



Spatial conservation prioritization for the East Asian islands: A balanced representation of multitaxon biogeography in a protected area network

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Abstract

Aim: On the basis of multitaxon biogeographical processes related to region-specific geohistory and palaeoclimate, we identified a balanced and area-effective protected area network (PAN) expansion in the East Asian islands, a global biodiversity hotspot.

Location: Japanese archipelago, Ryukyu archipelago and Izu-Bonin oceanic islands.

Methods: We modelled the distributions of 6,325 species (amphibians, birds, freshwater fish, mammals, plants and reptiles) using 4,389,489 occurrence data points. We then applied the Zonation software for spatial conservation prioritization. First, we identified environmental drivers underpinning taxon-specific biodiversity patterns. Second, we analysed each taxon individually to understand baseline priority patterns. Third, we combined all taxa into an inclusive analysis to identify the most important PAN expansions.

Results: Biodiversity patterns were well explained by geographical factors (climate, habitat stability, isolation and area), but their explanatory power differed between the taxa. There was remarkably little overlap between priority areas for the individual higher taxa. The inclusive prioritization analysis across all taxa identified priority regions, in particular in southern subtropical and mountainous areas. Expanding the PAN up to 17% would cover most of the ranges for rare and/or restricted-range species. On average, approximately 30% of the ranges of all species could be covered by the 17% expansion identified here.

Main conclusions: Our analyses identified top candidates for the expansion of Japan's protected area network. Taxon-specific prioritization was informative for understanding the conservation priority patterns of different taxa associated with unique biogeographical processes. For the basis of PAN expansion, we recommend multitaxon prioritization as an area-efficient compromise that reflects taxon-specific priority patterns. Spatial prioritization across multiple taxa provides a promising start for the development of conservation plans with the aim of long-term persistence of biodiversity on the East Asian islands.

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KEYWORDS

conservation biogeography, island biogeography, multitaxon approach, protected area network, reserve design, spatial conservation prioritization, Zonation software

1 | INTRODUCTION

The ongoing biodiversity crisis poses a grave threat to both global ecosystems and the global socio-economy (Naidoo et al., 2006). Establishing and managing protected area networks (PANs) is one of the most widespread and effective actions to maintain biodiversity (Moilanen, 2007; Possingham, Wilson, Andelman, & Vynne, 2006). In this context, spatial conservation prioritization (SCP), the activity of identifying areas important for achieving biodiversity conservation goals cost-effectively, has become one of the central methods of conservation planning (Kukkala & Moilanen, 2012; Moilanen & Arponen, 2011). Conservation biogeography provides a conceptual basis for the design of PANs that broadly capture key biodiversity attributes (Ladle & Whittaker, 2011; Whittaker et al., 2005), including those ecological and historical processes that underpin contemporary biodiversity pattern (Hawkins et al., 2003; Mittelbach et al., 2007; Ricklefs, 2004). SCP methods that are informed by biogeography can contribute to the efficient representation of evolution, historical contingency and species assembly processes (Ferrier, Faith, Arponen, & Drielsma, 2009; Kusumoto et al., 2017).

Biodiversity on islands exists in a naturally fragmented manner and is often characterized by endemism, especially on oceanic islands. Islands contribute substantially to global biodiversity; many of them are conservation priorities (Whittaker & Fernández-Palacios, 2007) and are ranked highly among global biodiversity hotspots (Mittermeier, Turner, Larsen, Brooks, & Gascon, 2011). Because of their distinct biogeographical history, the East Asian islands (which constitute Japan) serve as an ideal region in which conservation biogeographers can develop spatial prioritization analyses with the aim of long-term persistence of ecological and evolutionary potential. Geographical processes in the East Asian islands, such as landbridge connections with the continent and insularity in response to palaeoclimatic change, have shaped unique biodiversity patterns through taxon-specific dispersal and evolutionary diversification related to isolation and/or palaeoclimatic change (Kubota, Hirao, Fujii, Shiono, & Kusumoto, 2014; Shiono, Kusumoto, Yasuhara, & Kubota, 2018; Tojo et al., 2017). Despite the region's ecologically and/or evolutionarily distinctive biota, recent anthropogenic pressures have led to habitat loss, degradation and fragmentation, thereby threatening globally significant biodiversity (Kusumoto et al., 2015). Moreover, the Japanese PAN has a strong spatial bias towards less productive and remote areas (Kusumoto et al., 2017). Recently, the Japanese government has committed to expanding the coverage of Japan's terrestrial PAN to 17% of area, as agreed in the Convention on Biological Diversity's Aichi 11 target

(Ministry of Environment, 2012). Nevertheless, no comprehensive, ecologically justified spatial analysis has so far been carried out to identify PAN expansions that would capture Japan's biodiversity and biogeographical processes in an area-efficient and balanced manner.

The taxon-dependent biodiversity patterns and their underpinning ecological/evolutionary processes may be best captured by taxon-specific conservation planning that accounts for past losses suffered by the taxon, major threats present and cost-effectiveness of alternative conservation actions. Therefore, taxon-specific SCP analysis is useful for establishing baseline conservation priorities for individual taxa, especially from the viewpoint of conservation biogeography. However, the spatial incongruence of priority areas for different taxa may indicate that surrogacy assumptions do not work well (Franco et al., 2009) and separate conservation targets for individual taxa will lower the area efficiency of overall priority areas (Jenkins, Guénard, Diamond, Weiser, & Dunn, 2013). Hence, a multitaxon SCP approach is critically needed to secure key biogeographical processes across taxa that have different dispersal abilities and evolutionary histories, while accounting for overall area (cost) efficiency. Conservation practitioners may also emphasize taxonomic or species groups based on their contribution to ecosystem functions or economic values (Brown et al., 2013; Ellison et al., 2005; Sergio, Newton, & Marchesi, 2005), which may be implemented by taxon-specific weighting.

In this study, we develop a two-step SCP approach for identifying the most suitable PAN expansion areas in Japan, as a model of island conservation biogeography, to meet the 17% Aichi target. As a side product, we assess the performance of the current PAN in terms of biodiversity coverage. We based our prioritization on species distribution models built at a 1-km² resolution using a large amount of data on all native Japanese amphibians, birds, freshwater fishes, mammals, reptiles and vascular plants (6,325 species in total; in this study, we call these taxa or taxonomic groups). We first conducted an analysis of environmental drivers to clarify taxon-specific biodiversity patterns in relation to geohistory and palaeoclimate change. Second, we performed a taxon-specific SCP analysis to establish the priority patterns for each taxon, which also enabled investigation of the spatial congruence of priorities. In the third step, we combined data for all taxa into the same SCP analysis, both with and without the current PAN as a starting point. This multitaxon SCP analysis enabled us to identify cost-effective expansions of the Japanese PAN. Finally, we discuss the respective importance of single- versus multitaxon prioritization approaches for supporting spatial conservation planning in Japan.

2 | METHODS

2.1 | Study area

Japan (part of the East Asian islands), including the Japanese archipelago, the Ryukyu archipelago and the Izu-Bonin oceanic islands, is located off the eastern coast of Asia (Figure 1) and extends from the Holarctic to the Palaeotropical regions (Cox, 2001). During the Pliocene and Pleistocene, geographical processes in the Japanese and Ryukyu archipelagos intermittently divided one large regional biota into insular local communities, with periodic connections reforming through landbridge corridors (Hirao, Kubota, & Murakami, 2015; Millien-Parra & Jaeger, 1999). Even though these islands were never glaciated, climatic cooling and aridity became intensified (or buffered) at various sites, depending on the connection patterns of landbridges and the paths of warm ocean currents flowing into the Japan Sea (Kaizuka, 1980).

2.2 | Species distribution and phylogeny data

We created a geographical database of vascular plants, terrestrial vertebrates (mammals, birds, reptiles and amphibians; Table 1) and freshwater fishes to predict their distributions. This was done at 1-km grid resolution, resulting in an analysis with 377,589 cells with information. For vascular plants, we used the published database of species distributions (Kubota, Shiono, & Kusumoto, 2015). For vertebrates, we first compiled species checklists for Japan: amphibians and reptiles (Herpetological Society of Japan, 2012); freshwater fishes (Nakabō, 2013); birds (The Ornithological Society of Japan, 2012); and mammals (Abe et al., 2005). For each of these species, we collected occurrence information from previous literature and/or databases (see the Supporting Information Appendix S1 for the source list). Note that marine vertebrate species and migratory and stray birds were excluded. The compiled data sets held together 4,389,489 distribution data points for 6,325 species in total: 5,533

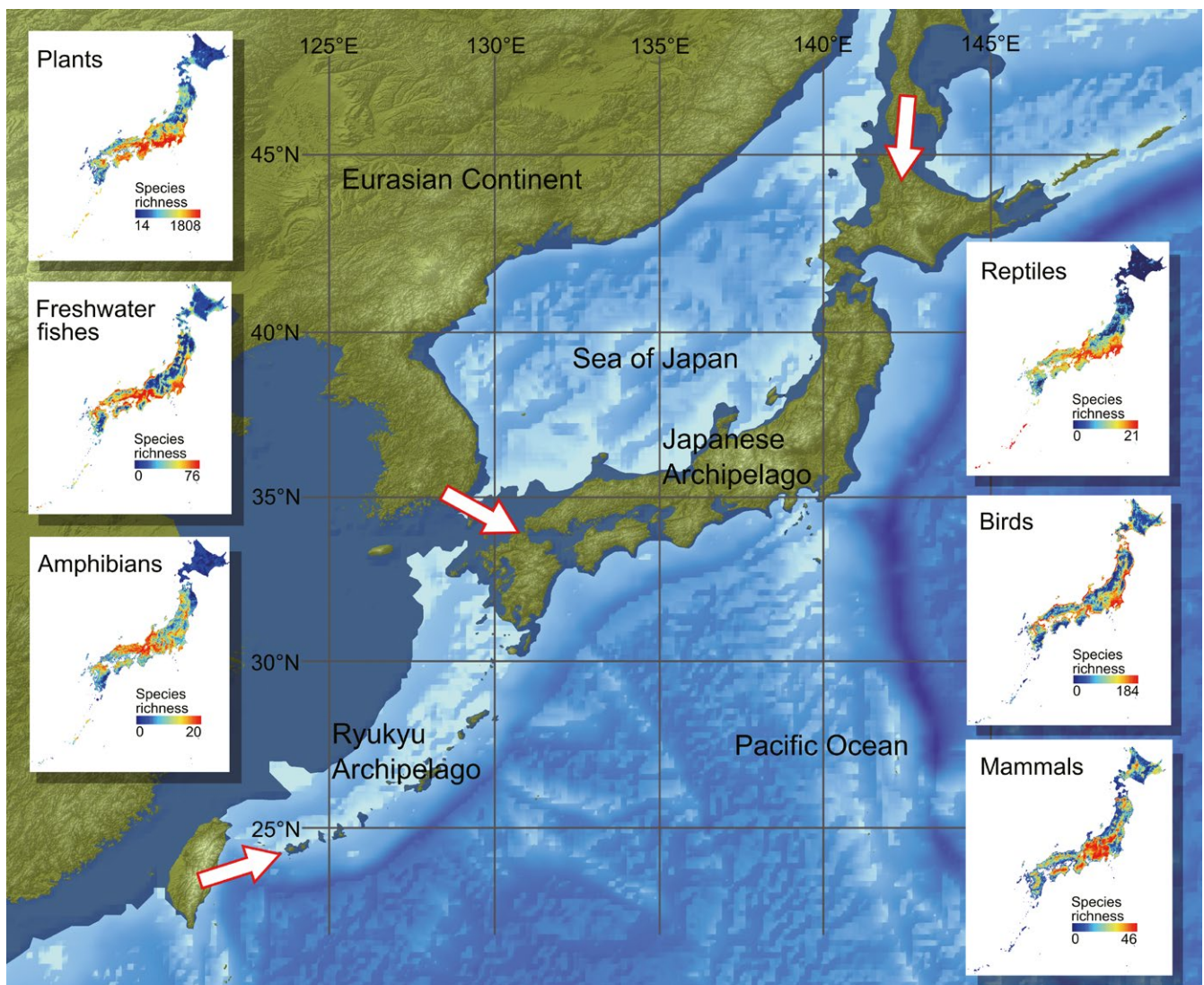


FIGURE 1 Map of East Asia. The green areas denote the current land areas. Dark blue areas show the landmass in the middle Pleistocene. Arrows describe major migration routes from the continental species pool to Japan. The small panels are geographical maps of species richness of each taxonomic group. The map is in the WGS84 geographical coordinate system

TABLE 1 Summary table of each taxon: number of total species, endemic species, endangered species and the number of occurrence data (N) used in species distribution modelling. Species extinction risk is based on the Japanese Red List category: critically endangered (CR); endangered (EN); vulnerable (VU); near threatened (NT); and data deficient (DD). Species range sizes are also shown (median, minimum and maximum within each taxon)

Taxon	N	No. of species								Range size (km ²)
		Total	Endemic	CR	EN	VU	NT	LC	DD	
Plant	210,733	5,533	1,819	389	361	542	223	3,995	23	27,083 (1–249,051)
Freshwater fish	431,038	210	84	36	33	20	16	96	9	16,224 (25–192,037)
Amphibian	45,007	71	59	1	9	11	15	34	1	4,927 (153–170,936)
Reptile	22,233	73	45	2	4	17	14	34	2	1,503 (5–162,970)
Bird	1,528,143	337	12	18	22	31	15	240	11	78,111 (1–244,032)
Mammal	255,735	101	46	6	8	9	11	62	5	48,583 (12–314,008)

vascular plants, 210 freshwater fishes, 71 amphibians, 73 reptiles, 337 birds and 101 mammals. Using these presence-only distribution data, we predicted the potential distribution of each species using MAXENT version 3.3.3 k (Phillips, Anderson, & Schapire, 2006). In the distribution models, we used environmental factors, including climatic, soil, geological, topographical and geographical conditions, as the predictor variables. We confirmed the accuracy of each model using the area under the receiver operating characteristic curve (Supporting Information Figure S1). We used the predicted suitability layer for each species in the subsequent spatial prioritization analyses. To evaluate the coverage of species range within a fraction of priority area, we also binarized (1/0) the predicted suitability using the sensitivity–specificity sum maximizer threshold (Jiménez-Valverde & Lobo, 2007). Kubota et al. (2015) provide a more detailed description of how this data set was developed.

To evaluate evolutionary distinctiveness for each species, we constructed a phylogenetic tree for each of the six taxa. We explain the procedure of phylogenetic reconstruction and calculation of evolutionary distinctiveness in the Supporting Information Appendix S1.

2.3 | PAN data

We extracted the spatial data of the PAs from Japan's National Land Numerical Information (<https://nlftp.mlit.go.jp/ksj-e/index.html>) and the World Database on Protected Areas (<https://www.protectedplanet.net>). We rasterized the polygon data sets for each of the protected area categories in Japan (mostly on the order of 10⁰ to 10³ km²) and classified them into three ranks based on the strictness of legal protection (high = economic activities are strictly forbidden; medium = public permission is required for economic activities; and low = other areas; Kusumoto et al., 2017). Subsequently, we created binary (1/0) maps of PAs for each rank at the 1-km grid cell level. In total, about 39% of the land area is designated as PAs (high = 2%,

medium = 7% and low = 31%). In this study, we focused on the high- and medium-ranked PAs, as effective and semi-effective PANs, respectively.

2.4 | Environmental data

We compiled a suite of environmental variables at 1-km grid cell resolution: current climate (JMA Mesh Climate Data 2002); past climate at the last glacier maximum (WorldClim; www.worldclim.org); land areas and elevation (Geospatial Information Authority of Japan; <https://fgd.gsi.go.jp/download/menu.php>); pyroclastic flows (volcanic activity); and lowland alluvial plains (the Geological Survey of Japan; www.gsj.jp/). To represent current climatic factors, we selected annual mean temperature and annual precipitation. To quantify historical climatic stability, we calculated differences in temperature and precipitation between the last glacier maximum and the present day. As geohistorical habitat stability measures, we used coverage of alluvial plains and pyroclastic flows, which represent drastic habitat change and possible local extinction events. Using the geographical location of each grid cell, we also calculated the shortest distance to the closest edge of the continent (Sakhalin, Korean Peninsula, or Taiwan). Note that all these variables have previously been proposed as potentially important factors explaining biodiversity distribution in the region (Kubota et al., 2015; Kubota, Kusumoto, Shiono, & Tanaka, 2017).

2.5 | Analysis of drivers that explain biodiversity patterns

To assess potential drivers of geographical biodiversity patterns, we conducted random-forest regression analyses. For each taxon, species richness, endemic species richness and the number of species with an evolutionary distinctiveness within the top 5% were set as

response variables. We set nine factors as the explanatory variables (please see previous section). In the estimation, we generated 1,000 regression trees for each run. We evaluated the relative importance of each explanatory variable based on the increase in mean squared error when the variable was permuted. To reduce computational load and to reduce potential effects of spatial autocorrelation, we randomly selected one of the 1-km grid cells in each 10 km by 10 km area and ran the random-forest model; we repeated this procedure 100 times. The analyses were implemented using the R package "randomForest" (Liaw & Wiener, 2002).

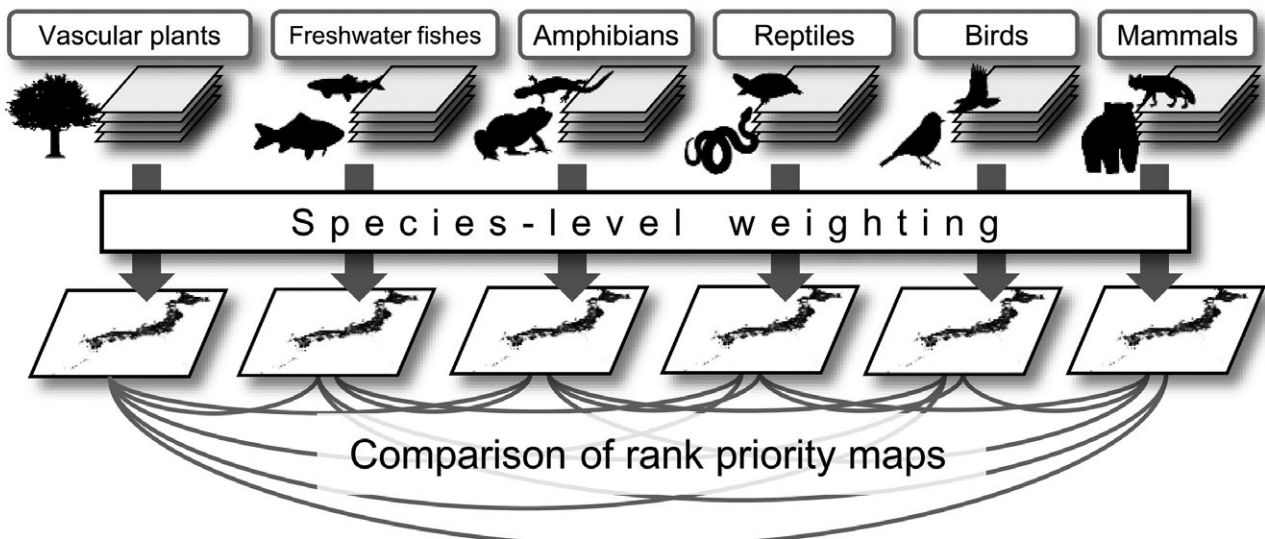
2.6 | Spatial conservation prioritization

For the SCP analyses, we used ZONATION software ver. 4.0 (Moilanen et al., 2014). Zonation produces a balanced, complementarity-based

ranking of conservation priority across the area of interest based on a set of input features. Starting from the full landscape, Zonation iteratively ranks and removes cells which lead to the smallest aggregate loss of conservation value, while accounting for total and remaining distributions of (potentially) weighted features and other relevant factors such as connectivity, costs or habitat condition. Using the predicted species distribution data for 6,325 species (the continuous suitability predictions), we conducted the spatial prioritization in two steps (Figure 2).

In the first analysis step, we ran the same set of prioritization variants (see Supporting Information Appendix S1) for each taxon separately. Within each taxon, we weighted each species by a compound weight of the Japanese Red List category (RLC; least concern = 1, near threatened = 2, vulnerable = 4, endangered = 6, critically endangered = 8, data deficient = 2); endemism (END;

Step 1 Per-taxon prioritization



Step 2 Inclusive analysis across multiple taxa

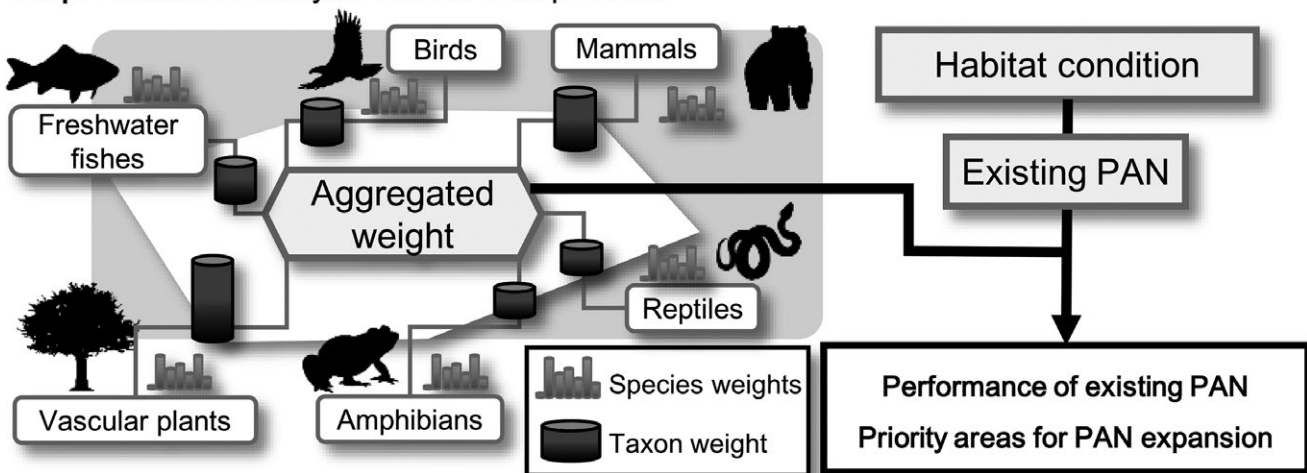


FIGURE 2 The conceptual framework of prioritization analysis in this study: The first step is per-taxon analysis for detecting biogeographical patterns of priority areas per taxon and revealing spatial inconsistencies between taxa; the second step is multitaxon analysis to identify priority areas for expansion of the existing protected area network in Japan

nonendemic = 1, endemic = 4) and evolutionary distinctiveness (EVD; scaled as minimum = 1 and maximum = 4). For a detailed description of the weights used, please see Supporting Information Appendix S1. The compound weight w for species i was calculated as follows:

$$w_i = \text{RLC}_i \times \text{END}_i \times \text{EVD}_i$$

In this analysis step, we ran the per-taxon analyses using both the core-area Zonation (CAZ) and additive benefit function (ABF) ranking methods in Zonation (Moilanen et al., 2014). CAZ emphasizes maintenance of high-quality locations for all species or other features (Moilanen et al., 2005). Using CAZ implies that trade-offs between features are discouraged and that the prioritization aims to retain core areas for all species even at the expense of cost efficiency. In contrast, the ABF minimizes aggregated extinction risk and implicitly places higher priority on species-rich cells, because they contribute to many species simultaneously (Moilanen, 2007). The ABF is generally a good choice if the features are acting as surrogates for a larger regional species pool and trade-offs between features are allowed to achieve cost-efficient coverage of species (Moilanen et al., 2014). Here, the ABF results are reported in the main text, with the CAZ results provided in the Supporting Information Appendix S1.

In the second step of the analysis, we ran a new set of prioritization analyses, this time including all species across all taxa to detect priority areas for expansion of the existing Japanese PAN (see Supporting Information Appendix S1 for details). To reflect the aggregate characteristics of each taxon, we complemented the taxon-specific weighting scheme with weight components reflecting the relative importance of the taxon to overall ecosystem functioning (ESF; vascular plants = 3, freshwater fishes = 1, amphibians = 0, reptiles = 0, birds = 1 and mammals = 2); ecosystem services provided (ESS; vascular plants = 6, freshwater fishes = 5, amphibians = 0, reptiles = 0, birds = 1 and mammals = 1); and overall number of species in the group (NSP; vascular plants = 3, freshwater fishes = 1, amphibians = 0, reptiles = 0, birds = 1 and mammals = 0) (Supporting Information Table S1). These weight components were then summed to form the aggregate weight for taxon j :

$$\text{AGG}_j = 1 + \text{ESF}_j + \text{ESS}_j + \text{NSP}_j$$

The weight w of species i in taxon j was then defined as follows:

$$w_{ij} = \frac{\text{RLC}_i \times \text{END}_i \times \text{EVD}_i \times \text{AGG}_j}{N_t}$$

where N_t is the number of species in taxon t . We chose to normalize the compound weight for each taxon with N_t to account for the rather different numbers of species in different taxa.

We also added a proxy for ecological condition into the analysis by using the inverse of the human influence index (HII, Sanderson et al., 2002), which is based on information about human populations,

accessibility and land use (see Kusumoto et al., 2017 for the details). HII was used as a condition layer in Zonation, that is, as a proxy layer indicating ecological condition from fully lost (0) to pristine (1). We used the existing PAN (high- and medium-rank) as a hierarchical analysis mask in Zonation. This forced the highest priorities into the high-rank PAs, followed by the medium-rank PAs and finally the nonprotected regions of the landscape. Use of the hierarchical mask implements gap analysis and cost-efficient gap filling: The top-priority, nonprotected areas are the most cost-effective complementary additions to the PAN (Lehtomäki, Tomppo, Kuokkanen, Hanski, & Moilanen, 2009).

2.7 | Comparing results

The Zonation priority rank map is a GIS-compatible raster that indicates the priority rank of each cell with a value between 0 (the lowest priority) and 1 (the highest priority) (Lehtomäki & Moilanen, 2013; Moilanen et al., 2014). We examined the spatial congruence among the taxon-specific priority ranks in two ways: Kendall's rank correlation and Jaccard's index. Kendall's Tau rank correlation was calculated using the full priority ranking, that is, the overall spatial congruence between solutions was compared. Jaccard's index was calculated for the grid cells that were in the top 17% fraction of priority ranks, that is, the similarity of high-priority areas was compared. We also analysed performance data automatically produced by Zonation. The performance curves thus produced quantify the fraction of the original distribution remaining for each biodiversity feature at all stages of the ranking process: They allow one to evaluate how much of the range of each species (or species group) can be covered by protecting a given fraction of the landscape.

We also compared the priority rank maps for the all-taxa analyses. In this case, we were primarily interested in (a) the expansion of the current PAN and (b) the performance of the expansion. We plotted performance data to study the potential impacts of alternative prioritization analyses that differed by weights used, the ranking rule ABF (and CAZ, see Supporting Information Appendix S1) and use of a condition layer or current PAN. We examined the distribution of species' ranges covered per taxon in the top 17% of areas both with and without accounting for the current PAN. Finally, we compared for each taxon the coverage of species ranges in the existing PAN and with the suggested expansions.

All postprocessing analyses and graphical works were implemented using the R software (version 3.4.0, R Core Team, 2017).

3 | RESULTS

The geographical patterns of species richness differed distinctly between the six taxa (Figure 1). The random-forest models involving current climate, geohistorical habitat stability, isolation and area effects explained biodiversity patterns generally well across the East Asian islands: The variance explained was 80.8% for amphibians,

76.6% for birds, 84.7% for freshwater fishes, 81.2% for mammals, 82.9% for plants and 84.5% for reptiles. The relative importance of variables showed intertaxon variation (Figure 3): Historical climatic stability was predominantly important for plants; coverage of alluvial plains especially for freshwater fishes; and isolation effects associated with elevation for mammals and birds, whereas area effects were relatively weak for reptiles, amphibians and freshwater fishes. Similar effects of environmental drivers were also observed for endemic species richness and evolutionary distinctiveness (Supporting Information Figure S2). These factors showed greater intertaxon variations in the relative importance of explanatory variables, particularly for elevation and distance from the continent, than did species richness.

In the SCP analysis, the Ryukyu archipelago was consistently identified as top priority for all taxa (Figures 1 and 4; Supporting Information Figure S3). For the East Asian islands, the spatial priority patterns had substantial differences between taxa. For amphibians, priority areas occurred in mountainous areas and/or southern parts of the islands. Priority areas for birds were distributed relatively evenly along coastal areas and only occasionally inland. For freshwater fishes, priorities were mainly distributed in lowland plains and around big lakes, and for mammals, in mountainous areas of middle part and in the northern island. For vascular plants, priority areas exhibited a more patchy distribution, especially in middle and southern parts of the islands. For reptiles, priority areas were mainly in the south-western part of the islands. At the prefectural level, Okinawa was the only prefecture consistently identified as a high conservation priority across all taxa (Supporting Information Table S2). There was marked variability between other prefectures with respect to priorities for different taxa.

The performance of the taxon-specific prioritizations varied relative to the range sizes and spatial co-occurrence of species in the taxon (Figure 5). For example, protecting 17% of the landscape purely based on species occurrences in a single taxon could achieve an average species range coverage of ~85% for reptiles and ~66% for amphibians. For birds, many of which are widely distributed, protecting 17% of the landscape could cover on average ~33% of species ranges. However, the priority rank patterns were spatially disparate between the taxa. Rank correlations based on all of the priority ranks between the taxa were weak (Table 2), and even negative between some pairs of taxa. The overlaps of the top 17% priority areas between the taxa (Jaccard's index) were also consistently low (Table 2).

The all-taxa analysis identified the north-eastern Japanese archipelago and the mountainous area in the middle part of the archipelago as the most important areas for PAN expansion (Figure 6a). As the top 9% of the prioritization was constrained to the current PAN, the potential expansion areas correspond to the top 9%–17% priority ranks (purple areas in Figure 6b). These areas were mostly found in the south-western part of the Japanese archipelago and in the Ryukyu archipelago. When the inclusive analysis was not constrained by the current PAN, the top areas resembled more the overall biogeographical patterns of taxa (Figure 6c,d). At the prefecture

level, Okinawa, Shiga, Yamanashi and Kochi were identified as the highest priority areas (Supporting Information Table S3).

As shown by the average performance curves, the marginal fraction of species ranges covered with additional protected area levels off for both high- and medium-ranked PAs (Figure 7a), but increases more steeply outside the current PAN (Figure 7a). Hence, large areas of top-priority land are located outside the current PAN. On average, 2%, 9% and 17% fractions of the landscape covered 3.8%, 10.3% and 25.2% of species ranges across all taxa (Figure 7a), but there was significant variation between taxa (Figure 7b–d). Amphibians and reptiles have less variation in the fraction of the ranges of individual species covered, and they could potentially gain much from a PAN expansion (Figure 7d). For all taxa, the coverage and representation of especially narrow-ranged species can be greatly improved by an expansion from 9% to 17% of land protected (Figure 8).

When the prioritization was not constrained by the current PAN, 2%, 9% and 17% fractions of the landscape covered 11.5%, 20.3% and 26.4% of the species ranges over all taxa (green curve in Figure 7a). If the prioritization is not constrained by the current PAN, it is possible to almost double the average species' range coverage within the 9% fraction. While amphibians and reptiles receive higher coverages than other taxa, freshwater fishes in particular are not well covered by the current PAN (Figure 7b–d).

The results were not substantially influenced by species or taxon weighting (Supporting Information Figure S4). The condition layer of HII, which penalizes areas with relatively higher human influence, had a large effect by greatly reducing the initial occurrence levels of species (Supporting Information Figure S4).

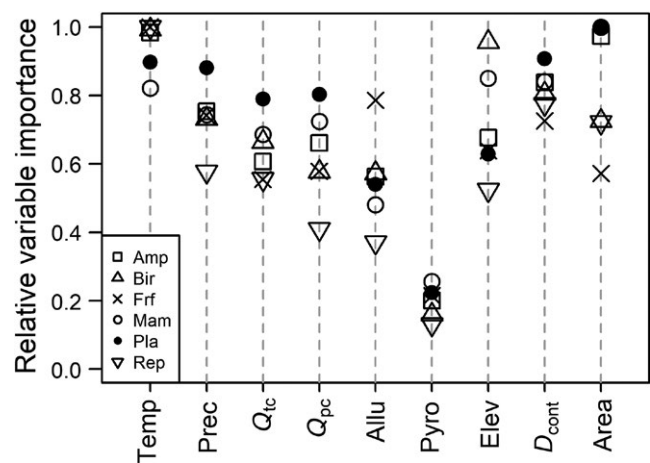


FIGURE 3 Relative importance of explanatory variables in the random-forest models for species richness of each of six taxonomic groups: amphibians (amp); birds (bir); freshwater fishes (frf); mammals (mam); vascular plants (pla); and reptiles (rep). The explanatory factors are mean annual temperature (Temp), annual precipitation (Prec), Quaternary temperature change (Q_{tc}) and precipitation change (Q_{pc}), coverage of alluvial plains (Allu) and pyroclastic flows (Pyro), elevation (Elev), shortest distance to the nearest continent (D_{cont}) and log-scaled land area (Area)

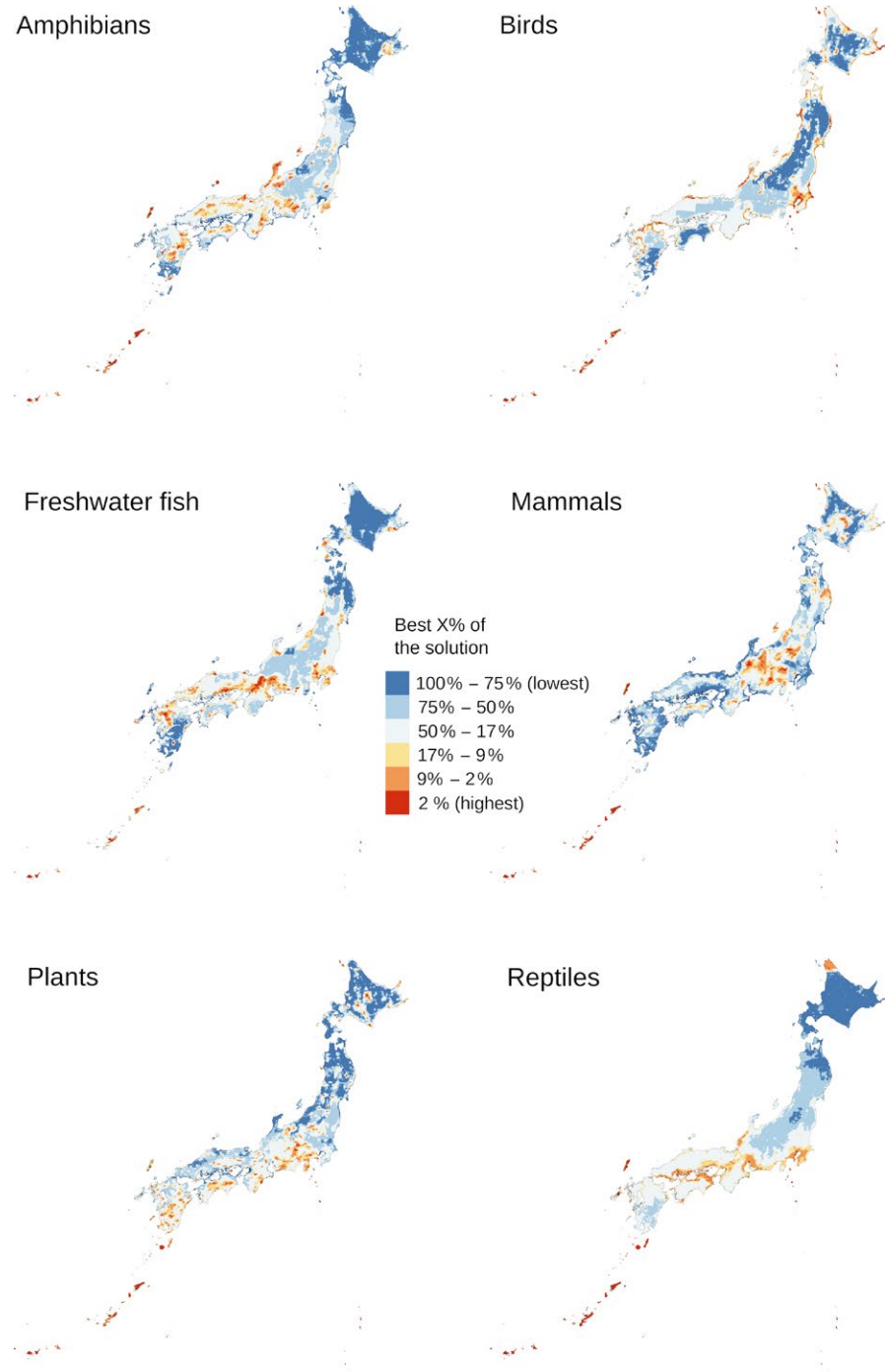


FIGURE 4 Priority rank maps computed for all taxa simultaneously using the additive benefit function algorithm that minimizes expected extinction rates. In this analysis, individual species had weights derived from the Red List category, endemism and evolutionary distinctiveness of the species. The projection used is WGS 84/UTM zone 54N

4 | DISCUSSION

Much of spatial conservation prioritization—especially when done in the context of centralized planning—is driven by so-called high-level objectives (Ferrier & Wintle, 2009; Shields, Šolar, & Martin, 2002). The failure of conservation actions may be caused by a low buy-in from local people affected by conservation actions and/or poorly defined objectives (Ferrier & Wintle, 2009; Game, Kareiva, & Possingham, 2013). In our case, the high-level objective was planning for the expansion of the Japanese PAN to meet the 17% area target defined by the Convention on Biological Diversity.

This objective itself is only one part of the broader Strategic Goal C: to improve the status of biodiversity by safeguarding ecosystems, species and genetic diversity (CBD, 2010). This is to be done with a focus on the representativeness, spatial configuration and complementarity of the PAN. However, what exactly constitutes “areas of particular importance for biodiversity and ecosystem services” (CBD, 2010) is more difficult to determine conceptually and practically. A universally shared notion of biodiversity simply does not exist, let alone a common understanding of how exactly biodiversity ought to be valued in (spatial) conservation prioritization.

TABLE 2 Kendall's Tau rank correlations (upper triangle) and Jaccard's index (lower triangle) between the priority ranks for the six taxa. Jaccard's index was calculated using the composition of cells that were included in the solution top 17% fraction (i.e., not accounting for the existing PAN). The priority rank was calculated by the additive benefit function (ABF) algorithm, which gives higher priority to cells that have comparatively many species with narrow ranges and/or high weights. All else being equal, species-rich cells are preferred to species-poor cells

	Amphibians	Birds	Freshwater fish	Mammals	Plants	Reptiles
Amphibians		0.077	0.289	0.153	0.260	0.373
Birds	0.099		0.298	-0.161	0.021	0.281
Freshwater fish	0.139	0.207		-0.062	0.092	0.412
Mammals	0.144	0.095	0.065		0.213	-0.042
Plants	0.179	0.106	0.098	0.241		-0.042
Reptiles	0.144	0.205	0.284	0.149	0.149	

Here, we first identified key priority areas that reflect taxon-specific biogeographical patterns and current conservation status (i.e., evolutionary distinctiveness, endemism and Red List category as weighting). This information is useful in assessing potential trade-offs and surrogacy between different taxa, as well as establishing taxon-specific baselines for further analyses. Meanwhile, in practice spatial conservation planning needs to balance between multiple taxa as well as to account for many real-life anthropogenic constraints. That is why in the second step we combined all species data into the same analysis and also accounted for human influence as well as the configuration of the current PAN. As a result, we could identify potential PAN expansion areas that have a balanced representation of all species included in the prioritization and that complement the current PAN in an area-efficient manner. Accounting for complementarity and human influence makes the prioritization potentially more cost-efficient and realistic for implementation. Below we first discuss aspects of taxon-specific conservation biogeography for safeguarding island biodiversity

and then, based on spatial prioritization of multiple taxa, assess the performance of the current Japanese PAN. Finally, we suggest ways in which our approach could be taken to the stage of implementation.

Because of pervasive shortfalls in our knowledge about biodiversity (Hortal et al., 2015), SCP is commonly based on surrogate species/taxa with the (often implicit) assumption that they represent biodiversity patterns more broadly (Di Minin & Moilanen, 2014; Rodrigues & Brooks, 2007). We used all native species of vascular plants and terrestrial vertebrates in Japan as surrogates for overall biodiversity (Caro & O'Doherty, 1999): Plant species assemblages have a fundamental role for other taxa through the creation of locally stable habitat conditions (Ellison et al., 2005); vertebrate species assemblages potentially provide a better representation of less charismatic biodiversity via their umbrella effects (Di Minin & Moilanen, 2014).

Taxon-specific biogeographical processes may explain the spatial incongruence of priority areas for individual taxa (Jenkins et al., 2013). The East Asian islands across Japan functioned as a refuge for the Tertiary relict flora (Kubota et al., 2014); thus, vascular plant assemblages in this region became diversified during geographically stable and isolated conditions reflecting insularity and orogeny over the Cenozoic (Kubota et al., 2017, 2015). In contrast to the terrestrial flora, the vertebrate biodiversity in this region is of relatively complex or recent origin and mainly diversified in the Quaternary (Ohdachi, Ishibashi, Iwasa, Fukui, & Saitoh, 2010; Otsuka & Takahashi, 2000). Thus, species accumulation in the western, middle and northern areas of Japan may reflect imprints of migration from the continent through landbridge connections via the Korean Peninsula and Sakhalin Islands (Figure 1). These connections occurred during the Ice Age and were amplified by subsequent in situ diversification of freshwater fishes (Watanabe et al., 2006), amphibians, reptiles (Ota, 1998, 2000; Takahashi, Otsuka, & Ota, 2008) and mammals (Millien-Parra & Jaeger, 1999; Motokawa, 2000). In addition, large-scale species diversity patterns of birds have been influenced both by migration from the tropics and the extratropical region after the Ice Age (Higuchi, 2012) and wintering or breeding areas in the temperate

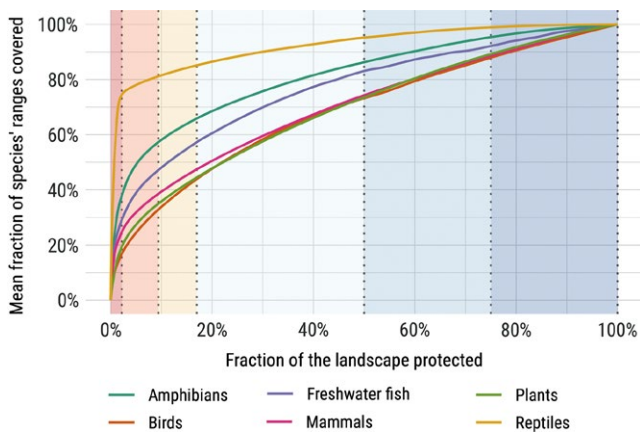


FIGURE 5 Performance curves for each per-taxon prioritization (Figure 2). Curves show the average fraction of species' occurrences covered (y-axis) in each taxon by a given fraction of the landscape (x-axis). The colours in the background correspond to the colour scheme of Figure 3. Curves are shown for all taxa, but each curve is based on a separate prioritization

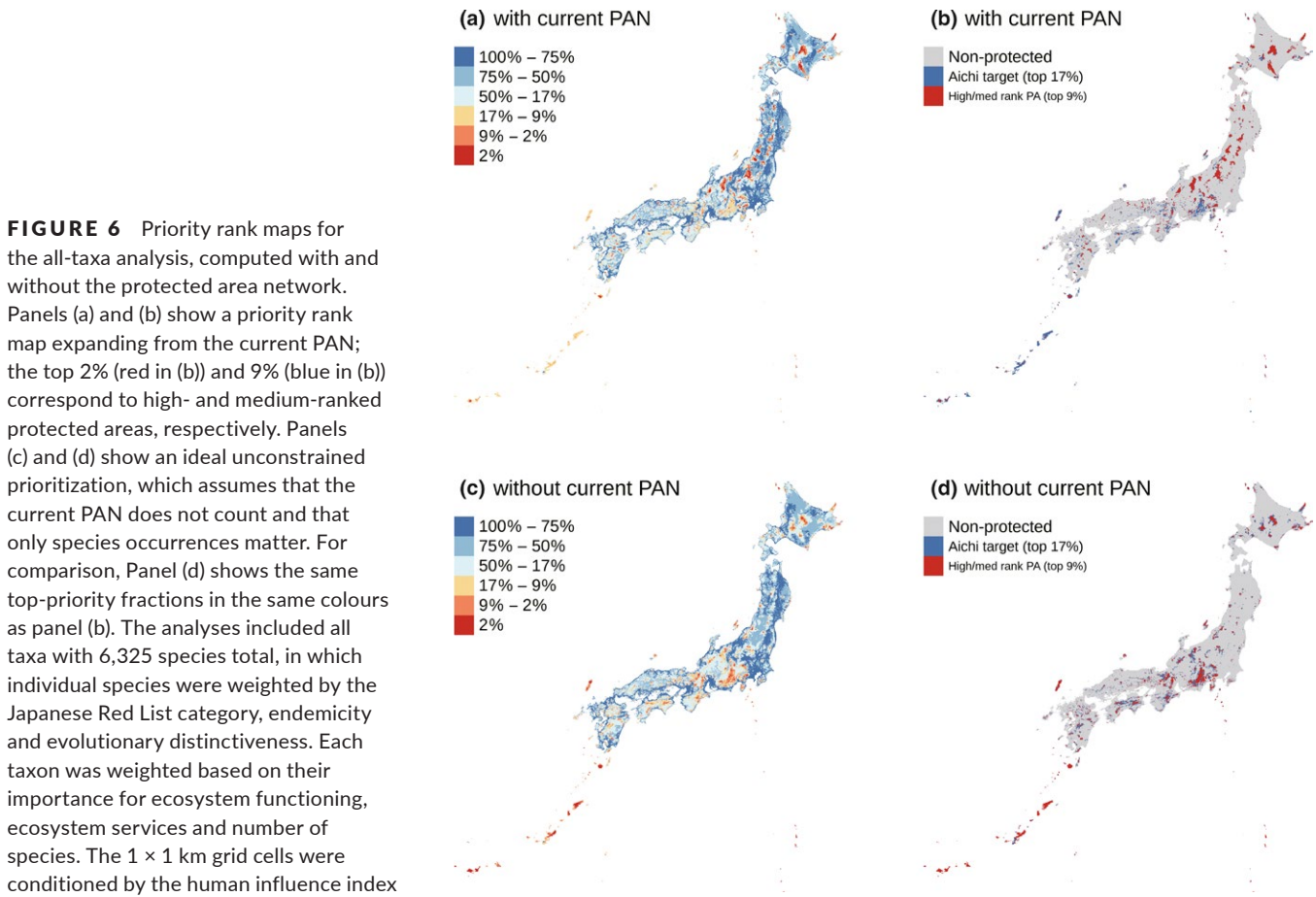


FIGURE 6 Priority rank maps for the all-taxa analysis, computed with and without the protected area network. Panels (a) and (b) show a priority rank map expanding from the current PAN; the top 2% (red in (b)) and 9% (blue in (b)) correspond to high- and medium-ranked protected areas, respectively. Panels (c) and (d) show an ideal unconstrained prioritization, which assumes that the current PAN does not count and that only species occurrences matter. For comparison, Panel (d) shows the same top-priority fractions in the same colours as panel (b). The analyses included all taxa with 6,325 species total, in which individual species were weighted by the Japanese Red List category, endemism and evolutionary distinctiveness. Each taxon was weighted based on their importance for ecosystem functioning, ecosystem services and number of species. The 1×1 km grid cells were conditioned by the human influence index

region (Yamaura, Katoh, Fujita, & Higuchi, 2005). Our results were consistent with these biogeographical processes: Intertaxon variations of biodiversity drivers involving geohistory and palaeoclimate changes (Figure 3) demonstrate that taxon-specific dispersal histories and habitat requirements jointly played a significant role in shaping biodiversity anomalies between taxa in the East Asian islands (Figure 1).

Information about species priorities (or weights) is typically used in strategic conservation planning (Arponen, Heikkinen, Thomas, & Moilanen, 2005; Marsh et al., 2007). Although subjective weighting may be controversial in biological justification (Possingham et al., 2002), equal weighting is also a weighting that requires justification. Here, we implemented a hierarchical weighting scheme across species and higher taxa, and found that the weighting had relatively little influence on the overall prioritization outcome (Supporting Information Figure S4). This is partially because of the large number of species distributions we used (6,325 species): Large number of species (or any other features) results in a priority ranking that is highly robust and stable regardless of moderate differences in feature weights (Kujala, Moilanen, & Gordon, 2018). This is because species (features) can only be protected where they exist; although their distribution sizes vary, many features occur in a more or less nested manner, and consequently moderate differences in weights lead to only

minor differences in the priority pattern. The nested pattern of species distributions is a factor that strongly supports stability of priority patterns (Arponen et al., 2005): For example, diversity hotspots for vascular plants showed significant spatial overlap between endemic species and all species in the East Asian islands (Kubota et al., 2015), indicating that representation of common species can be obtained within the geographical range of endemic species. Nevertheless, and despite comparatively minor effects on the pattern (Kujala et al., 2018), feature (here species) weighting is important for the efficiency and transparency of conservation decision-making, as it not only fine-tunes the prioritization results according to the requirements of decision-makers, but also makes those preferences explicit.

Our findings revealed major differences between the priority areas for different taxa that were driven by different biogeographical processes (Figures 3 and 4, Table 2). This implies that taxon-specific conservation prioritization is an efficient way to capture biodiversity patterns, including biogeographical backgrounds, for individual taxa alone. Depending on how broadly species within a taxon are distributed and to what degree they co-occur, even relatively small fractions of the landscape may be able to capture a large fraction of species' ranges (Figure 5), for a taxon. However, when multiple taxa are considered at the same time, trade-offs are usually inevitable. At the same time, these disparities imply that surrogacy

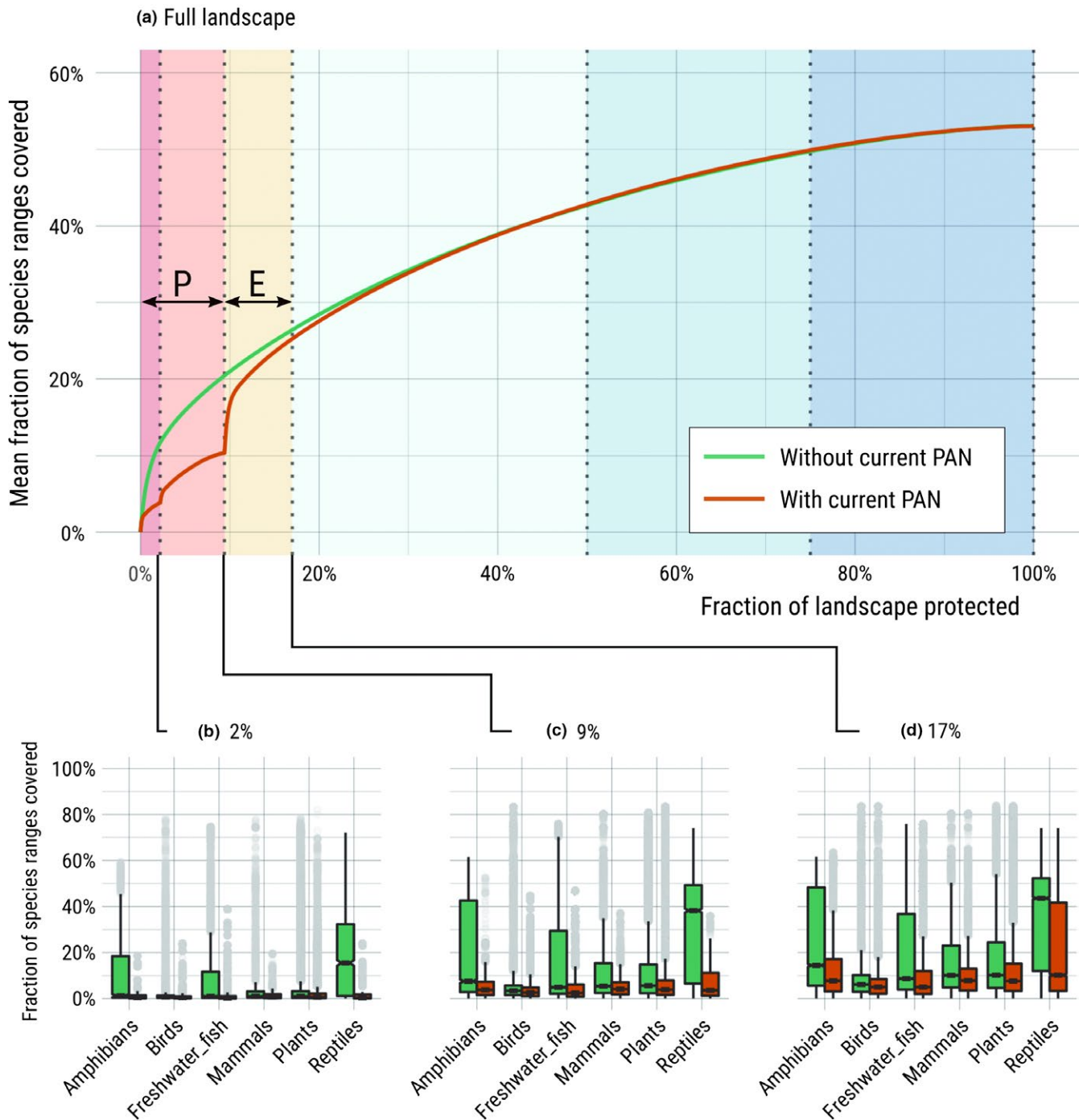


FIGURE 7 Panel (a) shows the average performance curves over all 6,325 species for the prioritization with the current PAN accounted for (orange) and not (green). The colours in the background correspond to the colour scheme in Figure 3. The best 9% show the section corresponding to the current PAN (red and orange background, arrow P). The following fraction up to 17% show what could be achieved by expanding the PAN to meet the 17% (Aichi 11) target (yellow background, arrow E). Because each grid cell was penalized by the condition (the human impact) layer, the maximal range coverage does not reach 100%. Box plots show the distribution of species ranges covered for each taxon in the high-ranked PAs (2%, (b)), medium-ranked PAs (9%, panel (c)) and with an expansion to 17% (Aichi 11 target, panel (d))

assumptions should be carefully tested for other taxonomic groups not included in this study because of insufficient data (e.g., invertebrates). Many previous conservation-planning studies have focused on identifying priority areas based on the geography of a specific taxon that has often been chosen subjectively, or based on data

availability (Andelman & Fagan, 2000; Grand, Cummings, Rebelo, Ricketts, & Neel, 2007). Designing a comprehensive and taxonomically unbiased PAN therefore requires concerted efforts to collect additional biodiversity information relevant for planning objectives (Meyer, Weigelt, & Kreft, 2016). Furthermore, we should carefully

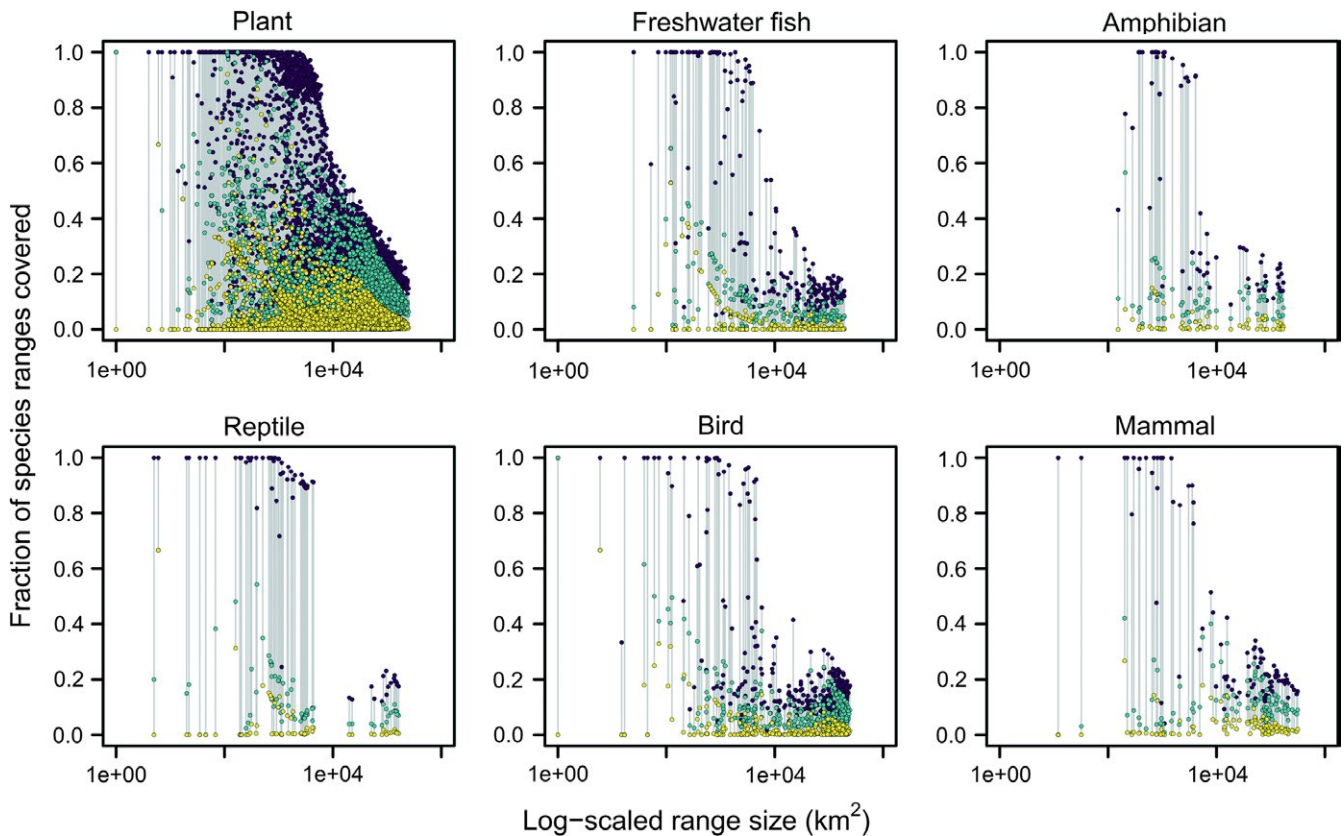


FIGURE 8 Relationship between the range size of a species and range coverage in different fractions of priority areas: 2% corresponding to the high-ranked existing protected areas (yellow), 9% corresponding to medium-ranked protected areas (turquoise) and 17% corresponding to the Aichi target 11 (purple). The priority ranking was conducted in the order of the nonprotected areas, then the medium-ranked protected areas and last the high-ranked protected areas. Note that the x-axes are logarithmic

consider the trade-offs between taxa in SCP to maximize the overall performance of PANs (Lentini & Wintle, 2015).

Our inclusive analysis accounting for the current PAN produced several important results, which were robust against subjective weighting of species/taxa. First, we showed that the current PAN is underperforming in terms of the coverage of the occurrence levels of 6,325 species in six different taxa (Figure 7). This finding is in line with a previous study concentrating on vascular plants only (Kusumoto et al., 2017). While the Japanese PAN is biased towards remote and unproductive areas (Kusumoto et al., 2017), the underperformance holds also when human influence is accounted for. Second, we identified the most area-efficient candidate expansion areas to meet the 17% Aichi target given the current PAN and estimates for ranges of species (Figure 6). The areas identified could capture considerable fractions of the ranges of especially narrow-ranged species (Figures 6 and 7). Redesigning the whole PAN while disregarding the current PAN would show even better performance (Figure 6 and 7). However, systematic expansion of the current PAN up to 17% improves the average range coverage to almost the same level (25.2%) as the unconstrained prioritization (26.4%). Redesigning the whole PAN is clearly infeasible, but selecting expansion areas based on prioritization can yield notable performance increases, especially for amphibians (~7 percentage point increase in

average performance) and reptiles (~9 percentage point increase in average performance).

Reaching the 17% terrestrial protection Aichi target necessitates effective design and implementation of the PAN expansion (Jenkins & Joppa, 2009; Pouzols et al., 2014) and possibly replacement of underperforming PAs (Fuller et al., 2010). The Japanese government promotes strategies and action plans mostly implemented at the local governance level of 47 prefectures. To date, however, systematic conservation planning, including SCP, has not been done because of both imperfect knowledge of the distribution of biodiversity and pressures from alternative land uses, for example, forest management (Kusumoto et al., 2017). Our approach balancing priority areas across multiple taxa provides a plausible method for conservation planning across a large number of biodiversity features (Regan et al., 2008; Smith-Patten & Patten, 2015) in Japan. Specifically, accounting for multitaxa biodiversity patterns shaped through taxon-specific biogeographical processes may lead to balanced conservation planning that secures overall conservation performance in terms of long-term persistence. Indeed, our inclusive analysis across taxa identified consistently important areas in both steps of our analysis, for example, in the south-western islands and mountainous areas in the middle part of Japan (Figures 4 and 5; Supporting Information Table S2).

We acknowledge that it would be beneficial to account for several additional factors. In the real-life implementation context, conservation prioritization typically involves actions rather than places or species (Brown et al., 2015). This implies that, in addition to spatially explicit biodiversity information, costs of conservation action (Evans et al., 2015) and threats to species have critical roles in making conservation decision (Tulloch et al., 2015). Our prioritization approach already uses a proxy for the condition of the species' habitats (the HII) and could accommodate other relevant information as well. Here again, the availability of reliable, spatially explicit data, rather than the technical capabilities of the prioritization procedure, is the limiting factor. More realistic treatment of the ecological connectivity requirements of species at multiple spatial scales in relation to the PAN would also be a useful improvement. Technically, this too could be incorporated using Zonation (Lehtomäki et al., 2009) assuming that the necessary ecological information is available. Finally, given that the Japanese national strategies and action plans are implemented at the local level of prefecture, a fully operationalized SCP approach would be greatly enhanced if it could account for potentially different objectives, preferences and constraints in different administrative units (i.e., prefectures). Again, this is not a matter of analytical capability but a question of data availability and resources for replicating analysis variants across prefectures.

In conclusion, our SCP analysis identified an area-efficient and balanced set of candidates for expansion of the existing PAN of Japan. Taxon-specific prioritization would be informative for developing conservation plans that represent island biogeographical processes; indeed, these processes have given rise to the unique biodiversity patterns we see today in the East Asian islands and are therefore themselves subjects for conservation actions. Such region-specific processes could be best captured by taxon-oriented, baseline conservation priorities that seek long-term persistence of biodiversity patterns for individual taxa. For practical planning, however, we recommend multitaxon prioritization as a balanced compromise design between taxon-specific priority patterns and key biogeographical processes that prevail across multiple taxa. Spatial prioritization is contingent on the choice of surrogate taxa that are characterized by different evolutionary processes. Our analyses were based on a large set of species distribution models never before used in such a manner. Although the amount of data we had available mitigates the subjective selection of biodiversity surrogates, there remains room for improvement. For example, data about insects were missing, and it is unknown how well plants act as surrogates for insects in this region. Implementing data-driven expansion of the PAN in Japan, which harbours a highly endemic biota, will contribute to increasing the conservation effectiveness of the world's biodiversity hotspots.

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DATA ACCESSIBILITY

All environmental GIS layers, habitat suitability models (except for rare species) and Zonation results generated for this study are available as raster grids from Zenodo: <https://doi.org/10.5281/zenodo.1462723>. The code used for preprocessing the data for Zonation analysis, analysing the results and generating most of the figures is available from <https://github.com/cbig/japan-zsetup> (will be archived in Zenodo once accepted).

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BIOSKETCH

The researchers involved in this study, belonging to Vrije Universiteit Amsterdam, University of the Ryukyus and University of Helsinki, share their interest on spatial conservation prioritization for biodiversity and biogeography in the East Asian continental Islands.

Author contribution: B.K. and Y.K. conceived the research idea. T.S., T.T. and B.K. constructed dataset. A.M. and J.L. designed the analytical framework. J.L. conducted the Zonation analyses. J.L. and B.K. conducted the posthoc analyses. J.L. made 1st draft of the paper, and all authors substantially contributed to revisions.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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