021; Ueta & Uemura, 2021). Species with aerial feeding, small fish-eating, and a preference for open habitats have been decreasing in Japan (Ueta & Sato, 2021; Ueta & Uemura, 2021). However, aerial-feeding species, including Barn swallow *Hirundo rustica*, and small fish-eating species, including Cattle egret *Bubulcus ibis*, have expanded their distribution on the Izu Islands. Human-settlement areas on the Izu Islands can act as refuges for these species because they are not heavily urbanised or modernised. For example, Barn swallow cannot breed in heavily urbanised areas without farmland or riparian areas (Osawa, 2015), and has been reported to breed on traditional houses with eaves on the Izu Islands (Hasegawa, 1990). Hence, we highlight that changes in assemblages on the mainland represent a critical mechanism driving changes in insular bird assemblages.

4.2 Taxonomic, functional and phylogenetic structures

We found that the larger the volume of the islands, the lesser the degree of decrease in species richness. Furthermore, species richness increased on the largest island. The negative correlation between colonised and extinct species richness, and the marginal associations between PC1-GEO and species richness or colonised species richness suggest that the target effect (Lomolino, 1990) is a crucial mechanism underlying changes in bird community structures. Species richness decreased on eight of the ten islands, which implies that the colonisation of species did not compensate for the decline in species richness due to their disappearance. Thus, bird assemblages on the Izu Islands are not in equilibrium between immigration and extinction.

Functional structures based on SES.MFD were more clustered in the current bird assemblages than in the historic ones on nine islands, especially less-isolated islands. The clustering tendencies of SES.FRic and SES.FDis became stronger on nine and eight islands, respectively. The negative associations between SES.FRic and weasel introduction indicate that functional richness, based on the volume of a convex hull (Laliberté et al., 2014), is decreased by the introduced predators. Therefore, functional clustering mainly occurs due to the loss of species located at the periphery of multivariate trait space. Phylogenetic structures became more clustered on eight islands. These findings suggest that functional and phylogenetic clustering strengthened in the current bird assemblages, thus constraining traits and phylogeny (Boyce et al., 2019; Si et al., 2017). In contrast, Schrader et al. (2023) reported that functional diversity of plant biota remained stable from 1956 to 1998 on environmentally stable islands with few human activities. The results of PGLS and phylogenetic comparisons

(Figure 4) suggest that functional and phylogenetic clustering was shaped by the colonisation of species from the mainland, especially on less-isolated islands, and the extinction of raptors and species with large clutches.

However, the landscape transformation of each island, represented by PC1-LAND-TF, and weasel introduction were not associated with the clustering of functional and phylogenetic structures in our GLM results, except for SES.FRic. The landscape transformation may have a small impact because more than 10% increases in afforestation and human-settlement areas were only observed in Toshima (Figure S10). The results indicate that weasel introduction has affected the bird community structures of the archipelago as a whole rather than on a single island, because birds can easily move to and from neighbouring islands. This interpretation is supported by the NMDS and LM findings, where differences in species composition along the pairwise geographical distance increased in the current bird assemblages, which suggests that colonisation and extinction on an island are associated with nearby islands (Wang et al., 2023). Ando et al. (2022) counted 4,954 Japanese wood pigeons *Columba janthina* that crossed the sea between Hachijo and Hachijo-kojima in May 2019. Decreases of wintering Izu thrush, which migrate seasonally among the islands, were observed in Niijima after the introduction of weasels in Miyake (Hasegawa, 1997). Hasegawa (1997) stated that Gray-faced buzzard eagle seemed to have declined in the Izu Islands after the rapid reduction of their prey, Okada’s five-lined skink, due to predation by weasels. Such a reduction in food resources causes breeding failure in raptors (Tapia & Zuberogoitia, 2018) and can collapse populations in the archipelago because fledged juvenile raptors move between islands before being recruited into a breeding population (Rodríguez et al., 2018). The mainland distribution ranges of Gray-faced buzzard eagle and Eastern buzzard, which disappeared from many islands, did not shrink in central Japan (Ueta & Uemura, 2021). Therefore, the strengthened functional and phylogenetic clustering across the archipelago is presumed to be due to the spillover effects of food resource reduction or direct predation by the introduced weasels on several islands, in addition to the colonisation of species from the mainland.

Apart from weasels, various other non-native species have been introduced to the Izu Islands (Hasegawa, 1999, 2017). For example, vegetation in Niijima was heavily modified by introduced Sika deer *Cervus nippon* (Hasegawa, 1997). Furthermore, predation by feral cats *Felis catus* on vertebrates and invertebrates reported in Mikura was not considered (Azumi et al., 2021; Tokuyoshi et al., 2020). As these introduced species potentially affect bird species distribution, the total impact of all exotic species on bird distribution remains an open question.

5. Conclusion

This study emphasises the need to integrate traditional island biogeography with the impact of human activities in the Anthropocene. Comparing data between the 1970s and 2010s–2020s empirically detected synchronisation between the mainland and island distributions of bird species, thereby supporting the hypothesis based on the ETIB. The PGLS results showed that the effect of changes in the mainland distribution of species was greater than that of almost all traits on changes in the insular distribution of species. Thus, our findings indicate that changes in community structure on the mainland indirectly modify insular communities. Furthermore, we found that species richness decreased, and functional and phylogenetic structures of bird assemblages on the Izu Islands became more clustered in the current bird assemblage, which suggest that traits and phylogeny became more strongly constrained from the historic to current times. Thus, bird assemblages on the Izu Islands are not at equilibrium between immigration and extinction. An association of these structural clusters was only detected with island volumes or isolation, and not with weasel introduction or landscape transformations, except for

SES.FRic. The lack of statistical association is assumed to be because the introduced weasels did not only have a direct impact on the bird assemblage of focal islands, but also had a spillover impact on nearby islands via overseas dispersal. Therefore, weasel introduction on one island led to the modification of biogeographic patterns and community structures on several islands of the archipelago. Islands act as potential sources, stepping stones, and colonisation targets (Wang et al., 2023). Changes in food web structure are directly linked to the evolution of prey (Landry Yuan et al., 2021) and changes in ecosystem functioning. Therefore, an empirical study on the spillover effects of introduced predators on prey communities on nearby islands is necessary to better understand the effects of human activities on oceanic islands.

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8. Figures & Tables with legends

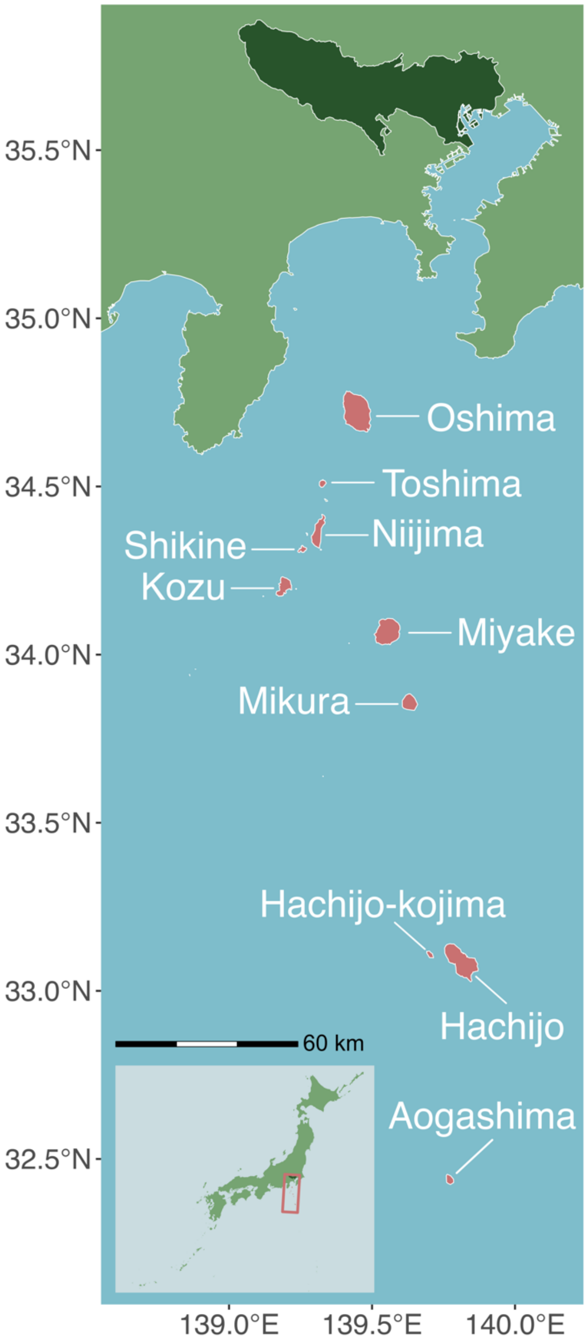

Figure 1 Map of the Izu Islands in Japan. The labelled islands (in red) were investigated in our study. Tokyo, where the breeding bird atlas program was conducted, is indicated in dark green on the mainland of Honshu. The red rectangle in the bottom panel indicates the Izu Islands in Japan.

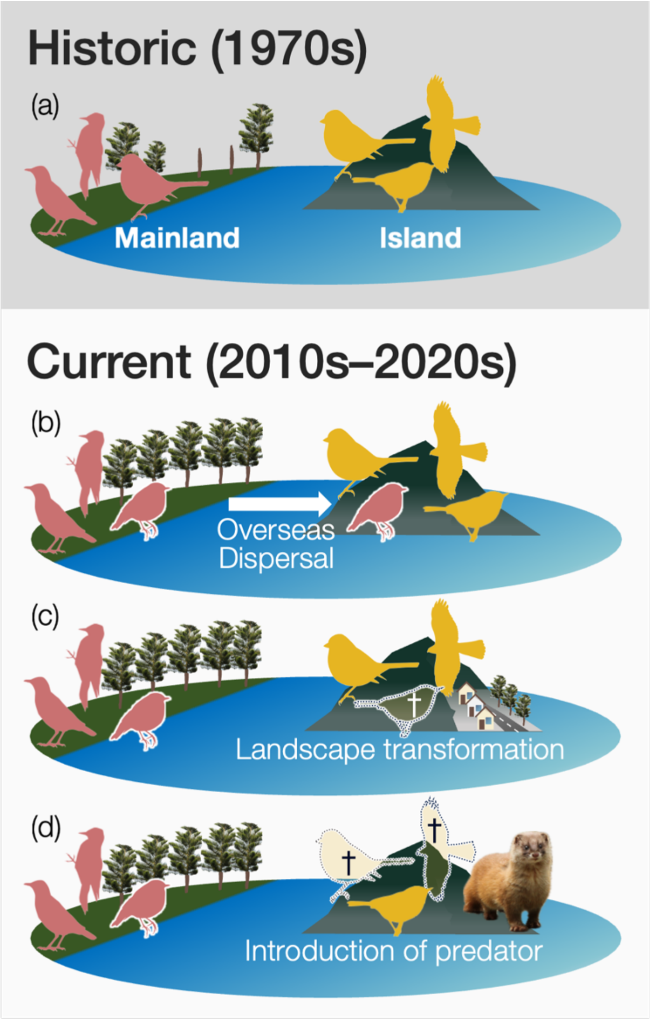

Figure 2 Schematic diagram of the mechanisms driving changes in insular bird assemblages on less isolated islands during the Anthropocene. (a) Assemblages in the historic time (1970s) after the period of high economic growth as a baseline for changes. Three scenarios were hypothesised. (b) When assemblages in the mainland changed, insular assemblage would change via overseas dispersal. As a result, species richness of islands near the mainland increases. (c) When human transformed landscape compositions, several forest-dwelling species would disappear. (d) When predators are introduced to an island, several native species and birds of prey would disappear from the introduced island. Moreover, species richness decreases and functional and phylogenetic structures cluster in islands with weasel introduction and landscape transformations. Silhouettes of birds retrieved from http://www.phylopic.org.

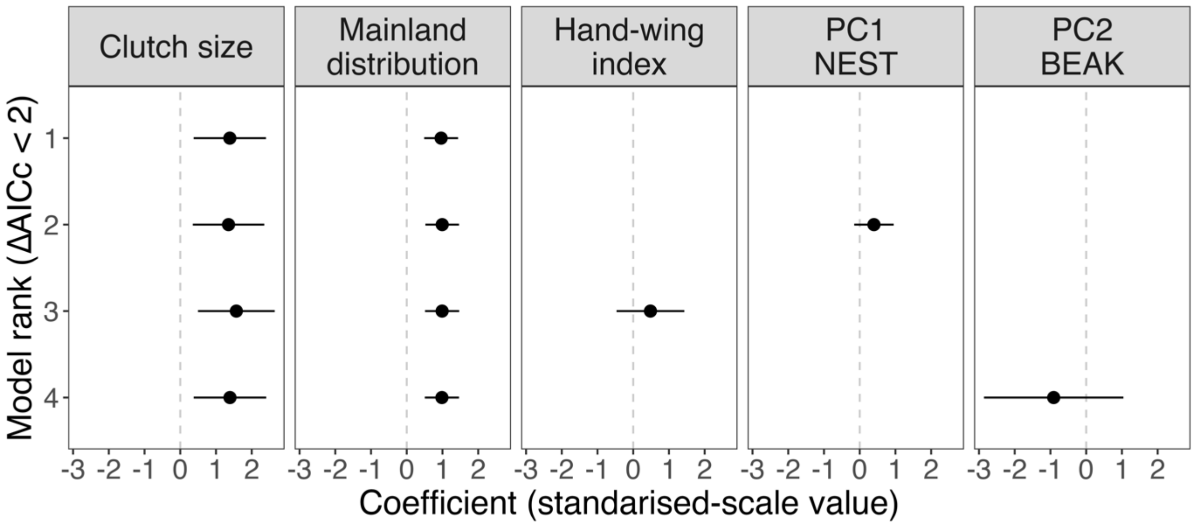

Figure 3 Model selection results of phylogenetic generalised least squares (PGLS) models examining the relationship between the changes in the numbers of recorded islands of each bird species on the Izu Islands from the historic (1970s) to current (2010s–2020s) times and eight species traits or the changes in mainland distribution. Four models with ΔAICc <2 are shown. All traits were standardised prior to analysis. Black circles and horizontal bars indicate point estimates and 95% CIs, respectively. Results of the null model and four traits were not shown because they were not selected as the models with ΔAICc <2. Mainland distribution: changes in the mainland distribution.

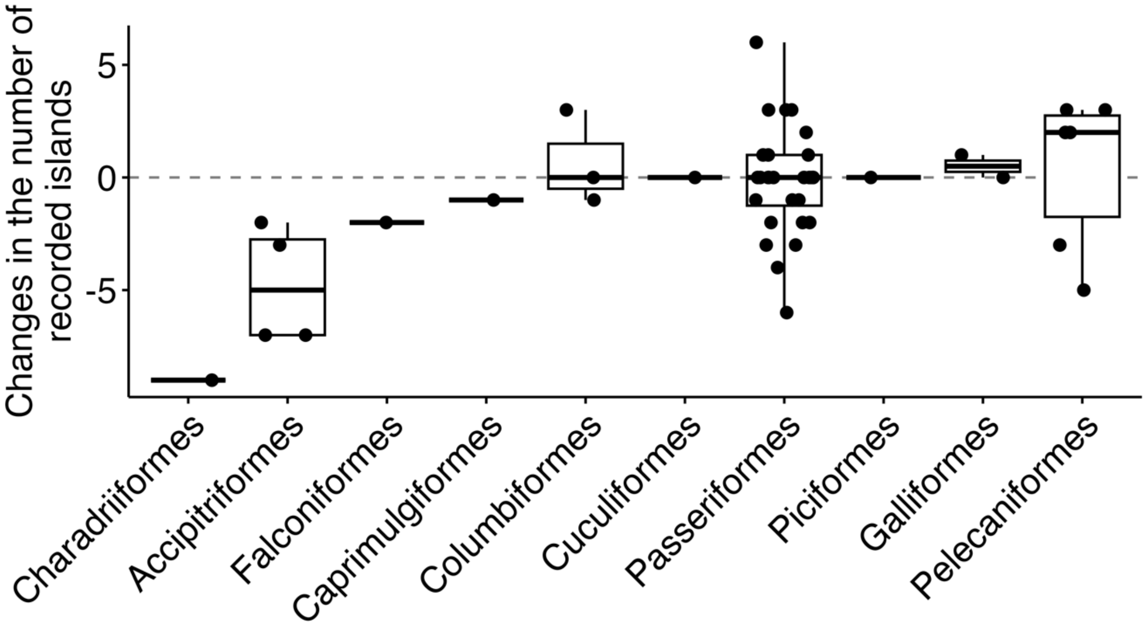

Figure 4 Changes in the numbers of recorded islands for each species of ten orders on the Izu Islands from the historic (1970s) to current times (2010s–2020s).

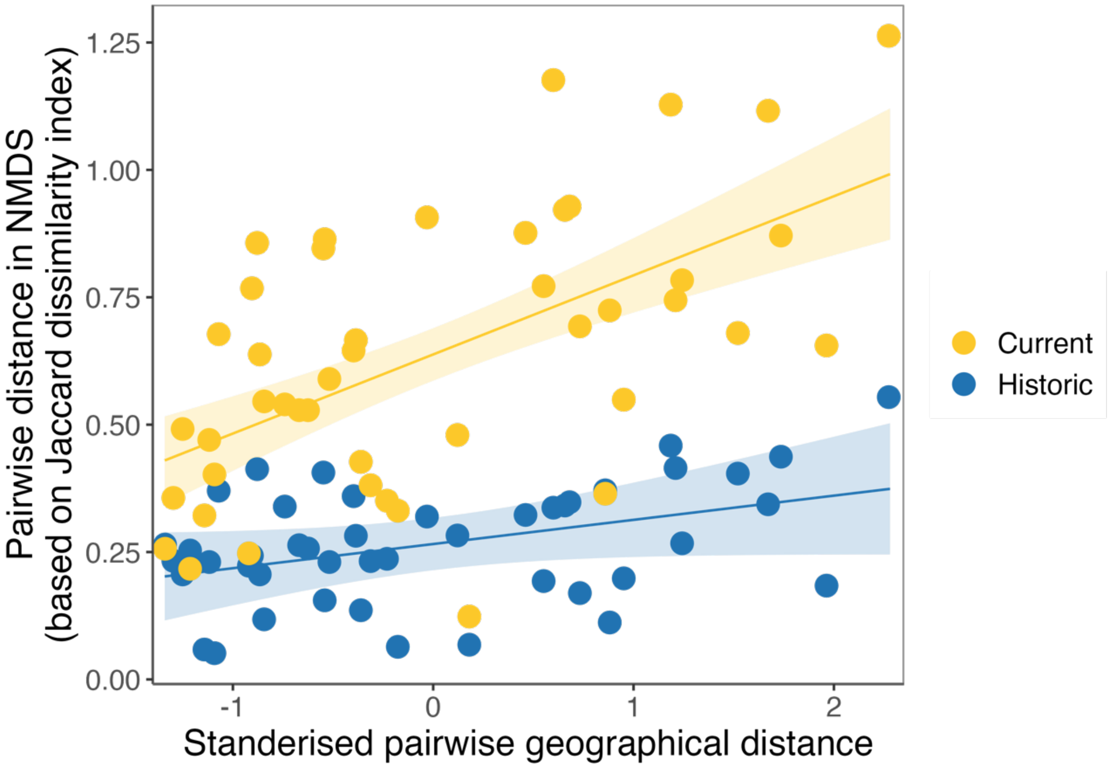

Figure 5 The association between inter-island pairwise distances on the two-dimensional non-metric multidimensional scaling (NMDS) ordination based on the species composition of each island in the historic (1970s, blue) to current times (2010s–2020s, yellow), and geographical distance. Solid lines show fitting with linear models and shaded areas represent the 95% confidence interval. The pairwise geographical distance, survey decades (historic and current), and the interaction term of these two variables were used as explanatory variables. All variables were selected in the models with ΔAIC <2.

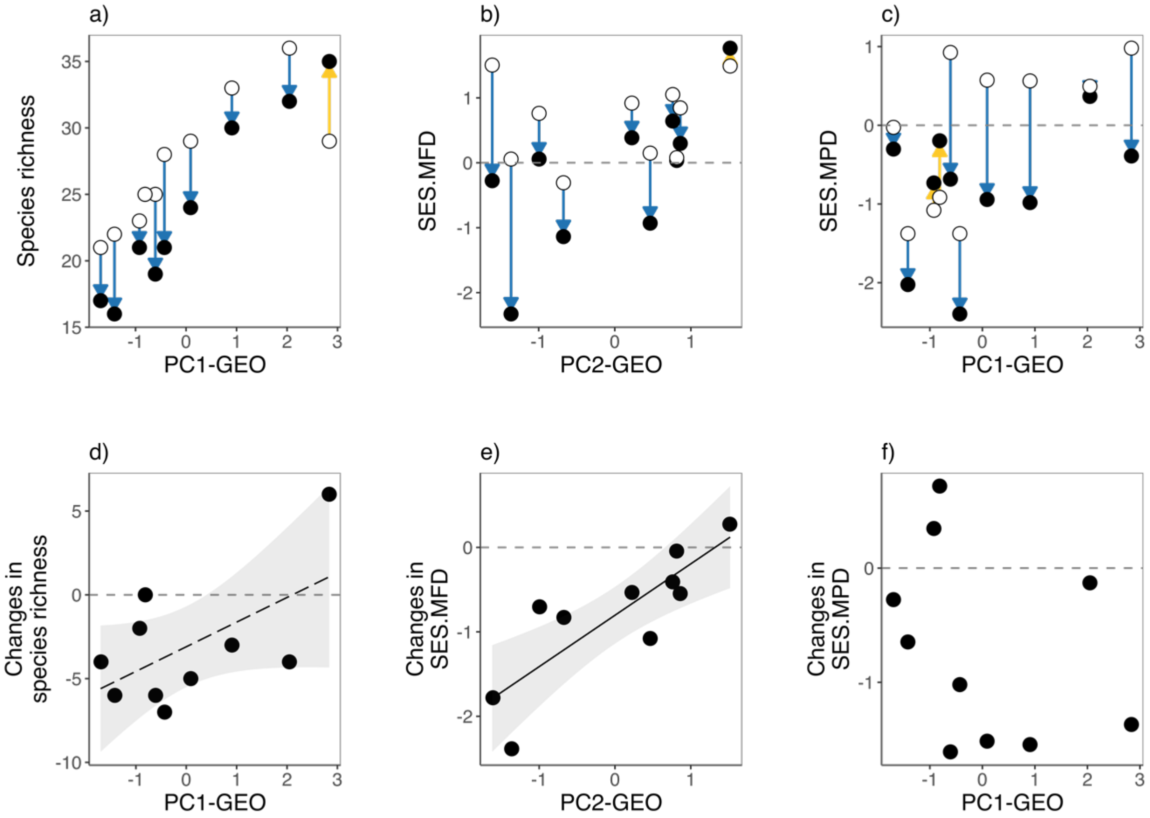

Figure 6 Observed species richness (a), SES.MFD (b), and SES.MPD (c) from the historic (1970s) to current (2010s–2020s) bird assemblages on ten islands in the Izu islands. Opened and filled circles indicate values in the historic and current bird assemblages, respectively. Blue and yellow arrows indicate negative and positive changes in the values, respectively. Changes in species richness (d), SES.MFD (e), and SES.MPD (f). Filled circles indicate the observed changes, and solid lines show fitting with generalised linear models (GLMs) for each diversity metric, and grey-shaded areas represent the 95% confidence interval. When the null model and models with explanatory variables were selected as the models with ΔAICc <2, the fitting was shown by long-dashed lines. The fitting is not shown when only the null model was selected. PC1-GEO represents island volume and volcanic activity, and PC2-GEO represents isolation. The explanatory variables selected in model selection procedures with ΔAICc <2 were used for the horizontal axis. However, PC1-GEO was displayed, despite the null model was the best for SES.MPD.

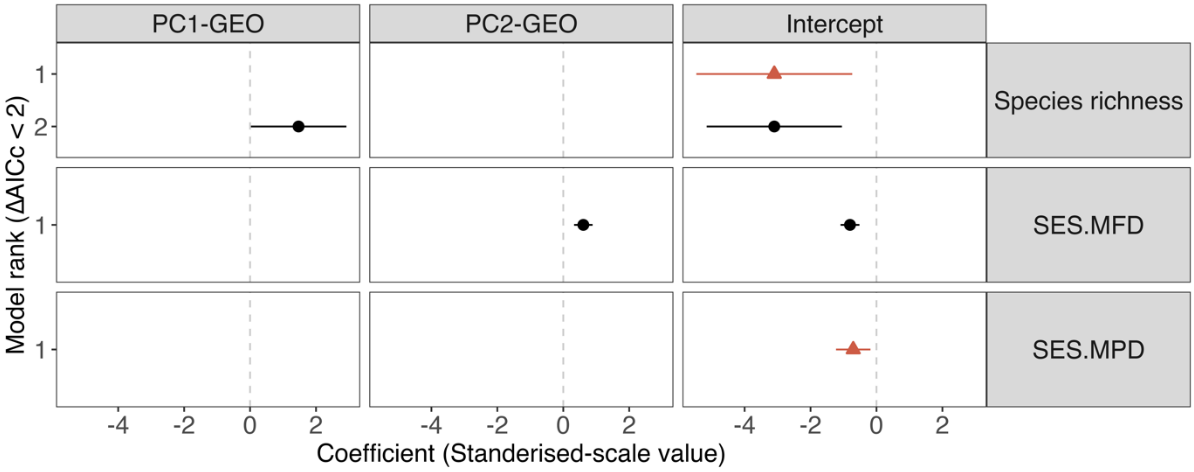

Figure 7 Model selection results from generalised linear models (GLMs) examining the relationship between the changes in taxonomic, functional, and phylogenetic bird community structures from the historic (1970s) to current times (2010s–2020s), and geographical and topographical characteristics of islands (PC1-GEO and PC2-GEO), weasel introduction, and landscape transformation (PC1-LAND-TF). PC1-GEO represents island volume and volcanic activity, and PC2-GEO represents isolation. All continuous explanatory variables were standardised by using principal component analysis, except for weasel introduction (factors). All models with ΔAICc <2 are shown. Two explanatory variables (weasel introduction and PC1-LAND-TF) were not displayed because they were not selected in the models with ΔAICc <2. Circles or triangles and horizontal bars indicate point estimates and 95% CIs. When the null model was selected as models with ΔAICc <2, indicated by the red triangle and horizontal bar.

Appendix S1

Ongoing collapse of avifauna in temperate oceanic islands close to the mainland in the Anthropocene

Daichi Iijima, Haruko Ando, Tohki Inoue, Masashi Murakami, Shun Ito, Shinpei Fukuda & Sato J. Nozomu

Section S1: Details of survey methods

Line transect surveys were conducted between May 16 to June 18 in 2017, and May 17 to June 2 in 2018. Transects were established according to an approximately 1 km^2 mesh (267 meshes) placed as a graticule over the map. Transects were set at approximately 1 km (mean = 1.19, median = 1.16, max = 3.30, min = 0.23, and se = 0.02; Figure S1). The surveys started between dawn and 9 a.m. for each mesh, except for several meshes in Aogashima and Mikura due to bad weather and other time constraints. The researchers walked at a speed of approximately 2 km/h along the transect and recorded species with distinctions within and beyond 50 m from the researchers. The researchers also recorded the abundance of species, and their behaviours.

The citizen science database from 2016 to 2021 was constructed based on the records of citizen bird watchers, collected using two entry forms of the breeding bird atlas (https://bird-atlas.jp/tokyo/data.html; https://bird-atlas.jp/index.html). Data was collected over time. We only used data recorded from May to June to adjust the time-scale for the line-transect census surveys. Furthermore, records obtained from the citizen researchers outside the line-transect survey time were collected. Information about mesh ID or latitude and longitude, date, bird species, number of individuals, and bird behaviour were collected from all data sources. When the data obtained from the forms did not include the number of individuals, the number of individuals was set to one.

Section S2: Focal species selection

Higuchi (1973) focused on terrestrial and freshwater bird species. Thus, eight orders were excluded: Anseriformes, Gruiformes, Podicipediformes, Charadriiformes, Gaviiformes, Procellariiformes, Ciconiiformes, and Pelecaniformes with the exception of Ardeidae (Higuchi personal communications). Nocturnal bird species were excluded from the analysis because Higuchi (1973) carried out nocturnal observations (Higuchi, personal communications) while the present bird investigations did not; Ural owl *Strix uralensis*, Northern boobook *Ninox japonica*, and Sunda scops-owl *Otus lempiji*. Eurasian woodcock *Scolopax rusticola* was not excluded despite being frequently observed during night, because it was commonly observed during the daytime in the 1970s, at least on Miyake (Higuchi, personal communications). We excluded species recorded only once throughout the study period from 2016 to 2021 and not reported in Higuchi (1973); Common cuckoo *Cuculus canorus*, Yellow rail *Coturnicops noveboracensis*, Chinese pond-heron *Ardeola bacchus*, Gray heron *Ardea cinerea*, Little egret *Egretta garzetta*, Oriental honey-buzzard *Pernis ptilorhynchus*, Northern goshawk *Accipiter gentilis*, Dollarbird *Eurystomus orientalis*, Ashy minivet *Pericrocotus divaricatus*, Tiger shrike *Lanius tigrinus*, Eastern crowned warbler *Phylloscopus coronatus*, Japanese leaf warbler *P. xanthodryas*, Middendorff's grasshopper warbler *Helopsaltes ochotensis*. Although Kamchatka leaf warbler *P. examinandus* was recorded more than once in our field survey, it was strongly suggested to be transient and temporary stays during migration were excluded from the analysis. Eurasian Woodcock and Asian House Martin *Hirundo rustica* were not excluded despite being recorded only once, because they were recorded on several islands by Higuchi (1973). We excluded two wintering bird species in Japan; Dusky thrush *Turdus eunomus* and Black-faced bunting *Emberiza spodocephala*. We included two introduced species: Japanese pheasant *Phasianus colchicus* and Chinese bamboo partridge *Bambusicola thoracicus* (Hasegawa, 2017) because they were introduced into the Izu Islands before 1970 (Higuchi 1973) except for the introduction of Japanese pheasant into Toshima between 1974 and 1975 (Kawai et al., 1978). These two species were also included in the list of Higuchi (1973).

Section S3: Categorisation of vegetation

We re-categorised vegetation into 13 categories: evergreen broad-leaved, deciduous broad-leaved, and bamboo forests, shrubland, wetland, grassland, sand dune, natural bare ground, afforested, cultivated, and human-settlement areas, water surface, and coniferous forest on the coastal cliffs (Figure S10). Water surface was excluded from the analysis because several small swamps were not well represented on the map. Furthermore, the coniferous forest on the coastal cliff was excluded from the analysis because it was identified only in the maps at a scale of 1:25,000.

Section S4: Species traits

Morphology is associated with important dimensions of their ecology, which should affect species distribution on islands. Specifically, the beak-related morphology is linked to the size and type of diet of birds (Hsu et al., 2014; Pigot et al., 2020; Wheelwright, 1985). We used the principal component axis 2 (PC2) of a principal component analysis (PCA) as the bill shape (Neate-Clegg et al., 2023) on the three morphological traits related to beak (beak length from culmen, beak width, and beak depth) because PC1 is highly correlated with body mass (Pigot et al., 2020). The hand-wing index provides insights into the dispersal ability of birds (Claramunt et al., 2012). These morphologies were obtained from a published morphological database (AVONET; Tobias et al., 2022). The ecological dimensions of the species were obtained from the Japanese avian trait database (Javian; Takagawa et al., 2011) unless otherwise noted. Cold tolerance of species can contribute to bird community structures on the Izu Islands, because the air temperature on the Izu Islands has increased (Landry Yuan et al., 2021). The northern limit of the wintering distribution range of each species can be used as a surrogate for cold tolerance (Root, 1988). Thus, the northernmost latitudes of wintering and resident distributions were examined for each species based on a distribution map (Birdlife International and NatureServe, 2015). Body mass is another indicator of physiological tolerance (Swanson & Garland, 2009). The mean value was calculated when the range of body mass or those between sex were shown in the database. Microhabitat preferences and diets can be linked to changes in bird community structures because many ground-dwelling vertebrates and invertebrates are heavily consumed by introduced weasels (Hasegawa, 1999). The foraging strata were examined based on the proportional use of water below the surface, water around the surface, ground, understory, mid-canopy, upper canopy and aerial according to Elton trait 1.0 (Wilman et al., 2014). Diets were investigated based on whether the birds eat each food or not, i.e., insects, fishes, earthworms, frogs, lizards, mammals, birds, fruits, seeds, and leaves. The nesting microhabitat of species was evaluated because the predation risk by weasels was higher in nests closer to the ground (Hamao et al., 2009). Thus, we investigated whether the species nests in each microhabitat or not, i.e. on trees including tree hollows, in the understory, on the ground, on cliffs, and in human settlements. A life-history trait, the clutch size was negatively correlated with extinction risk in birds (Bennett & Owens, 1997). Therefore, we examined the clutch size of each species. The mean of the minimum and maximum values was used as the range for the database. For the clutch size of White-bellied green-pigeon *Treron sieboldii*, the data presented by Del Hoyo et al. (2019) were used because of the lack of available data in the Javian. For the blood parasite cuckoo species, the nesting microhabitat was investigated based on their main host species on the Izu Islands: Japanese bush warbler *Horornis diphone*, Ijima's leaf warbler *P. ijimae*, Styan's grasshopper-warbler *Locustella pleskei*, and Eurasian wren *Troglodytes troglodytes* (Hamao, 2011; Higuchi, 1998). The clutch size of the cuckoo species was set to one because chicks of these species are raised alone in the nest of host species (Higuchi, 1995). In total, 27 traits within seven categories were used in the analysis.

Section S5: Bird assemblages on the mainland in Japan

Data from the Breeding Bird Atlas of Tokyo were used to examine changes in distribution ranges in Tokyo, mainland Honshu (Ueta & Sato, 2021). The program started in the 1970s (1973–1978) and subsequently in the 1990s (1993–1997) and the 2010s–2020s (2016–2021), and surveyed the distribution of bird species with the support of citizen scientists. In total, 279 meshes were surveyed throughout the program. Each mesh had a survey transect of approximately 1 km, including the environments representative of that mesh. The transect was walked twice during the breeding season at a speed of about 2 km per hour in each program period. The species and their abundance within and beyond 50 m were recorded. In addition, observation records of citizen bird watchers were collected during each period. The number of meshes in which each species was recorded during each program period was examined.

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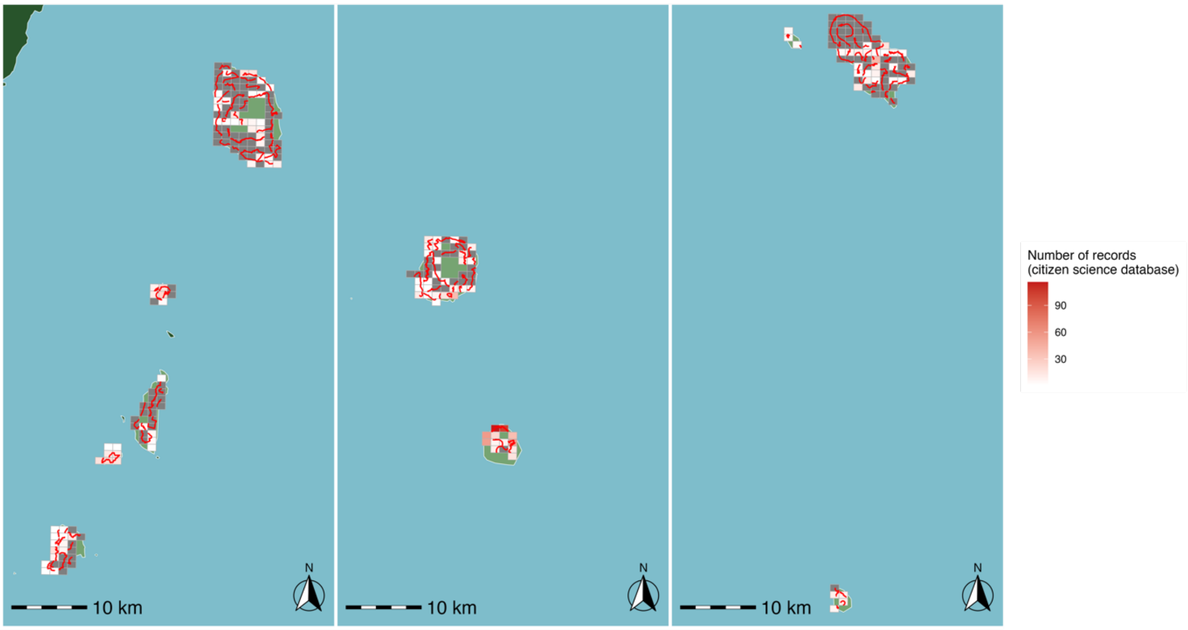

Figure S1 Surveyed 1 km^2 resolution meshes located on the Izu Islands. The left, centre, and right panels show the five nearest islands, two islands in the middle, and three isolated islands, respectively. Red line in each mesh represents the transect. Dark orange meshes have large numbers of records, white meshes have low numbers of records, and grey meshes have no records in the citizen science database. Green areas indicate unsurveyed locations. The total number of meshes was 267: Oshima, 78; Toshima, 8; Niijima, 19; Shikine, 5; Kozu, 23; Miyake, 49; Mikura, 8; Hachijo, 70; Hachijo-kojima, 2; and Aogashima, 5.

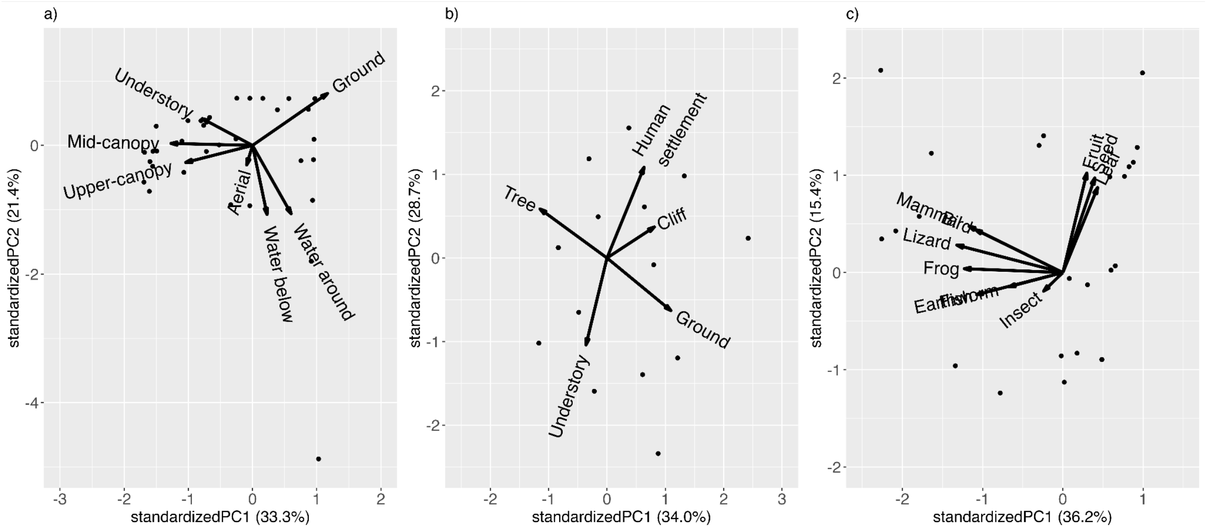

Figure S2 Principal component analysis (PCA) ordination biplot for (a) foraging strata, (b) nesting microhabitat, and (c) diet of 48 bird species. Each species trait was represented as vectors.

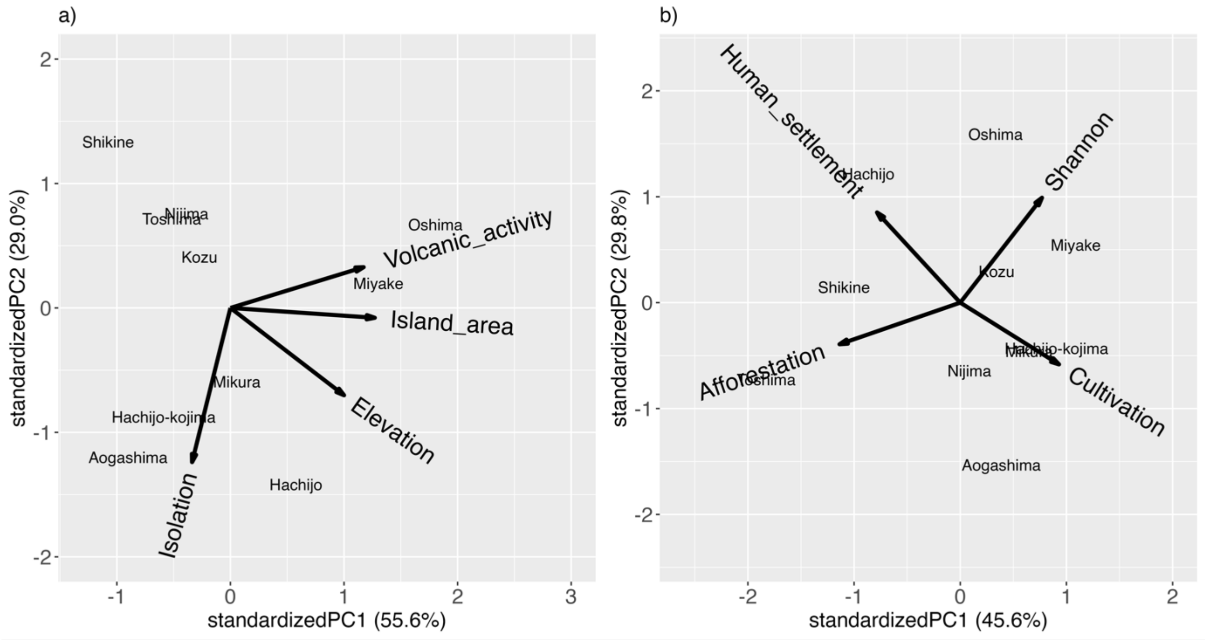

Figure S3 Principal component analysis (PCA) ordination biplot for (a) the geographical and topographical characteristics of islands and (b) landscape transformation. Each variable was represented as vectors.

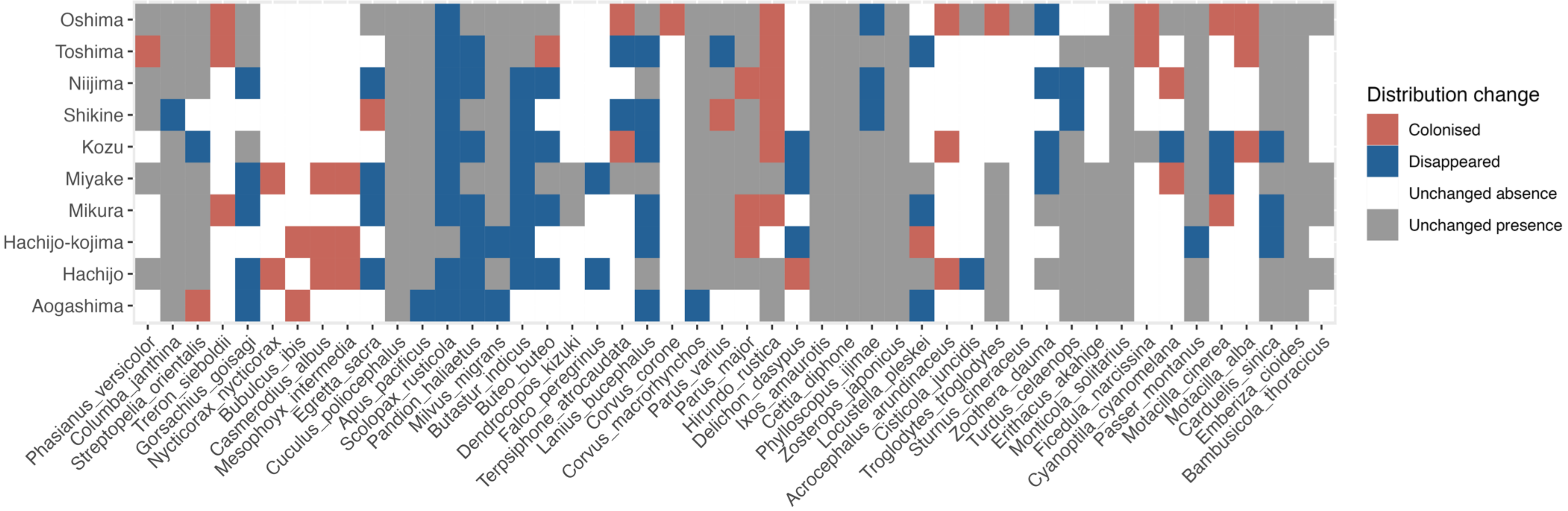

Figure S4 Changes in bird community structures through colonisation or disappearance on the ten islands in the Izu Islands. Tiles coloured by red, blue, white, and grey indicate colonisation, disappearance, unchanged absence, and unchanged presence, respectively, of each species between the historic (1970s) and current times (2010s–2020s).

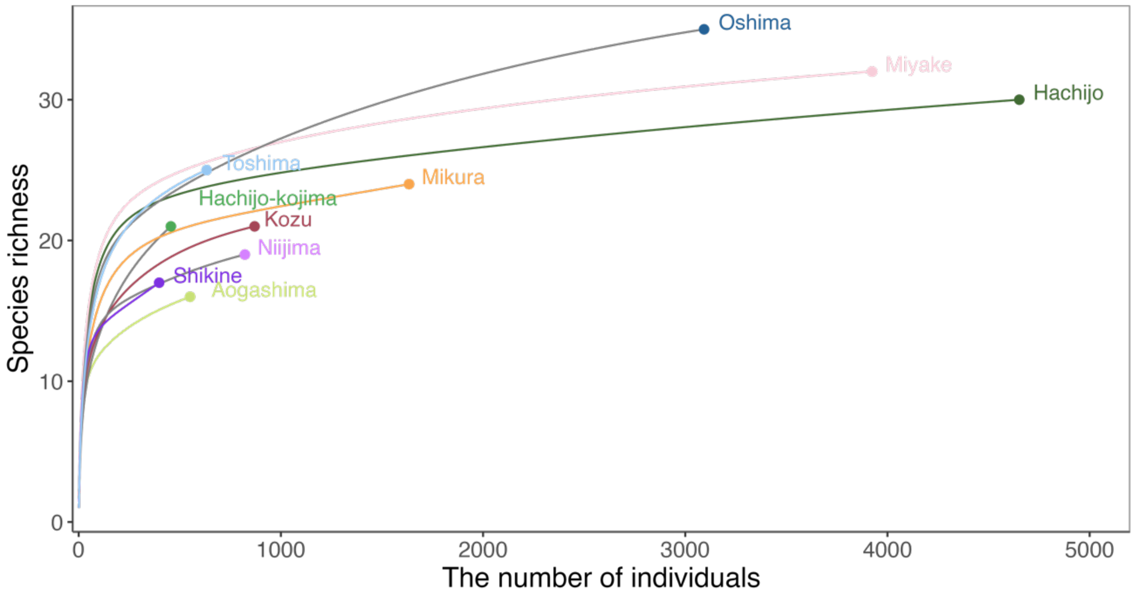

Figure S5 The species accumulation curve computed based on the individual-based interpolation for each island. Dots indicate observed species richness and the number of individuals.

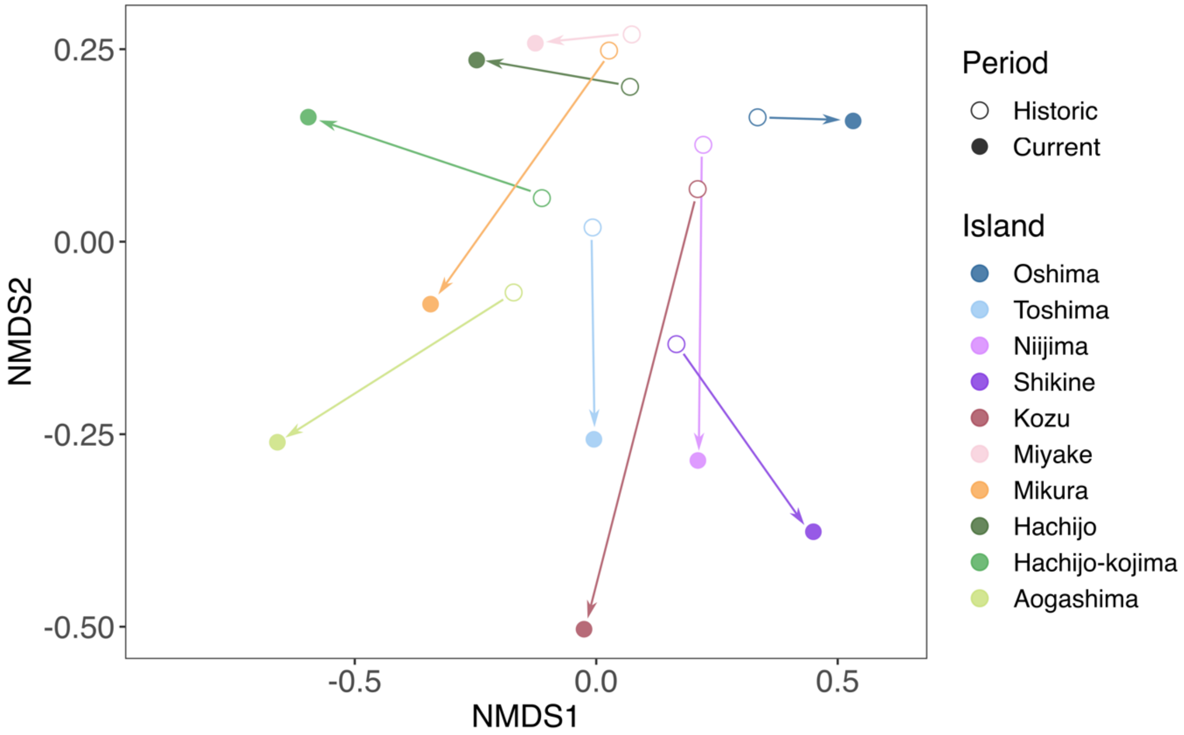

Figure S6 Two dimensional non-metric multidimensional scaling (NMDS) based on the species composition of the assemblage on ten islands in the historic (1970s) and current times (2010s–2020s). Stress = 0.18. Open and filled circles indicate the bird community structures in the historic and current times, and are connected by coloured arrows.

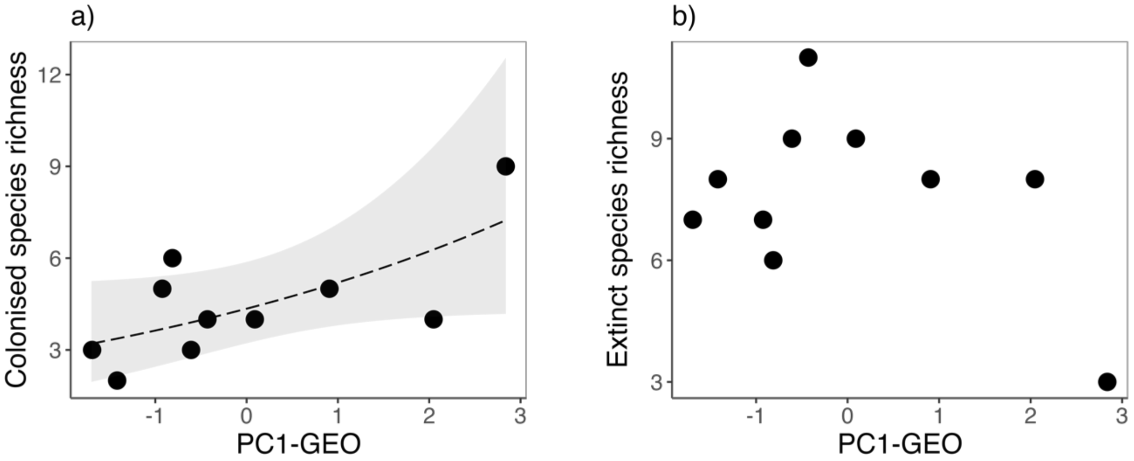

Figure S7 (a) Colonised and (b) extinct species richness of each island. Filled circles indicate the observed values, and lines show fitting with generalised linear models (GLMs), and grey shaded areas represent the 95 % confidence interval. When the null model and models with explanatory variables were selected as the models with ΔAICc <2, the fitting was indicated by long-dashed lines. The fitting is not shown when the null model was the best model. PC1-GEO represents island volume and volcanic activity, and PC2-GEO represents isolation. The explanatory variables selected in model selection procedures with ΔAICc <2 were used for the horizontal axis.

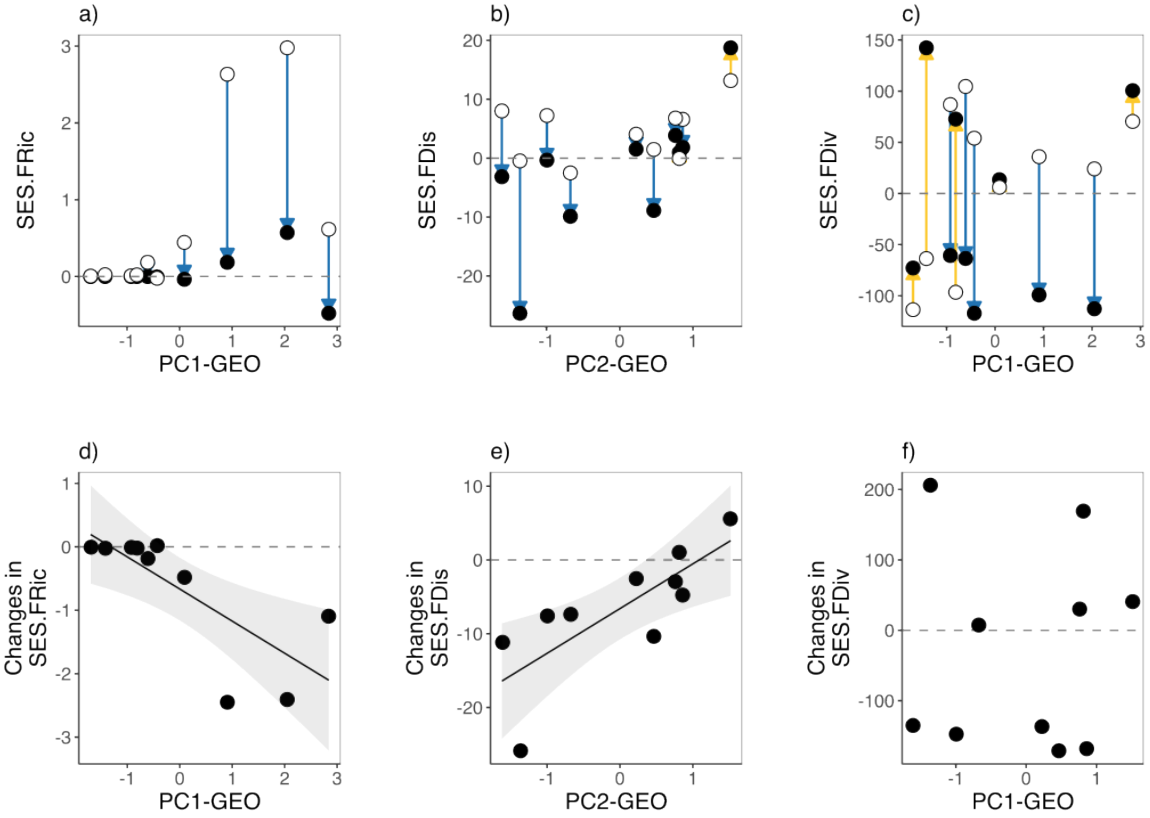

Figure S8 Observed SES.FRic (a), SES.FDis (b), and SES.FDiv (c) from the historic (1970s) to current (2010s–2020s) bird assemblages on ten islands in the Izu islands. Open and filled circles indicate the values in the historic and current bird assemblages, respectively. Blue and yellow arrows indicate negative and positive changes in the values, respectively. Changes in SES.FRic (d), SES.FDis (e), and SES.FDiv (f). Filled circles indicate the observed changes, and solid lines show fitting with generalised linear models (GLMs) for each diversity metric, and grey shaded areas represent the 95 % confidence interval. The fitting is not shown when only the null model was selected. PC1-GEO represents the island volume and the volcanic activity, and PC2-GEO represents the isolation. The explanatory variables selected in model selection procedures with ΔAICc <2 were used for the horizontal axis. However, PC1-GEO was displayed despite the null model being the best for SES.FDiv.

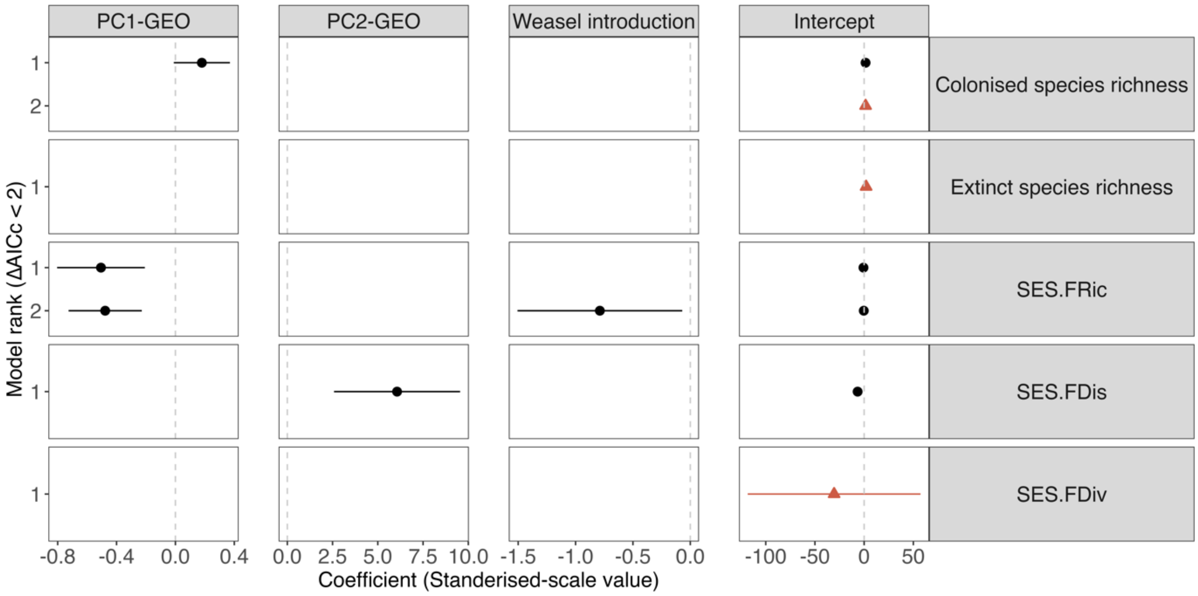

Figure S9 Model selection results from generalised linear models (GLMs) examining the relationship between the changes in functional structures from the historic (1970s) to current times (2010s–2020s), and geographical and topographical characteristics of islands (PC1-GEO and PC2-GEO), weasel introduction, and landscape transformation (PC1-LAND-TF). All continuous explanatory variables were standardised by using principal component analysis, except for weasel introduction (factors). All models with ΔAICc < 2 are shown. An explanatory variable (PC1-LAND-TF) was not displayed because they were not selected in the models with ΔAICc <2. Circles or triangles and horizontal bars indicate point estimates and 95% CIs. When the null model was selected as models with ΔAICc <2, which was shown by a red triangle and a red horizontal bar.

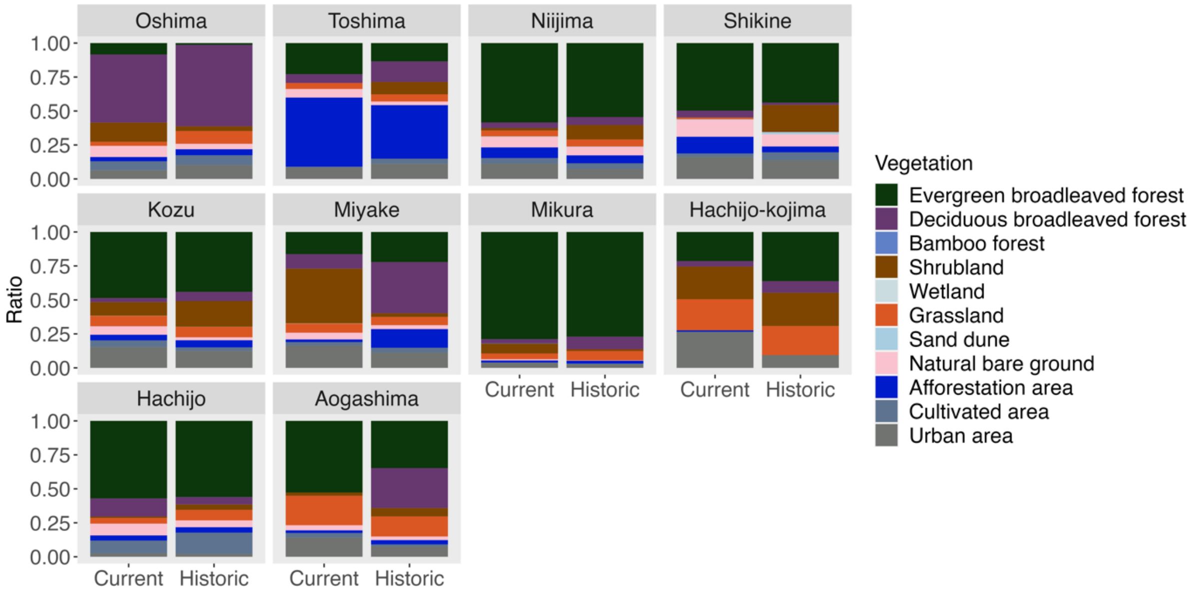

Figure S10 Ratio of the 11 categories of vegetation on each island in the 1970s and 2010s.

Table S1 Traits of birds and their categories. Trait categories are shown in bold type. Equal weights were given to each of the seven trait categories and to each trait within categories to calculate the functional distance.

Traits	Variable	Weight
Morphology (Beak)		
PC2	Continuous	1
Morphology (Dispersal ability)		
Hand-wing Index	Continuous	1
Cold tolerance		
the northernmost latitude	Continuous	1
Susceptibility to extinction in insular species		
Body mass	Continuous	1
Foraging strata		
Upper-canopy	Continuous	0.142
Aerial	Continuous	0.142
Mid-canopy	Continuous	0.142
Understory	Continuous	0.142
Ground	Continuous	0.142
Water around the surface	Continuous	0.142
Water below the surface	Continuous	0.142
Diet		
Insect	Binomial	0.1
Fish	Binomial	0.1
Earthworm	Binomial	0.1
Frog	Binomial	0.1
Lizard	Binomial	0.1
Mammal	Binomial	0.1
Bird	Binomial	0.1
Fruit	Binomial	0.1
Seed	Binomial	0.1
Leaf	Binomial	0.1
Nesting microhabitat		
Tree	Binomial	0.2

Understory	Binomial	0.2
Ground	Binomial	0.2
Cliff	Binomial	0.2
Human settlement	Binomial	0.2
Life history		
Clutch size	Continuous	1

Table S2 Coefficient of the mainland distribution change, simple linear regression models for each species based on the recorded number of meshes in Tokyo in 1973, 1993, and 2017. The number of recorded meshes in each year was used as the objective variable, and the year was used as the explanatory variable. The coefficient of years was used as the coefficient of the mainland distribution change. The coefficient for four insular bird species was set to zero, which is shown by bold type. Seven species with no records on mainland Tokyo were excluded from the analysis. The point estimate and standard error (se) of coefficient of years for each species were presented.

Species	Coefficient	se	Species	Coefficient	se	Species	Coefficient	se
Phasianus colchicus	-0.53	0.32	*Buteo buteo*	-0.02	0.07	*Acrocephalus orientalis*	-0.29	0.19
Columba janthina	**0**		*Dendrocopos kizuki*	1.91	0.48	*Cisticola juncidis*	-0.92	0.30
Streptopelia orientalis	0.11	0.44	*Falco peregrinus*	0.02	0.01	*Troglodytes troglodytes*	0.13	0.30
Treron sieboldii	0.92	0.65	*Terpsiphone atrocaudata*	-0.05	0.36	*Spodiopsar cineraceus*	-0.11	0.56
Gorsachius goisagi			*Lanius bucephalus*	-1.68	1.41	*Zoothera dauma*	-0.21	0.30
Nycticorax nycticorax	0.05	0.30	*Corvus corone*	1.30	0.10	***Turdus celaenops***	**0**	
Bubulcus ibis			*Corvus macrorhynchos*	1.44	0.07	*Luscinia akahige*	-0.22	0.09
Ardea alba	0.57	0.09	*Poecile varius*	1.11	0.41	*Monticola solitarius*	0.21	0.11
Mesophoyx intermedia			*Parus minor*	0.73	1.39	*Ficedula narcissina*	1.19	1.39
Egretta sacra			*Hirundo rustica*	-0.48	0.29	*Cyanoptila cyanomelana*	0.58	0.70
Cuculus poliocephalus	0.09	0.86	*Delichon dasypus*	-0.22	0.37	*Passer montanus*	-0.14	0.05
Apus pacificus	0.00	0.05	*Hypsipetes amaurotis*	0.85	0.13	*Motacilla cinerea*	-0.87	0.70
Scolopax rusticola			*Cettia diphone*	0.50	0.89	*Motacilla alba*	2.04	0.62
Pandion haliaetus			***Phylloscopus ijimae***	**0**		*Chloris sinica*	-1.48	0.83

Milvus migrans	0.30	0.18	*Zosterops japonicus*	2.84	0.43	*Emberiza cioides*	-1.98	0.75
Butastur indicus			***Locustella pleskei***	**0**		*Bambusicola thoracicus*	-2.14	1.69

Table S3 Model selection results of phylogenetic generalised least squares (PGLS) models examining the relationship between the changes in recorded numbers of island of each bird species on the Izu Islands from the historic (1970s) to current times (2010s–2020s) and species traits or the distribution in the mainland. All traits were standardised prior to analysis. All models with ΔAICc <2 and a null model are shown. Point estimates were shown with standard errors in parentheses. Mainland distribution: changes in the mainland distribution; Latitude, the northernmost latitude of wintering and resident distribution.

Model	Intercept	Clutch size	Mainland distribution	Hand-wing index	PC1 FOOD	PC1 NEST	Latitude	PC1 FORAGING STRATA	PC2 BEAK	Body mass	AICc	delta
1	0.18 (±1.6)	1.39 (±0.52)	0.96 (±0.24)								192.6	0
2	0.15 (±1.59)	1.32 (±0.51)	0.99 (±0.24)			0.37 (±0.28)					193.3	0.69
3	-0.02 (±1.62)	1.57 (±0.55)	0.99 (±0.24)	0.48 (±0.48)							194.12	1.52
4	0.37 (±1.62)	1.39 (±0.52)	0.98 (±0.24)						-0.91 (±1.00)		194.29	1.69
Null	0.00 (±1.93)										205.19	12.59

Table S4 Model selection results from linear models (LMs) examining the effect of pairwise geographic distance and survey decade on the pairwise distance in the ordination of non-metric multidimensional scaling (NMDS). We included an interaction term (Geo.dist x Decade). All models with ΔAIC <2 and a null modelare shown. Point estimates were shown with standard errors in parentheses.

Model	Intercept	Geographical distance	Decade (Present)	Geo.dist x Decade	AIC	delta
1	0.2658 (±0.0259)	0.0475 (±0.026)	0.3721 (±0.0366)	0.1078 (±0.0368)	-53.72	0
Null	0.4518 (±0.0293)				28.04	81.76

Table S5 Model selection results from generalised linear models (GLMs) examining the relationship between the changes in taxonomic, functional, and phylogenetic bird community structures from the historic (1970s) to current times (2010s–2020s), and geographical and topographical characteristics of islands (PC1-GEO and PC2-GEO), weasel introduction, and landscape transformation (PC1-LAND-TF). All explanatory variables were standardised prior to analysis. All models with ΔAICc <2 and a null modelare shown. Point estimates were shown with standard errors in parentheses.

Community structures	rank	Intercept	PC1-GEO	PC2-GEO	PC1 LAND-TF	Weasel introduction	AICc	delta
Species richness	1 (Null)	-3.1 (±1.21)					59.81	0
	2	-3.1 (±1.05)	1.47 (±0.74)				60.08	0.27
Colonised species richness	1	1.47 (±0.15)	0.18 (±0.1)				42.62	0
	2 (Null)	1.5 (±0.15)					42.67	0.05
Extinct species richness	1 (Null)	2.03 (±0.11)					46.9	0
SES.MFD	1	-0.80 (±0.15)		0.61 (±0.15)			20.72	0
	Null	-0.80 (±0.25)					28.26	7.53
SES.MPD	1 (Null)	-0.70 (±0.27)					29.6	0
SES.FRic	1	-0.67	-0.51				28.44	0

		(±0.22)	(±0.15)					
	2	-0.35 (±0.23)	-0.48 (±0.13)			-0.79 (±0.37)	29.36	0.92
	Null	-0.67 (±0.31)					32.84	4.40
SES.FDis	1	-6.60 (±1.82)		6.06 (±1.78)			71.10	0
	Null	-6.60 (±2.68)					75.80	4.70
SES.FDiv	1 (Null)	-30.51 (±44.81)					132.11	0