Global conservation of species' niches

Jeffrey O. Hanson, Jonathan R. Rhodes, Stuart H. M. Butchart, Graeme M. Buchanan, Carlo Rondinini, Gentile F. Ficetola & Richard A. Fuller

Abstract

Environmental change is rapidly accelerating, and many species will need to adapt to survive[1]. Ensuring that protected areas cover populations across a broad range of environmental conditions could safeguard the processes that lead to such adaptations[1,2,3]. However, international conservation policies have largely neglected these considerations when setting targets for the expansion of protected areas[4]. Here we show that—of 19,937 vertebrate species globally[5,6,7,8]—the representation of environmental conditions across their habitats in protected areas (hereafter, niche representation) is inadequate for 4,836 (93.1%) amphibian, 8,653 (89.5%) bird and 4,608 (90.9%) terrestrial mammal species. Expanding existing protected areas to cover these gaps would encompass 33.8% of the total land surface—exceeding the current target of 17% that has been adopted by governments. Priority locations for expanding the system of protected areas to improve niche representation occur in global biodiversity hotspots[9], including Colombia, Papua New Guinea, South Africa and southwest China, as well as across most of the major land masses of the Earth. Conversely, we also show that planning for the expansion of protected areas without explicitly considering environmental conditions would marginally reduce the land area required to 30.7%, but that this would lead to inadequate niche representation for 7,798 (39.1%) species. As the governments of the world prepare to renegotiate global conservation targets, policymakers have the opportunity to help to maintain the adaptive potential of species by considering niche representation within protected areas[1,2].

Main

In response to the biodiversity crisis, 195 governments have signed the Convention on Biological Diversity (https://cbd.int). Signatories have pledged to conserve habitats that support 'key evolutionary processes' (Article 8, Annex I of the convention)—in part, by conserving at least 17% of the Earth's terrestrial and inland water areas and 10% of coastal and marine areas (especially areas of particular importance for biodiversity), through ecologically representative systems of protected areas and other effective area-based conservation measures (Aichi Target 11, https://www.cbd.int/sp/targets/). Because habitat heterogeneity can foster local adaptations to local conditions, a well-designed system of protected areas would conserve populations in suitable habitats that contain different environmental conditions (that is, a representative sample of the realized niche of each species) and—in turn—maximize the persistence of species[1,2,10]. However, despite progress in understanding how much habitat is available for species in protected areas[5,6,11], very little is known about how well protected areas cover the diversity of environmental conditions that affect the adaptive potential of any given species. As consideration is already being given to a new framework for conserving biodiversity, it is imperative that conservation scientists and policymakers understand how much progress has been made towards protecting biodiversity and how best to shape future conservation targets.

Here we assess the representation of the realized climatic niches (hereafter, niches) of species by protected areas globally. We obtained maps of the extent of suitable habitat (hereafter, habitat maps) for the majority of the world's known bird (n = 9,670)[5,6], terrestrial mammal (n = 5,070)[7] and amphibian (n = 5,197)[8] species, and subdivided the habitat map of each species into 10 partitions on the basis of climatic conditions[12] (see Extended Data Fig. 1 for sensitivity analysis). For each species, we calculated a target percentage of its global geographic distribution to be covered by protected areas, decreasing from 100% for species with less than 1,000 km2 of habitat to 10% for those with

more than 250,000 km2 of habitat, and linearly interpolated on a log-linear scale between these thresholds[11,13]. We then applied the global geographic representation target of each species to each of its climatic partitions to assess niche representation. Next, we overlaid the partitioned habitat maps of all species with the boundaries of protected areas[14] (Extended Data Fig. 2) and identified which species are inadequately represented because their target level of coverage is not met. To understand how accounting for species' niches might alter conservation priorities, we generated two spatial prioritizations to identify areas needed to reach targets for the partitioned and unpartitioned habitat maps of each species. We used data on Key Biodiversity Areas—defined as 'sites that contribute significantly to the global persistence of biodiversity'[15]—to explore the contribution that their protection would make to conserving species' niches. We overlaid maps of the boundaries of Key Biodiversity Areas[16] with the protected area and partitioned habitat maps, and compared their performance with randomly selected localities of a similar extent.

We found that 18,097 (90.8%) species do not have their niche adequately represented by existing protected areas (Fig. 1). Although 5,384 (27%) species have their overall distribution adequately represented by protected areas, existing protected areas only cover—on average—28.2% of species' climatic partitions. Furthermore, 9,651 (48.4%) species do not have any of their climatic partitions adequately represented. Of these species, 2,385 are listed as globally threatened on the Red List of the International Union for Conservation of Nature (IUCN)[17]. Although challenges remain in detecting local adaptations[18], there are documented examples among imperilled species. For example, foothill populations of the globally vulnerable Italian agile frog (Rana latastei) appear to exhibit adaptations to their colder surroundings that are absent from lowland populations[19] (Extended Data Fig. 3, Supplementary Information section 1). As none of the climatic partitions of this species is adequately protected, further environmental modifications could limit its ability to adapt to changing conditions. In China, populations of the globally vulnerable giant panda (Ailuropoda melanoleuca) show spatial patterns in parts of their genome that underpin immune-system function[20]. On average, only 18.6% of the habitat in each of the climatic partitions of this species overlaps with protected areas—far less than the 88.5% target calculated for its limited geographic range (Extended Data Fig. 4, Supplementary Information section 2). Similarly, populations within the breeding distribution of the great snipe (Gallinago media) show spatial patterns in parts of their genome that affect immune-system function[21], and only one of its ten climatic partitions is adequately represented by protected areas (Extended Data Fig. 5, Supplementary Information section 3).
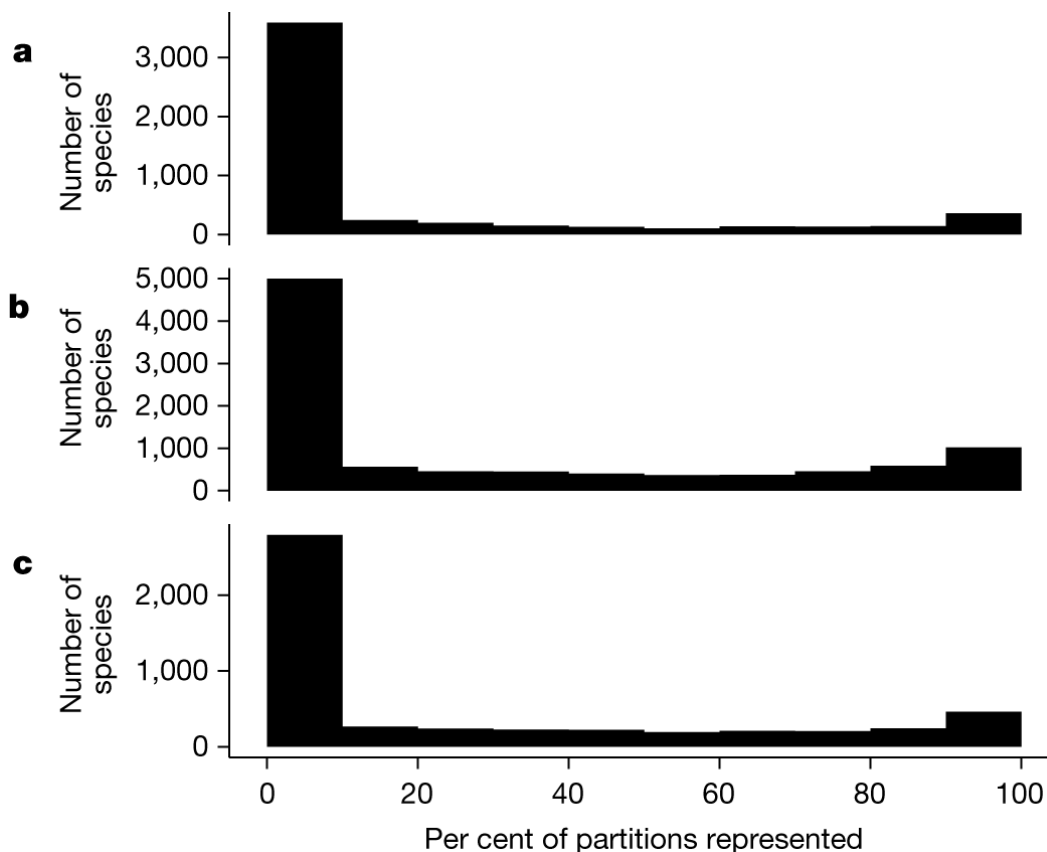
Fig. 1: Coverage of species' niches by existing protected areas. a–c, The percentage of climatic partitions adequately represented by protected areas for different amphibian (n = 5,197) (a), avian (n = 9,670) (b) and mammalian species (n = 5,070) (c). The representation of climatic partitions was assessed by overlaying the partitioned habitat maps of each species with maps of protected areas, and determining whether the total amount of habitat in protected areas met a target threshold for each partition.

We identified priority areas for the expansion of protected areas to represent species' niches (Fig. 2a). When combined with existing protected areas, these priority areas encompass 33.8% of the Earth's land and inland water—exceeding the 17% target in Aichi Target 11. Some of the highest concentrations of priority areas are located in global biodiversity hotspots[9]. For example, the tropical Andes—where steep environmental gradients and complex topographies have driven evolutionary processes[22], resulting in unparalleled levels of biodiversity[9]—stand out as critical for the expansion of protected areas. The Cape floristic region (a floral diversity hotspot near the southernmost tip of Africa) and Madagascar are evolutionary powerhouses that also contain many priority areas[23,24]. Further east, more priority areas occur along the Himalayas, an evolutionary epicentre for bird species[25], and throughout the species-rich island nations of Southeast Asia and the Pacific. Outside of recognized biodiversity hotspots, more priority areas are distributed throughout Africa, Asia, Europe and Northern America. Although they mostly occur in smaller concentrations, these areas are critical for comprehensively covering species' niches.
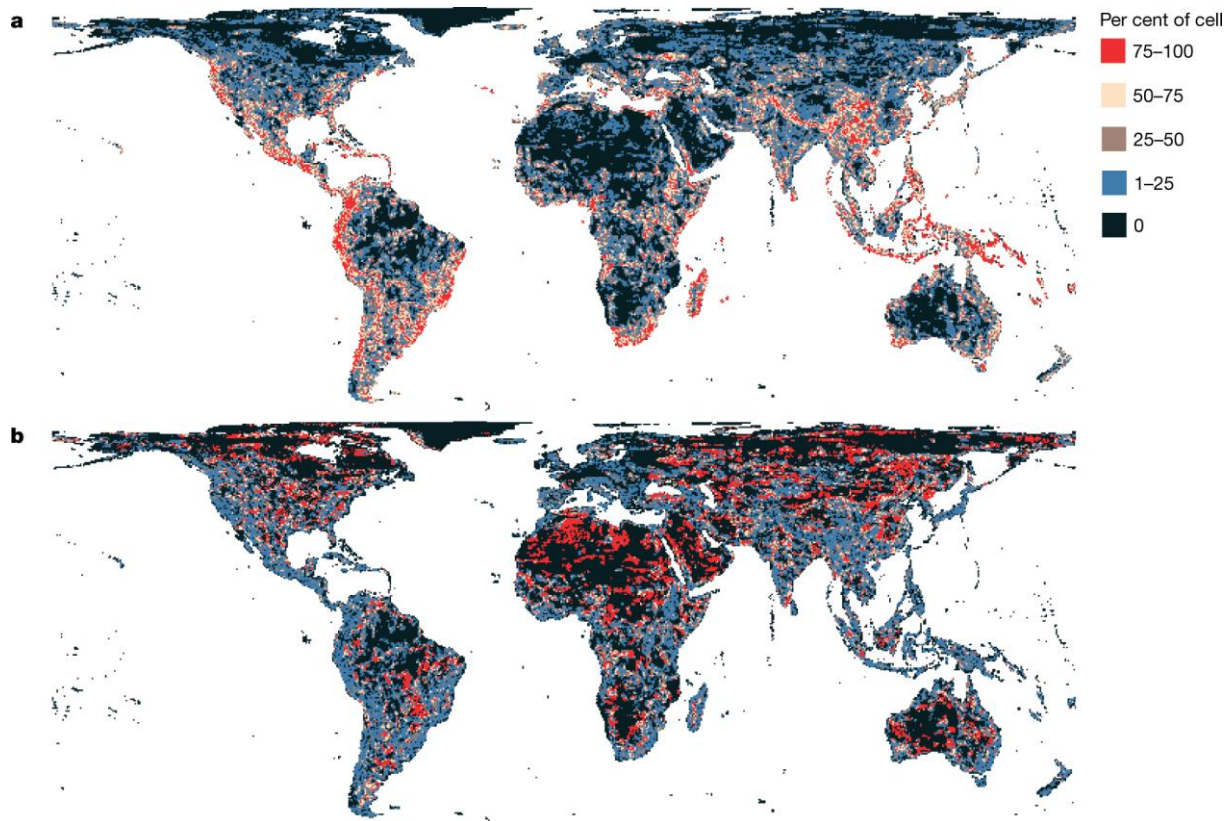
Fig. 2: Priority areas for covering species' niches. a, Spatial prioritization for expanding the global system of protected areas to represent the breadth of environmental conditions found across the geographic ranges of species (n = 19,937). b, Areas that would increase the representation of species' niches that are missing when species' niches are not considered during reserve selection. To aid visual interpretation, data show the proportion of 25-km2 planning units selected in 2,500-km2 grid cells.

Most previous prioritizations for the establishment of protected areas, although informative, have not accounted for the adaptive potential of species1. To understand how accounting for species' niches might alter conservation priorities, we created a second prioritization using the unpartitioned maps to exemplify conventional approaches. When combined with existing protected areas, this second prioritization encompassed 30.7% of the Earth's land (Extended Data Fig. 6)—further highlighting that the 17% target in Aichi Target 11 is insufficient for biodiversity representation. Despite covering only 3.2% less of the Earth's land than the niche-based prioritization, this prioritization did not adequately represent the niches of 7,798 (39.1%) species. Many of the 295,224 priority areas identified in the niche-based prioritization that are absent from this prioritization (shown in red in Fig. 2b) are located in extreme environments, such as the Sahara desert and the Boreal forests of Canada and Russia. These findings demonstrate that prioritizations need to explicitly account for species' niches and further show that the strategic placement of protected areas can yield substantial returns13.

Establishing protected areas to cover terrestrial Key Biodiversity Areas would result in 3,363 (16.9%) species with adequately represented niches. This would raise the average percentage of adequately represented climatic partitions per species from 28.2% to 39.4%, and the number of threatened species with adequately represented niches from 200 to 421—approximately 67% more effective than protecting random localities. The protected area coverage of Key Biodiversity Areas is currently used to monitor progress towards global targets (for example, Aichi Target 11 and Sustainable Development Goals 14 (https://sustainabledevelopment.un.org/sdg14) and 15

(https://sustainabledevelopment.un.org/sdg15)), and these findings further illustrate their importance[26].

Our results show that Article 8 of the Convention of Biological Diversity has been insufficiently implemented to conserve habitats that contribute to the adaptive potential of species. Because international policies currently lack targets for protecting evolutionary processes in wild populations[4] or explicit targets for protecting Key Biodiversity Areas that would help to conserve species' niches, one strategy to address this shortfall would be to set explicit targets under the next framework for biodiversity to be adopted through the convention. Since 2010, the targets set under the Strategic Plan for Biodiversity (https://www.cbd.int/sp/) have stimulated conservation efforts. However, many recently established protected areas are in places that are less important for biodiversity[11,13,26]. Therefore, targets created for the conservation of biodiversity processes must be both readily understood and carefully crafted to avoid negative outcomes (for example, by following 'specific, measurable, ambitious, realistic, and time-bound' (SMART) protocols)[27,28].

As a basis for developing targets for the conservation of areas to maintain species' niches, there are several important considerations. First, many important locations already may be effectively conserved through 'other effective area-based conservation measures' (Aichi Target 11), such as indigenous reserves and community-managed areas outside formal protected areas[29]. We were unable to assess this because comprehensive global-scale data are not yet available[30]. Second, different environments are important for different species[2]. We recognized this by subdividing the distributions of species into multiple climatic partitions; this step could be refined for narrower geographic and taxonomic scales and additional aspects of species' niches. Third, habitats that are not important for representing species' niches could be important for the long-term persistence of species for other reasons[2], as with climate refugia[1]. Fourth, genetic factors are also important[2,4]. Although techniques do not yet exist that can assess genetic diversity cheaply enough for large-scale deployment, evidence is emerging that environmental data can be an effective surrogate[3]. Because sites can be recognized as Key Biodiversity Areas if they support distinct genetic diversity for threatened or geographically restricted species[15], further work is needed to determine whether such sites can be identified using surrogates.

The Convention on Biological Diversity highlights the importance of conserving habitats that promote evolutionary processes. However, this has not been explicitly addressed in the targets to be met by 2020. Effectively conserving such habitats give species a greater chance of long-term persistence.

Methods

No statistical methods were used to predetermine sample size. The experiments were not randomized and investigators were not blinded to allocation during experiments and outcome assessment.

Data

We compiled a map delineating the protected areas of the world (Extended Data Fig. 2) by downloading the World Database on Protected Areas (WDPA)[14], and preparing it for analysis following best practices[31]; code is available at https://github.com/jeffreyhanson/global-protected-areas. First, we reprojected the database to an equal-area coordinate system (World Behrman; ESRI: 54017). Second, we excluded UNESCO (United Nations Educational, Scientific and Cultural Organization) biosphere reserves[32] and sites with an unknown or proposed designation status. Third, we extracted protected areas that were represented only by a point locality, reprojected them to an equidistant coordinate system (World Equidistant Cylindrical; ESRI: 54002), buffered them according to their reported area and merged them with the main dataset. Finally, we spatially dissolved overlapping areas and removed slivers. After cleaning the data using these procedures, we overlaid the protected areas onto a grid (5 × 5-km resolution) and identified which cells had more than half of their land inside protected areas (using 1:10 m Natural Earth data; https://www.naturalearthdata.com).

Although this meant that grid cells with less than 50% coverage by protected areas were treated as having zero coverage by protected areas, these grid cells contained only 7.3% of the total protected-area estate. Next, we overlaid the boundaries of terrestrial Key Biodiversity Areas[16] with the grid to identify areas that contain sites that are important for conserving biodiversity. Processing was completed using the R statistical computing environment (version 3.4.1)[33]. Spatial analyses were conducted using ArcMap (version 10.3.1), Python (version 2.7.8), and the sp[34] and raster[35] R packages.

We obtained extent of suitable habitat maps, also known as Area of Habitat maps[36], for most of the world's amphibian[8], avian[5,6] and terrestrial mammalian species[7] (excluding 773 species with no mapped suitable habitat). In brief, these maps were produced using the global range maps of each species (obtained from https://www.iucnredlist.org/). Next, for each species, areas were removed if they are outside of the elevational limits of that species or if they contain unsuitable land-cover or habitat types (on the basis of the IUCN Red List assessment for the species)[5,6,7,8]. As a consequence, these maps contain far fewer commission errors than the range maps that are typically used in assessments of global conservation[5,6,7,8]. Although smaller-scale assessments could account for variation in habitat suitability using continuous measures of suitability from environmental niche models[37], such data are not available globally for the taxa examined here. All maps were reprojected to an equal-area coordinate system (World Behrman; ESRI: 54017) and standardized to the same spatial grid by calculating the proportion of suitable habitat in each pixel (5×5-km resolution). Although we were unable to accommodate migratory mammals in our dataset (owing to insufficient data on their migration patterns), we included 1,689 migratory bird species in our dataset by processing and analysing each of their breeding, non-breeding and passage distributions separately[31].

Populations in different environmental settings may exhibit different local adaptations[38], and such local adaptations may have a role in the species' adaptation to climate change and long-term persistence[1,39]. To assess the protection of populations in different environmental settings, we subdivided the species' habitat maps into climatic partitions using global climatic data (19 layers at a resolution of 2.5′)[12,40]. This climatic dataset was produced using remote sensing, and it therefore provides accurate information for remote areas where meteorological stations are absent[12]. Specifically, we used this approach for the following reasons. First, although techniques are available for assessing and prioritizing the establishment of protected area with consideration for intraspecific variation that do not require partitioning species' geographic distributions[41], these techniques currently do not scale to conservation planning scenarios that involve thousands of species. Second, although some approaches involve conserving geophysical features instead of species' distributions[42], these approaches need to be complemented with methods that explicitly consider existing patterns of biodiversity to enhance the long-term persistence of biodiversity[43]. Third, available genetic and population data are not spatially comprehensive enough across the entire geographic extent of most vertebrate taxa at scales that are relevant for informing the establishment of protected areas[44]. Fourth, even if such data were available, future research is needed to develop the tools for supporting decision-making that can directly operationalize evolutionary and population models to guide land-use policy. Fifth, environmental data can in some circumstances serve as a surrogate—albeit an imperfect one—for adaptive genetic variation[3].

The species' distributions were subdivided into distinct climatic partitions using the following steps. We first aggregated and resampled the climatic maps to match the spatial extent and resolution of the species' habitat maps. For each species, we then overlaid the climatic layers with their habitat map, masked the climatic data to places that contained suitable habitat and subjected the masked climatic data to a principal components analysis. On average, the first two principal components explained 99.76% ± 0.41 s.d. of the climatic variation associated with areas covered by the habitat map of each species (Supplementary Table 1). Next, we used the scores from the first two principal components to perform a k-means cluster analysis to subdivide the habitat map of each species into ten distinct

climatic partitions. Because results might vary depending on the number of clusters that is used to partition species' niches, we conducted a sensitivity analysis in which we subdivided species' niches into varying numbers of clusters and calculated how well the niches of these species are represented. This analysis showed that our results are robust to variation in the number of clusters used to subdivide species' niches: in all cases, the vast majority of species have poorly represented niches (Extended Data Fig. 1).

We used k-means cluster analyses to create climatic partitions for each species, because this process yields partitions that are suitable for representing the environmental niches of species in spatial prioritizations. Specifically, this analysis would subdivide the species' niches using roughly equal-sized spherical classifications on the basis of the main gradients of environmental conditions. As a consequence, a prioritization must spread out conservation effort across the whole species' niche when a suitable number of clusters is used to create the environmental partitions. To further justify this methodology, we note that clustering methods that use nonspherical clusters[45] are not well-suited to our particular task because a prioritization based on these clusters will not necessarily spread out conservation effort as evenly across the species' niches. Furthermore, clustering methods that aim to identify an optimal number of clusters on the basis of clear divisions in multidimensional data[46] would also not be well-suited to our particular task. This is because we aim to represent environmental conditions throughout each and every species' niche—even if the niche of a particular species forms a singular cluster in multidimensional environmental space, it is still important to represent environmental conditions that comprise different parts of that singular cluster.

Analysis

We created representation targets for each species on the basis of the unpartitioned and the partitioned habitat maps. Targets for the unpartitioned habitat maps were set following standard practices for global gap analyses and prioritizations[11,31,47], except that instead of using the range sizes of species to set the targets, here we used the total extent of suitable habitat for each species. Although the habitat maps provide a more accurate estimate of the areas available for species' persistence[6,48], it should be noted that (i) because the habitat maps delineate fewer areas for representation than range maps, applying the same methods to calculate the targets as in previous studies[49] is likely to result in higher proportional representation targets; (ii) these maps probably over-estimate the available habitats for species in areas that have recently experienced habitat destruction (as they were produced nearly a decade ago); and (iii) because areas that historically contained suitable habitat for a given species and that have since become unsuitable were excluded from this analysis (for example, areas converted to urban land use), the representation of species' climate niches may be worse than reported here[50].

In brief, species with less than 1,000 km2 of suitable habitat were assigned a 100% target for their unpartitioned map (1,802 amphibians, 893 avian and 645 mammalian species), species with more than 250,000 km2 of suitable habitat were assigned a 10% target for their unpartitioned map (712 amphibians, 4,518 avian and 1,868 mammalian species) and species with an intermediate amount of suitable habitat were assigned a target by log-linearly interpolating values between the previous two thresholds (2,683 amphibians, 5,190 avian and 2,557 mammalian species; migratory bird species were assigned targets for each seasonal distribution separately). Additionally, to prevent species with very large suitable habitats from requiring excessively large amounts of area to be protected[11], the targets for species' distributions larger than 10,000,000 km2 were capped at 1,000,000 km2. This cap affected only 206 (1%) species, and sensitivity analyses showed that it had little effect on our results (Extended Data Fig. 1).

After calculating distribution-level percentage targets for each species, we then calculated partition-level percentage targets for each species' climatic partition. For each species, each of its climatic partitions was assigned the same percentage target as the species' distribution-level target. These partition-level percentage targets were then expressed as area-based targets using the total amount of

habitat available for the species in a given partition. Thus, the total amount of habitat required for the geographic distribution of each species did not differ between the targets set for the partitioned and unpartitioned maps, although setting targets to capture a representative sample of the niche of each species would probably increase the size of the solution (because the prioritization is forced to spread out across the species' geographic distributions)[51]. Furthermore, although species with very small suitable habitats are likely to have lower climatic and genetic variation among their partitions compared to species with larger extents of suitable habitat, these species also require a large proportion of their habitat to be under protection owing to their elevated extinction risk; for example, species with less than 1,000 km2 of suitable habitat require 100% of their habitat to be protected, and so representing a large range of environmental conditions will probably exert little influence on prioritizations for these species. One limitation of this approach is that all climatic partitions for a given species are assigned equal targets, although some climatic partitions may require greater protection than others (for example, refugia)[1].

We generated prioritizations using the target-based minimum set formulation of the reserve selection problem (similar to the Marxan decision support tool)[52]. Because this formulation is constrained by biodiversity targets, it does not make trade-offs between different species. Specifically, the prioritizations were generated using the 5×5-km planning units and land area as a measure of acquisition cost. First, we generated a niche-based prioritization using the partitioned habitat maps of all the species, and their corresponding targets, to identify priority areas for conservation. Second, we generated a distribution-level prioritization using the unpartitioned habitat maps and their corresponding targets to understand how failing to account for species' niches can alter priorities. Although these two prioritizations resulted in an increased number of smaller (≤ 25 km2) reserves when added to the existing system of protected areas (Extended Data Fig. 7), such reserves only comprised 1.6% and 1.11% (for niche-based and distribution-level prioritizations, respectively) of the resulting system of protected areas. Both prioritizations were solved to within 1% of optimality using Gurobi (version 8.1.0)[53] and the prioritizr R package[54]. Following standard practice, Antarctica was omitted from land coverage statistics[11].

We calculated how well each species is represented by the (i) existing global system of protected areas; (ii) this existing system plus planning units that have over half their land contained inside Key Biodiversity Areas; (iii) this existing system plus the niche-based prioritization based on the partitioned habitat maps; and (iv) this existing system plus the distribution-level prioritization based on the unpartitioned habitat maps. First, we assessed which species are adequately represented under each of the four maps using the species' partitioned habitat maps and their corresponding targets. Second, we assessed which species are adequately represented under each of the four maps according to the species' unpartitioned habitat maps and their corresponding targets. These assessments are provided in the Supplementary Information (Supplementary Table 2) and Extended Data Fig. 8.

We evaluated the effectiveness of expanding the global system of protected areas to include Key Biodiversity Areas, compared with adding random terrestrial areas (Extended Data Fig. 9). To achieve this, we calculated how many 5×5-km planning units outside of protected areas currently contain terrestrial Key Biodiversity Areas, and then generated 1,000 sets of randomly selected planning units that each contained the same number of planning units as that covered by Key Biodiversity Areas. We then assessed the effectiveness of protecting Key Biodiversity Areas by comparing the number of additional species' niches that are adequately represented when adding terrestrial Key Biodiversity Areas to the protected area system with the average number of additional species' niches that are adequately represented when adding the randomly selected grid cells.

Reporting summary

Further information on research design is available in the Nature Research Reporting Summary linked to this paper.

Data availability

The climatic data12,40, WDPA (http://www.protectedplanet.net)14, and World Database of Key Biodiversity Areas (http://keybiodiversityareas.org)16 are freely available online. The habitat maps can be obtained from their creators5,6,7,8. All other data are available in an online digital repository, https://doi.org/10.5281/zenodo.1035485. Source Data for Figs. 1, 2 and Extended Data Figs. 1, 2, 6–9 are provided with the paper.

Code availability

All code is available in an online digital repository at https://doi.org/10.5281/zenodo.1035485.

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