Key Biodiversity Areas and Important Plant Areas can help build ecologically representative Protected and Conserved Area networks to meet 30-by-30

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Abstract

Expanding the global network of Protected and Conserved Areas (PCAs) to cover 30% of the planet by 2030 (30-by-30) is mandated in the Global Biodiversity Framework. However, if PCA expansion is undertaken hastily, it risks inadvertently overlooking important species or ecosystems and entrenching existing spatial and taxonomic biases. We investigate, across 28 countries, whether sites identified as important for biodiversity, specifically Key Biodiversity Areas (KBAs) and Important Plant Areas (IPAs), capture environments and species outside the current PCA network, and thus the extent to which they could help build an ecologically representative pathway towards 30-by-30. We find that KBAs, IPAs and PCAs cover significantly different environments in 23 of 28 countries. Inclusion of KBAs and IPAs in PCA networks could increase mean national environmental representation from 62.4 to 81.4%. Per unit area, KBAs and IPAs were more effective than PCAs at encompassing threatened and endemic species. While PCAs covered the highest mean proportion of species' ranges (23.4%), KBAs and IPAs together captured the ranges of 919 additional species, 575 of which are threatened and 539 nationally endemic. Encouragingly, comparing outcomes from 2010-2024, we find that cells inside KBAs or IPAs were 4.4 times more likely to become PCAs than cells outside. This suggests that programmes to identify important areas for biodiversity are already influencing PCA placement with potentially improved outcomes for representative biodiversity conservation.

Introduction

Protected areas are the cornerstone of spatial conservation planning (Lewis et al., 2019). Increasingly, these are augmented by other effective area-based conservation measures (OECMs), which lie outside of protected areas but are managed and governed for long-term *in situ* biodiversity conservation, sometimes alongside other key objectives such as water management (Dudley et al., 2018; Jonas, et al., 2024a). The importance of protected areas and OECMs, collectively known as Protected and Conserved Areas (PCAs), is illustrated by Target 3 of the Kunming-Montreal Global Biodiversity Framework (GBF), which seeks to conserve 30% of Earth for nature by 2030, also referred to as 30-by-30 (CBD, 2022; Appendix S1). There are now roughly 287,000 protected areas and 6,300 OECMs in 244 countries and territories, covering 17.6% of terrestrial land and inland waters (UNEP-WCMC & IUCN, 2024b). Achieving 30-by-30 will therefore require the current PCA network to expand at a pace far exceeding that of recent decades (UNEP-WCMC & IUCN, 2024a). Moreover, to meet Target 3, this expansion must deliver a network that is ecologically representative and well-connected (CBD, 2022). Using areas already identified as important for biodiversity to guide the expansion of PCAs may help to accelerate this process, while ensuring effective representation of diverse environments and taxa.

Areas of particular importance for biodiversity, hereafter termed “important areas”, include a range of internationally recognised sites that either support biological processes, have high irreplaceability or ecological integrity, or are globally important for the persistence of threatened and endemic species or ecosystems (Darbyshire et al., 2017; Eken et al., 2004). However, they do not provide formal protection themselves. These include Important Bird and Biodiversity Areas (IBAs), Important Plant Areas (IPAs), Alliance for Zero Extinction sites, B-ranked sites, Important Fungus Areas and Prime Butterfly Areas, many of which sit under the umbrella of Key Biodiversity Areas (KBAs) (Plumptre et al., 2024). The Global Standard for the Identification of KBAs (KBA Standard) builds on long-term lessons from other important areas, particularly IBAs, setting out 11 criteria under five broad categories that underpin KBA identification for species and ecosystems (IUCN, 2016). This approach aims to support the evidence-based identification of areas of particular importance for biodiversity to guide monitoring and conservation efforts and halt nature loss.

There are more than 16,500 KBAs, 11,500 of which are terrestrial and freshwater, including legacy KBAs that pre-date the KBA Standard and are yet to be reassessed under its criteria (BirdLife International, 2024a). KBAs are intended to be taxonomically broad, although approximately 57% of the qualifying elements of KBAs are vertebrates. Plants may be underrepresented in the global KBA network, however there are now more distinct trigger species of plants (6,814) than birds (6,059), although less than 13% of KBAs are actually triggered by plant species (BirdLife International, 2024b), and there is an expectation of more plant trigger species because there are at least 30 times more plant species than birds. KBAs have only been assessed comprehensively across multiple taxonomic groups, under the KBA Standard, in 11 countries to date (Plumptre et al., in revision), and there is a need to do so in all countries. Furthermore, spatial and taxonomic biases in sampling efforts have led to data gaps for some species and regions (Hughes et al., 2021), potentially undermining ecological representation in important areas, the identification of which relies on available data.

The concurrent and complementary IPA programme, developed in 2002 by Plantlife International and extended to tropical regions through the Royal Botanic Gardens, Kew's, Tropical Important Plant Area (TIPA) programme, uses criteria tailored to plants, focusing on threatened species, botanical richness and threatened habitats (Anderson, 2002; Darbyshire et al., 2017). IPAs may improve the representation of plants in conservation planning by encompassing sites rich in threatened and endemic/range-restricted plant species, particularly in countries with limited overlaps between IPAs and protected areas (Richards et al., 2023). Indeed, at COP16, voluntary complimentary actions relating to Target 3 of the GBF were adopted, focusing on identifying, protecting, managing and monitoring important areas for plant diversity (CBD, 2024). Under revisions to the IPA criteria, IPAs may additionally be triggered through the presence of concentrations of socioeconomically and culturally important plant species (Darbyshire et al., 2017). Effectively managed IPAs can thus synergise sustainable development and biodiversity conservation goals (Kor & Diazgranados, 2023). In total, 76 countries have engaged with IPAs (Kor et al., 2025), and there are approximately 2,500 sites published in the Plantlife IPA database and on the Tropical Important Plant Areas portal.

The placement and designation of protected areas is influenced by social, cultural and economic drivers (Joppa & Pfaff, 2009; Loucks et al., 2008). For example, they may be biased towards sites with low opportunity costs, such as higher elevation land with minimal agricultural value, and thus they do not necessarily target the most important areas for biodiversity (Joppa & Pfaff, 2009; Venter et al., 2018; Visconti et al., 2019). By comparison, important areas are identified using evidence-based criteria specifically designed to target such sites (Eken et al., 2004; Smith et al., 2019; Plumptre et al. 2024). While important areas may contribute to the delineation of PCAs, they are not always priorities for conservation and PCA establishment. This is either because of competing land-use demands, for example some land areas are greater priorities for crop and livestock production or commercial development

(Hoffmann, 2022), or because planners with limited resources may prioritise other conservation features that KBAs do not inherently target, such as sites that are important for local ecosystem services (Smith et al., 2019).

Nonetheless, the coverage of KBAs by protected areas and OECMs is an official indicator used for monitoring the progress of GBF Target 3 and Sustainable Development Goals 14 and 15 (CBD, 2022; United Nations, 2015). Currently, the average PCA coverage of terrestrial and freshwater KBAs is 44% (BirdLife International, 2024b), and previous work has shown the importance of OECMs in overlapping with unprotected KBAs (Donald et al., 2019). Meeting 30-by-30 is unlikely to be achievable through protected area expansion alone (Butchart et al., 2015), but OECMs can contribute meaningfully to achieving the GBF targets (Jonas et al., 2024b), and there is potential for important areas to also feed into OECM identification to accelerate this process.

The Convention on Biological Diversity defines ecological representation in PCAs as the incorporation of “adequate samples of the full range of existing ecosystems, ecological processes and regions” (CBD, 2022). Here, to measure and compare ecological representation across countries, we use environmental space, comprised of bioclimatic, topographic and soil variables, and species ranges, consisting of mammals, birds, reptiles, amphibians and plants, as proxies for ecosystems, ecological processes and regions. We thus consider more ecologically representative conservation networks to be those that encompass a greater diversity of a given country’s environmental variation and species from different taxonomic groups. This framing enables comparisons of ecological representation between countries and their PCAs, KBAs and IPAs. Building ecologically representative PCA networks is critical for ensuring that different taxonomic groups and biogeographic conditions are effectively and equitably protected and conserved (Butchart et al., 2015; Mammides et al., 2021; UNEP-WCMC & IUCN, 2024a). If important areas are to guide the expansion of protected areas and OECMs, it is essential that these networks are also ecologically representative or increase the representation of target ecosystems or groups of underrepresented taxa, or we risk perpetuating existing biases within PCA networks.

Across 28 countries, we investigated and compared how well PCAs and important areas represent environmental space – a proxy for a given country’s total environmental variation – and species’ ranges (Figure 1). First, we evaluate changes in the environmental representation of PCAs through time and quantify additional environmental coverage by important areas. Second, we test whether PCAs, KBAs and IPAs occupy significantly different environmental space and evaluate the variables characterising their differentiation. Third, we examine whether taxonomic representation differs between PCAs and important areas and test whether important areas capture additional threatened and endemic species outside of PCAs. Finally, we evaluate evidence for important areas catalysing PCA designations and thus whether they may provide an evidence-based guide for informing the expansion of PCAs to meet the GBF targets.

Methods

Protected and Conserved Areas and areas of particular importance for biodiversity

We identified 28 countries with PCA networks and programmes to identify important areas including KBAs, IBAs and IPAs (Appendices S2 & S3), though we recognise that site identification is largely an ongoing process with no defined completion point. We collated data for PCAs from the World Databases on Protected Areas (WDPA) and OECMs (WDOECM) (UNEP-WCMC & IUCN, 2024b), KBAs and IBAs from the World Database of Key Biodiversity Areas (WDKBA) (BirdLife International, 2024a, 2024b) and IPAs from Plantlife International (2023), the Tropical Important Plant Areas Explorer portal (RBG Kew, 2024) and Kor and Diazgranados (2023). India and China do not have comprehensive, openly available protected area data on the WDPA, so we supplemented their PCA data with protected area polygons from OpenStreetMap (Appendix S4). All analyses were undertaken in R (R Core Team, 2023), using the packages sf (Pebesma, 2018), raster (Hijmans, 2023a), adehabitatHR (Calenge, 2023), vegan (Oksanen et al., 2022) and terra (Hijmans, 2023b). Data visualisation was performed in the R package ggplot2 (Wickham, 2016).

We note that many KBAs are based on IBAs, which have been identified over the past four decades. Across our studied countries, around 93% of the total area within IBAs was also within the boundaries of KBAs. We thus exclude IBAs from the main analyses presented here, but include them in our environmental representation analysis in the Supporting Information for reference.

Expansion of environmental space through time

We collated 31 environmental variables for climate (Fick & Hijmans, 2017), topography (EROS, 2017; Jarvis et al., 2008) and soil (Poggio et al., 2021) (Appendix S5). We calculated slope, roughness, aspect, topographic position index (TPI) and terrain ruggedness index (TRI) using the terrain function in the R package terra (Hijmans, 2023b). Variables were reprojected to a Mollweide equal-area projection with a spatial resolution of 30 arc-seconds (~1 km at the equator). To assess multicollinearity between predictors, we sampled 50,000 points stratified across all 28 countries' combined geographic space, extracted the environmental data and measured correlation between variables using Spearman's rank correlation coefficient. We removed highly correlated ($r > 0.7$) variables and any remaining variables with a moderate to high variance inflation factor (> 5) to mitigate multicollinearity, resulting in 13 retained variables (Appendix S5). Then, for each country, we extracted the retained environmental data from a geographically stratified sample of points and conducted principal component analysis to characterise its background environmental space. Background environmental space here refers to the multivariate representation of the overall variation in environmental conditions across a given country. This approach enables direct comparisons of environmental representation for a given area through space or time (Appendix S6). We scaled the number of sampled points in each country by the respective country's geographic area, with a minimum threshold of 1,000 points to ensure the smallest countries had sufficiently large samples for analyses and a maximum threshold of 50,000 points to avoid excessive computational load in the largest countries. The extracted environmental data were z-transformed prior to our analyses, standardising to a mean of 0 and standard deviation of 1.

To test whether the expansion of PCAs in geographic space through time was associated with increasing coverage of environmental space, we characterised each point that fell within a PCA by the time period in which that PCA was designated (pre-1960, pre-1970, pre-1980, pre-1990, pre-2000, pre-2010, pre-2020 or pre-2024). The year of designation, establishment, inscription or adoption was missing from 6.1% of our PCAs and the date that each KBA polygon was added to the database was missing from 4.5% of KBAs. Therefore, we randomly allocated these PCAs/KBAs a year from another PCA/KBA in the same country following Butchart et al. (2015).

First, we produced minimum convex polygons (MCPs) for each time period from the first and second principal components, fitting 99% MCPs to avoid artificially inflating temporal expansions based on outlier points (Appendix S7). We plotted polygons sequentially to visualise the expansion of PCA networks in environmental space through time. Second, we tested the extent to which important areas, since their inception, encompass environmental space outside of, or overlapping with, PCA networks. To understand the relationship between coverage of geographic space and environmental space, we used linear regression to estimate the slope of this association separately for PCAs, KBAs and IPAs, using the natural logarithm of environmental and geographic coverage.

Representation of environmental space

To test whether PCAs and important areas occupy different parts of environmental space within each country, we again applied principal component analysis on the same stratified sample of background points and determined which points fell within the country's PCAs, KBAs and IPAs. We fitted 99% MCPs for PCAs, KBAs and IPAs to prevent artificially inflating differences based on outlier points, and 100% MCPs for each country's background environmental sample to ensure that the entire spectrum of its environmental conditions was captured. The loadings of and variance explained by each of the principal components is displayed in Appendices S8 & S9.

We calculated the proportion of each country's background environmental space covered by PCAs, KBAs and IPAs. To determine whether important areas provide additional environmental coverage beyond PCAs, we quantified the proportion of each country's environmental space that was covered by KBAs and IPAs but not PCAs. To test for statistically significant differences in the coverage of environmental space across PCAs, KBAs and IPAs, we conducted permutational multivariate analysis of variance (PERMANOVA) and post-hoc pairwise adonis tests with Bonferroni correction. We first performed PERMANOVA nationally to examine evidence for differentiation within countries, using a 10-km spatially thinned sample of points to avoid pseudoreplication, and 999 permutations (Appendix S10). We also performed PERMANOVA across all countries together to evaluate overall environmental differentiation between PCAs, KBAs and IPAs, using a sub-sample of 10,000 points. We preserved the original data structure in this sub-sample by maintaining both the proportion of points between countries and the distribution of points per area (PCA, KBA and IPA) within each country.

To determine which variables were associated with environmental differentiation between PCAs, KBAs and IPAs, we plotted the density distribution of each variable for each area and the background sample across all countries together, using the raw environmental extractions from all stratified points. Then, using a sub-sample of 10,000 points, as above, we conducted Kruskal-Wallis tests and post-hoc Dunn's tests with Bonferroni correction on each variable to identify significant differences in the distribution of environmental variables across PCAs, KBAs and IPAs. We also compared the median raw values of each variable across areas using the entire sample of environmental data.

Representation of species' ranges

We collated range data from the IUCN Red List for 2,527 threatened (Critically Endangered, Endangered and Vulnerable) and 12,480 not threatened (Near Threatened and Least Concern) plant, bird, mammal, amphibian and reptile species (the latter two are hereafter grouped as herptiles) that had ranges overlapping at least one of the studied countries (IUCN, 2024). Following the KBA guidelines (KBA Standards and Appeals Committee of IUCN SSC and IUCN WCPA, 2022), we filtered the dataset to retain only the range polygons coded as extant or probably extant and native, reintroduced or assisted colonisation, leaving 2,473 threatened and 12,413 not threatened species. As the IUCN Red List does not yet contain comprehensive spatial polygon data for plant species – 86% of the threatened and 87% of the not threatened red-listed plant species in our studied countries did not have range maps – we generated ranges for an additional 2,394 threatened and 10,102 not threatened plant species that had Red List occurrence records using these point data and the subLocRapoport function from the rCAT package (Moat et al., 2020). This function connects a species' known presences via the least possible distance through a Euclidean minimum spanning tree (eMST) and calculates the mean propinquity of the given set of points (Rapoport, 1982). We used automated barrier and buffer distances for each species calculation of two times the mean branch length of the eMST and the mean branch length of the eMST, respectively. For species with two or fewer Red List occurrence records, we instead polygonised each point by adding a 10 km buffer. After filtering the species ranges and generating range maps for the unmapped plant species, our final dataset contained 4,867 threatened and 22,515 not threatened species.

We rasterised the species ranges and country, PCA, KBA and IPA polygons to a spatial resolution of 5 km with a Mollweide equal-area projection. To evaluate the representation of different taxonomic groups in PCAs and important areas, we calculated pairwise overlaps between each species' range and each country's PCAs, KBAs and IPAs and quantified the proportion of each species' national range within each of those areas. Each species was characterised by its IUCN Red List category, threat status (threatened or not threatened) and endemism status (we considered a species to be endemic if every cell in its global range fell within the given country). In total, 4,416 threatened and 21,540 not threatened species had ranges overlapping at least one of the studied countries (Appendix S11).

We assessed taxonomic representation in three ways. First, we plotted the mean and standard error of overlap percentages between species from each taxonomic group, threat/endemism status and conservation network (i.e. PCAs, KBAs and IPAs). We used a chi-squared test of independence to determine whether the number of threatened species with ranges overlapping PCAs, KBAs and IPAs was associated with the taxonomic group. Second, to account for differences in the geographic extent of PCAs, KBAs and IPAs, we divided each species' overlap percentage by the number of cells covered by the country's given conservation network and plotted these weighted values. Finally, we quantified and characterised, by taxonomic group, IUCN Red List category and endemism status, the number of additional species with ranges overlapping KBAs or IPAs that did not intersect PCAs in any of the studied countries.

Impact of important areas on Protected and Conserved Area designations

We tested whether cells identified as important areas before 2010 were more likely to subsequently be designated as PCAs than cells outside of important areas. For each cell, we determined whether it contained any part of the respective country's PCAs and KBAs or IPAs in 2010 and 2024 and assigned a binary value. We then excluded any cells that were inside PCAs prior to 2010. We performed chi-squared tests for each country and across all countries together to test for statistically significant associations between unprotected cells in 2010 and corresponding cells in 2024 and thus whether cells within a KBA or IPA were more likely than expected to become a PCA over time. Specifically, we compared all unprotected cells in 2010 that were "inside an important area" and "outside an important area" with the same cells in 2024 that were either "protected/conserved" or "still unprotected/unconserved". We used odds ratio and Cramer's V to evaluate the chi-squared outputs.

Results

Temporal expansion of Protected and Conserved Areas and important areas in geographic and environmental space

Between 1960 and 2024, mean coverage of environmental space by PCAs (excluding India and China), averaged across the studied countries, rose from 10.2% to 62.1% (Appendices S12 & S13), whereas mean coverage of geographic space by PCAs only reached 16.6%. The coverage of environmental space by PCAs, KBAs and IPAs was significantly positively associated with the coverage of geographic space in all three networks (PCA: $\beta = 0.20$, $p < 0.01$; KBA: $\beta = 0.15$, $p < 0.01$; IPA: $\beta = 0.25$, $p < 0.05$) (Figure 2A). Coverage of geographic space explained approximately 56.0% of the variance (adjusted R^2) in environmental coverage for PAs, 26.5% for KBAs and 34.8% for IPAs. Area type (PCA, KBA or IPA) was not a significant predictor of environmental coverage, suggesting no meaningful difference in trends.

Across the studied countries, KBAs and IPAs contributed significantly to increasing environmental representation through time (Figure 3; Appendix S14). Since their inception, KBAs and IPAs covered, on average, 19.7% of overall environmental space outside of PCAs by 2010, 21.4% by 2020 and 20.1% by 2024. Environmental space covered by both PCAs and important areas together totalled 45.0% in 2010, 56.9% in 2020 and 58.4% in 2024. Several countries where PCA networks were not increasingly environmentally representative through time, such as Syrian Arab Republic and Türkiye, had particularly large contributions by KBAs and IPAs to additional environmental representation.

Representation of environmental space

On average, KBAs covered the largest proportion of total environmental space (mean = 71.6%, standard deviation = ± 12.7%), followed by PCAs (62.4 ± 20.1%) and IPAs (56.6 ± 23.9%) (Table 1; Figure 4; Appendix S15). Environmental coverage by all three networks combined averaged 81.5% (± 9.4%), ranging from 54.7% in China to 97.6% in the British Virgin Islands. Additional coverage by important areas, outside the environmental space occupied by PCAs, averaged 14.7% (± 16.0%) for KBAs and 14.4% (± 17.2%) for IPAs. Analysis across all studied countries found that environmental coverage differed significantly across PCAs, KBAs and IPAs ($F = 61.7$, $p = 0.001$) (Appendix S16). At the national level, environmental coverage differed significantly across PCAs, KBAs and IPAs in 23 (82.1% of) countries. Post-hoc comparisons revealed significant differences between PCAs and KBAs in 16 countries, PCAs and IPAs in 17 countries and KBAs and IPAs in 18 countries.

Of the 13 retained environmental variables, 11 (not aspect or TPI) showed significant differences in their distribution across PCAs, KBAs and IPAs (Figure 2B, Appendix S17). KBAs were significantly different from PCAs for 10 variables, IPAs from PCAs for 11 variables and IPAs from KBAs for 8 variables. Comparisons of median values and pairwise assessments of distributions of significantly different environmental variables showed that IPAs represented sites with a greater nitrogen and clay content, elevation, slope, precipitation seasonality (Bio15) and precipitation of the coldest quarter (Bio19), and a lower sand content, mean diurnal range in temperature (Bio2), isothermality (Bio3) and mean temperature of the wettest (Bio8) and driest (Bio9) quarters, compared to PCAs (Appendix S17). Compared to PCAs, KBAs followed the same pattern as IPAs for all environmental variables except isothermality (Bio3), which, unlike in the case of IPAs, was higher in KBAs relative to PCAs, although this difference was not statistically significant. Generally, the magnitude of difference between variables was greater between IPAs and PCAs than between KBAs and PCAs.

Representation of species' ranges

Across all taxa and IUCN Red List categories, PCAs covered an average of 23.4% of species' ranges, KBAs 20.9% and IPAs 8.7%. PCAs, KBAs and IPAs covered, on average, a higher proportion of threatened or endemic species' ranges than not threatened species ranges, for nearly all taxonomic groups (Figure 5A). The only exception was for birds and IPAs, where not threatened species were narrowly better represented on average. KBAs, despite covering a smaller average proportion of countries' geographic space than PCAs, captured a higher mean proportion of threatened herptiles (+8.4%), mammals (+0.3%) and plants (+1.7%), and endemic herptiles (+6.7%) mammals (+7.9%) and plants (+0.3%) than PCAs. Threatened (-0.8%) and endemic birds (-0.9%) were, surprisingly, marginally worse represented in KBAs compared to PCAs. IPAs, as the smallest network in geographic space, understandably incorporated the lowest proportion of species' ranges for all taxa and combinations of threat and endemic status. However, threatened plant species (mean = 13.7%, standard deviation = ± 0.4%) were the best represented threatened taxonomic group in IPAs (birds = 8.3 ± 0.6%; herptiles = 11.8 ± 0.8%; mammals = 11.4 ± 0.8%). By contrast, PCAs were less representative of threatened plant species (24.2 ± 0.5%) than threatened birds (24.8 ± 0.9%), herptiles (27.4 ± 0.9%) and mammals (28.3 ± 1.1%). We found a statistically significant association between the distribution of species from each taxonomic group across each conservation network ($X^2 = 81.2$, $p < 0.01$) (Appendix S18).

When accounting for differences in the geographic size of each area, IPAs were the most effective at capturing threatened groups of species (Figure 5B). This was especially the case for threatened plant species, which were better represented per unit area in IPAs than PCAs or KBAs (IPA = 0.055 ± 0.005% per 25 km^2 cell; PCA = 0.039 ± 0.005%; KBA = 0.048 ± 0.006%). IPAs were also the most effective network at capturing endemic plant species, per unit area (IPAs = 0.027 ± 0.003% per cell; PCAs = 0.016 ± 0.003%; KBAs = 0.021 ± 0.003%).

Across the studied countries, PCAs incorporated the ranges of 24,574 distinct species (21,009 not threatened; 3,565 threatened), KBAs 25,021 (21,098 not threatened; 3,923 threatened), and IPAs 18,223 (16,011 not threatened; 2,212 threatened). Together, the three networks overlapped with 25,493 species, 3.7% more than PCAs alone (Table 2). KBAs and IPAs together captured the ranges of 919 additional species that do not overlap with PCAs, 575 of which are threatened and 539 nationally endemic (Appendix S19). Of those additional species, 404 were exclusively found in KBAs (238 threatened; 246 endemic) and 107 exclusively in IPAs (68 threatened; 69 endemic). KBAs and IPAs together were particularly effective at capturing the ranges of additional plant and herptile species, overlapping with 374 and 158 threatened and 342 and 165 endemic species, respectively.

Impact of important areas on Protected and Conserved Area designations

From 2010 to 2024, cells within KBAs or IPAs were significantly more likely to become PCAs compared to cells outside of important areas ($X^2 = 6073.24$, $p < 0.01$) (Appendices S20 & S21). The odds of cells inside KBAs or IPAs becoming a PCA were approximately 4.4 times higher than the odds of cells outside of KBAs or IPAs becoming a PCA (95% CI: 4.23–4.59; p

< 0.001). However, the strength of association was quite weak, with a low-moderate effect size (V = 0.12), because overall only 4.62% of cells became PCAs in the 14-year survey period. Chi-squared tests for each of the studied countries (excluding three that did not have at least one positive integer in each part of the contingency table) revealed statistically significant associations for 16 countries (Appendix S21). Across these countries, the mean Cramer's V was 0.18 (± 0.20), with the strongest association observed in Croatia (V = 0.68) and the weakest in Tunisia (V < 0.01).

Discussion

Important areas increase environmental representation of PCA networks

To meet ambitious area-based conservation targets agreed in the Kunming-Montreal Global Biodiversity Framework (CBD, 2022), countries must decide how and where to expand their PCA networks. Moreover, this expansion should seek to increase the representation of diverse ecosystems and species. Our analysis tests the extent to which "important area" programmes can guide and accelerate this process. Compared to PCAs, we find that KBAs and IPAs encompass significantly different environmental space in 82% of studied countries with established PCA, KBA and IPA networks. If combined with PCAs, KBAs and IPAs could increase the environmental representation of countries' existing PCA networks by 14.7% and 14.4%, respectively (Table 1). Patterns of differentiation, and hence the additionality provided by important areas, appear strongest in arid countries including Algeria, Libya and Syrian Arab Republic. Whereas for Croatia, Nepal and the UK, the three networks are largely concordant, and, through time, important areas have largely covered parts of environmental spaces that are already represented by PCAs.

Our analysis identified that KBAs and especially IPAs are typically wetter and colder than PCAs (Figure 2B), potentially reflecting the distribution of species that meet the criteria of the KBA Standard or IPA programme. That IPAs were generally associated with higher elevation sites, compared to PCAs, may reflect the fact that IPAs can be triggered by range-restricted plant species (Darbyshire et al., 2017), and endemic plant species richness is often positively correlated with elevation (Trigas et al., 2013). This result is nonetheless surprising, given that protected areas have been previously criticised for being biased towards higher elevation sites (Joppa & Pfaff, 2009). Our findings conversely suggest that some higher elevation sites, where threatened, endemic and/or range-restricted species occur, are still in need of protection.

Interestingly, we find no significant difference between the beta coefficients of PCAs, KBAs and IPAs in the association between the coverage of geographic and environmental space, suggesting that no network is significantly more or less efficient at capturing environmental space, though the slope for IPAs is the steepest. PCA designation and important area identification are driven by different approaches. Our results empirically show that this results in networks differentiated in environmental space, with systematic biases in, for example, elevation and different precipitation and temperature variables. Together these findings emphasise the ability of important areas to capture different bioclimatic, topographic and pedological attributes that are complementary to existing PCA networks and thus have significant added value.

Important areas increase representation of threatened and endemic species

Many PCA networks seek to encompass a substantial proportion of the species present in a country, although they do not always target the most important places for biodiversity (Plumptre et al., 2024). We find that, unsurprisingly, important areas encompass numerous additional species not found inside country's PCA networks, many of which are threatened, endemic or both (Appendix S19). Per unit area, we show that KBAs and IPAs more successfully target threatened species than PCAs, probably because criterion A of the KBA standard and IPA programme is explicitly designed to capture threatened biodiversity (Darbyshire et al., 2017; IUCN, 2016). This supports previous work that has shown that KBAs, for example, better represent threatened or near-threatened species than would be expected by chance (Lansley et al., 2025). However, an alternative explanation is that species are more likely to be threatened if found outside of PCA networks, where formal protection and/or *in situ* conservation is likely lacking. This could be explained, at least in part, by the fact that some countries, such as the United Kingdom, have PCAs that were established prior to the comprehensive red-listing of certain taxa. Either case represents a compelling argument for further integration of important areas within PCA networks.

Our analysis of species representation also sought to test a key concern, that plants may be underrepresented in conservation planning. Over 70% of vascular plant species have not yet had their conservation status formally assessed (Bachman et al., 2024), and the IPA programme is currently more limited in geographic scope than KBAs, with KBAs covering more than double the total land area as IPAs within the 28 studied countries (Appendix S3). We thus hypothesised that plants may be underrepresented in national PCA networks. As expected, our analysis shows that PCAs, KBAs and IPAs differ in their coverage of species ranges across taxonomic groups. Overall PCAs and KBAs currently cover the ranges of more plant species than IPAs, due to these networks being much larger. After correcting for network size, IPAs encompass a greater proportion of plant ranges (especially threatened and endemic plants) than PCAs or KBAs (Figure 5B). This may be expected given that IPA criteria are specifically tailored to represent important features of plant diversity patterns, but it underscores the value of combining a range of taxonomically specific tools to identify the most important areas for biodiversity when considering future PCA networks. The value of ensuring representation of plants in PCAs is epitomised by the estimate that three-quarters of undescribed plant species may be threatened with extinction (Brown et al., 2023). Our findings emphasise that KBA and IPA approaches are complementary and together could improve progress towards Target 3 of the Global Biodiversity Framework.

Important areas are associated with subsequent formal protection

A key question underpinning global area-based conservation is whether important areas currently catalyse formal protection as PCAs. Indeed, indicator 15.1.2 of the Sustainable Development Goals monitors the proportion of terrestrial KBAs covered by protected areas, and it has similarly been adopted as an official indicator used for monitoring progress towards GBF Target 3 (CBD, 2022). In 2020, 20.2% of terrestrial and inland water KBAs fell entirely within protected areas and OECMs, while 33.8% were not fully covered (UNEP-WCMC & IUCN, 2021). We find a significant relationship between unprotected cells inside important areas in 2010 and the protection status of corresponding cells in 2024. Cells inside important areas were 4.4 times more likely to become protected than cells outside of important areas. This suggests that KBAs and/or IPAs may catalyse legal protection or OECM designation, however countries have adopted a multitude of approaches to PCA designation and thus the effect of being an important area appears relatively weak compared to other drivers. For example, in Eastern Europe, where statutory protection of IPAs is most common, IPA protection was largely driven by their inclusion in Natura 2000 sites, suggesting that transition countries used IPAs to expand their PCA network upon joining the EU, rather than IPAs explicitly catalysing protection as such (Kor et al., 2025).

Challenges and limitations

There are three important caveats. Firstly, our environmental space analysis uses minimum convex polygons to estimate coverage. Whilst this method enables comparisons of environmental coverage across countries and networks, it is not informative about the density of coverage of any given environment. In practice, this means that networks can appear similar but be weighted strongly towards different ecosystems. Therefore, our method could be considered conservative in only finding differentiated networks where there is complete absence of overlap in environmental conditions. Furthermore, in using 99% MCPs for the temporal analysis, which inherently involves the differential calculation of outliers across time periods, some countries (especially Guinea) show declines in environmental coverage by

PCAs even if this is not the case. Second, we assume that expanded environmental space means that more ecosystems of conservation value will be encompassed by PCA/important area networks. In reality, this may not be the case because other drivers, such as land use, can influence whether the potential ecosystem is present. In this case, because important areas are identified using empirical evidence of a species' or ecosystem's presence, we contest that increased environmental and species' range coverage would be associated with increased conservation value. Nonetheless, this emphasises the importance of a rolling programme of re-assessment for important area status. Finally, we reiterate that KBA or IPA status does not make a site an immediate priority for conservation management, as this should be assessed based on a number of factors that include local opportunities, threats, costs and resourcing (Maxwell et al., 2020). Many important areas for biodiversity overlap with areas impacted by and important for humans, where designating a PCA can be challenging (Yang et al., 2020). In these instances, OECM designation may be an appropriate alternative to legislated protection.

Conclusions

Conserving and protecting a range of the planet's environments and species from diverse taxonomic groups and regions is critical for supporting ecosystem services, maintaining ecosystem functioning and, more broadly, meeting the Global Biodiversity Framework's targets. Our findings demonstrate that KBAs and IPAs, two examples of areas of particular importance for biodiversity, extend the environmental coverage of countries even with relatively well developed PCA networks. In addition, they capture the ranges of species, especially threatened and endemic plants and herptiles, that are not represented within the existing PCA network. Many countries already recognise and use important areas in their National Biodiversity Strategies and Action Plans (Plumptre, 2021), and we show that complementary approaches such as IPAs are particularly good at identifying sites for plants. We suggest that, given the limited time in which to achieve the Global Biodiversity Framework's 2030 Targets, supporting and accelerating evidence-based important area identification is a practical strategy to enable informed PCA expansion.

Acknowledgements

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Data availability

Spatial data for IPAs is available through RBG Kew's Tropical Important Plant Area Explorer (https://tipas.kew.org/), the Figshare data repository from Kor & Diazgranados (2023), and via a data enquiry to Plantlife International (https://www.plantlifeipa.org/gisdata). KBA and IBA data can be obtained through formal GIS data requests on the Key Biodiversity Area (https://www.keybiodiversityareas.org/kba-data/request) and BirdLife International (https://datazone.birdlife.org/site/requestgis) websites. Data for PCAs can be downloaded from the World Database on Protected Areas and OECMs (https://www.protectedplanet.net/en). The R code required to process the data, replicate these analyses and visualise the results will be made available in the following GitHub repository: https://github.com/joeflangley/Ecological-Representation.

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Tables and Figures

Table 1. Coverage of environmental space by Protected and Conserved Areas (PCAs), Key Biodiversity Areas (KBAs) and Important Plant Areas (IPAs), based on principal component analysis of 13 environmental variables and displayed in descending order of combined environmental coverage.

Environmental Representation							
	Environmental coverage by PCAs (%)	**Environmental coverage by pairwise combinations of PCAs, KBAs and IPAs (%)**			**Additional environmental coverage by KBAs and IPAs outside of PCAs (%)**		**Combined environmental coverage of PCAs, KBAs and IPAs (%)**
Country	PCA	PCA / KBA	PCA / IPA	KBA / IPA	KBA	IPA	Total
Virgin Islands, British	82.65	77.23	82.65	78.57	1.34	14.92	97.57
Croatia	85.40	83.77	77.73	82.98	6.92	8.28	94.72
Israel	80.76	58.85	59.25	40.59	8.08	5.52	94.35
North Macedonia	86.80	73.90	81.86	74.60	7.02	2.24	93.99
Lebanon	35.35	35.35	35.35	88.01	55.23	52.79	90.70
Morocco	78.85	73.66	58.13	59.24	4.94	8.80	89.82
Montenegro	80.57	65.46	62.74	61.43	7.48	2.98	89.48
Albania	62.41	58.90	52.66	57.21	23.97	4.81	86.37
India	78.30	77.67	19.27	18.98	4.51	1.63	84.43
Bhutan	82.18	74.69	59.57	59.71	2.21	0.14	84.39
United Kingdom	80.96	70.15	65.73	65.62	1.75	2.47	84.38
Algeria	44.08	32.28	5.19	20.05	33.66	19.23	82.14
Syria †	20.73	18.40	20.34	69.68	52.26	60.27	81.97
Colombia	79.81	74.15	27.86	27.84	2.15	0.00	81.96
Türkiye	30.84	30.84	30.49	74.89	49.08	46.21	81.71
Nepal	68.53	67.15	61.26	70.34	11.02	11.14	81.58
Tunisia	73.07	66.48	21.43	20.01	0.85	5.30	79.20
Palestine, State of	63.16	61.90	54.52	60.43	13.15	7.38	77.14
Ethiopia	58.06	56.01	26.92	30.92	18.68	4.24	76.99
Guinea	49.93	44.72	39.00	59.03	26.82	20.21	76.86
Bolivia ‡	75.30	74.72	6.55	6.55	0.93	0.00	76.22
Jordan	52.02	49.98	34.86	44.39	24.00	9.74	76.21
Pakistan	74.39	66.99	15.48	13.78	0.02	1.77	76.15
Cameroon	43.55	38.74	34.88	57.34	22.85	30.82	74.56
Egypt	62.13	53.99	56.58	59.27	6.59	10.54	73.75
Mozambique	42.80	41.80	34.37	42.65	9.98	26.51	71.00
Libya	20.66	12.96	20.66	26.97	15.08	43.86	65.54
China	53.14	51.27	37.60	37.69	1.27	0.70	54.66
Mean	62.37	56.86	42.25	50.31	14.71	14.37	81.35

‡ Plurinational State of Bolivia; † Syrian Arab Republic

Table 2. Coverage of species' ranges by Protected and Conserved Areas (PCAs), Key Biodiversity Areas (KBAs) and Important Plant Areas (IPAs), based on overlap analysis of threatened and not threatened plants, mammals, birds and herptiles and displayed in descending order of the number of combined species ranges in PCAs, KBAs and IPAs.

Species Representation							
	Number of species ranges in PCAs	Number of species ranges in pairwise combinations of PCAs, KBAs and IPAs			Number of additional species ranges in KBAs and IPAs and not PCAs		Combined number of species ranges in PCAs, KBAs and IPAs
Country	PCA	PCA / KBA	PCA / IPA	KBA / IPA	KBA	IPA	Total
Colombia	8614	8414	5340	5297	132	15	8758
Bolivia ‡	4953	4932	2645	2641	72	0	5025
China	4524	4488	2921	2965	234	72	4778
Cameroon	3568	3468	3381	3445	96	124	3703
India	3616	3583	1795	1795	80	4	3698
Mozambique	2614	2572	2463	2562	132	144	2771
Ethiopia	2453	2415	1932	1959	114	51	2580
Guinea	2337	2212	2087	2062	3	3	2342
Nepal	1507	1501	1472	1495	46	33	1560
Bhutan	1364	1354	1264	1272	25	22	1400
Türkiye	724	724	724	1139	464	433	1206
Pakistan	1194	1101	661	647	7	0	1201
Morocco	931	913	796	794	1	0	932
Algeria	829	759	694	711	23	17	852
Croatia	834	826	815	812	1	0	835
Albania	779	761	765	761	4	5	786
Syria †	586	582	581	731	168	154	755
Egypt	700	677	666	662	46	6	746
North Macedonia	714	705	693	692	6	3	720
Israel	676	665	670	698	38	37	715
Tunisia	691	681	513	513	6	0	697
Montenegro	687	666	678	660	5	0	692
Lebanon	551	546	545	611	89	66	640
Jordan	576	574	559	586	56	28	632
United Kingdom	631	613	611	601	0	0	631
Palestine	528	528	515	526	50	12	579
Libya	383	371	363	434	98	88	492
Virgin Islands, British	416	415	416	423	8	16	432
Global	24574	24204	17687	18009	812	515	25493

‡ Plurinational State of Bolivia; † Syrian Arab Republic

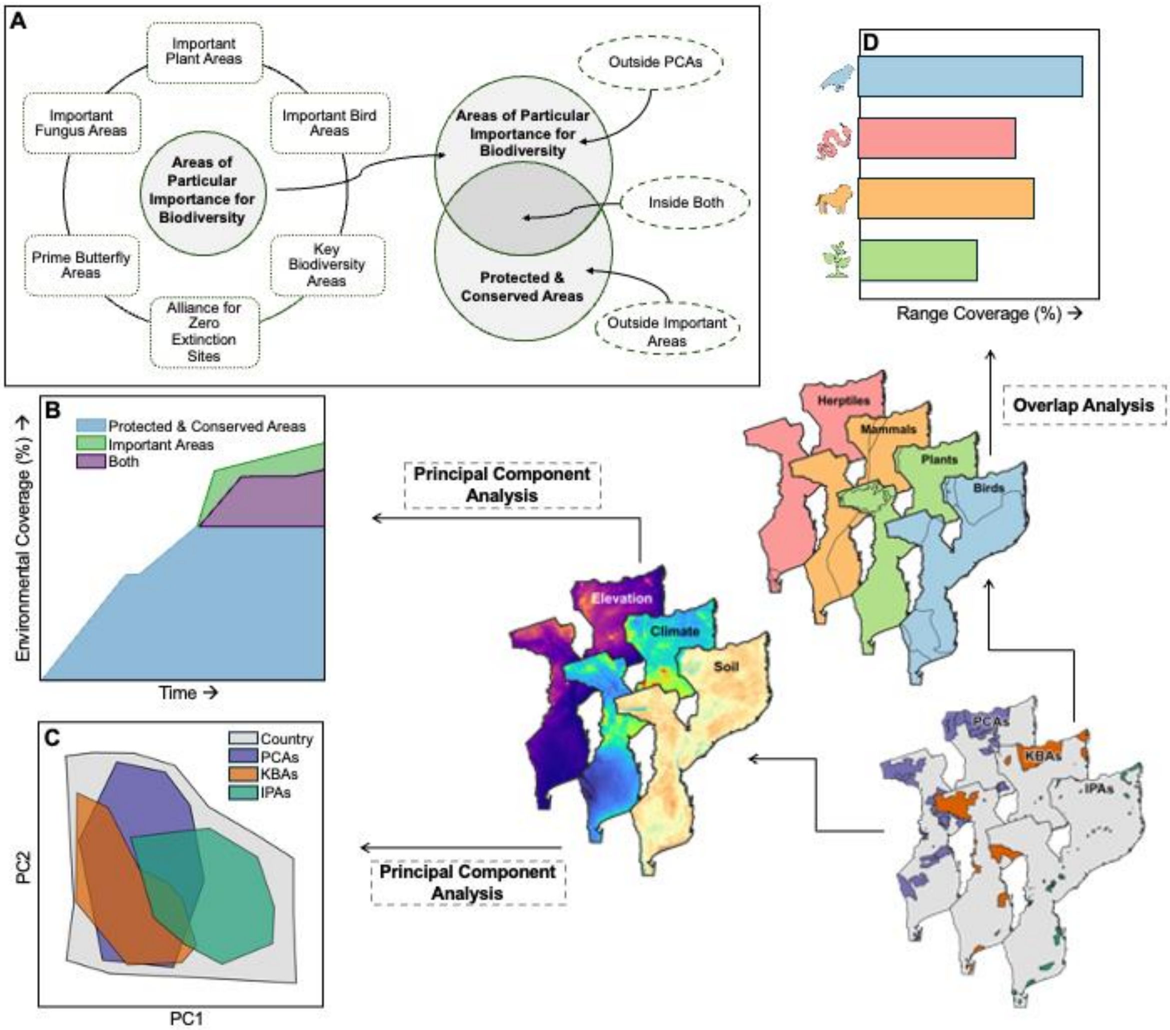


Figure 1. Framework used for assessing ecological representation in Protected and Conserved Areas (PCAs) and areas of particular importance for biodiversity (important areas). (A) Examples of important areas and delineation between sites that are only inside important areas, only inside PCAs or overlapping both important areas and PCAs. (B) Representation of environmental space through time by PCAs and important areas. (C) Differential representation of environmental space by PCAs and important areas. (D) Representation of bird, mammal, herptile and plant species' ranges by PCAs and important areas.

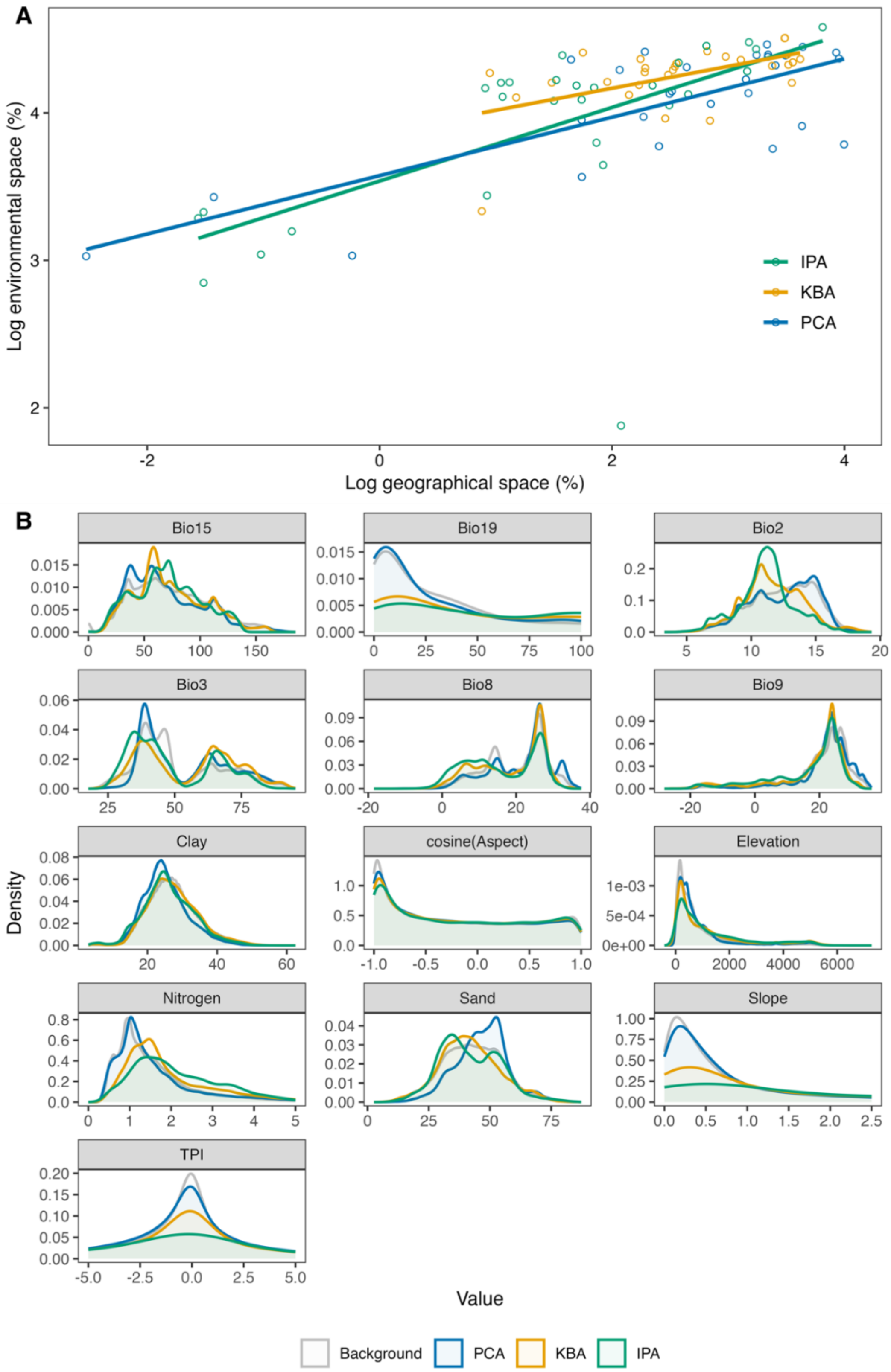


Figure 2. (A) Association between log-transformed geographic and environmental coverage for Protected and Conserved Areas (PCAs), Key Biodiversity Areas (KBAs) and Important Plant Areas (IPAs), based on linear regression. (B) Density distribution of raw environmental variables illustrating environmental differentiation between PCAs, KBAs and IPAs and overall background environmental variation. Bio15 = precipitation seasonality; Bio19 = precipitation

of coldest quarter; Bio2 = mean diurnal temperature range; Bio3 = isothermality; Bio8 = mean temperature of wettest quarter; Bio9 = mean temperature of driest quarter; TPI = topographic position index.

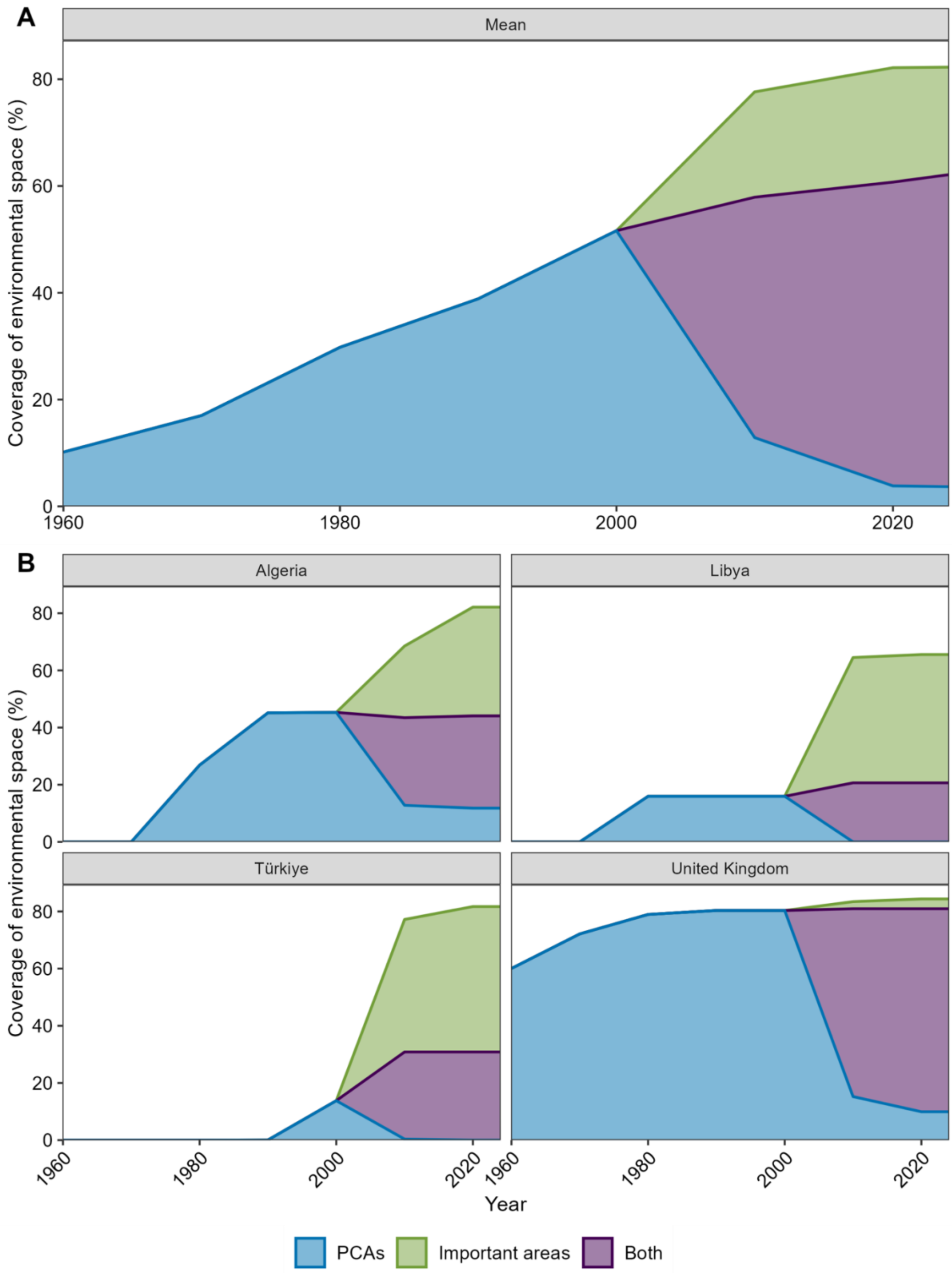


Figure 3. Cumulative coverage of environmental space by Protected and Conserved Areas (PCAs) and areas of particular importance for biodiversity (important areas) through time, based on principal component analysis of 13 environmental variables. (A) Mean expansion across all 28 studied countries. (B) Expansion for four countries with different rates of and/or contribution of networks to this trend.

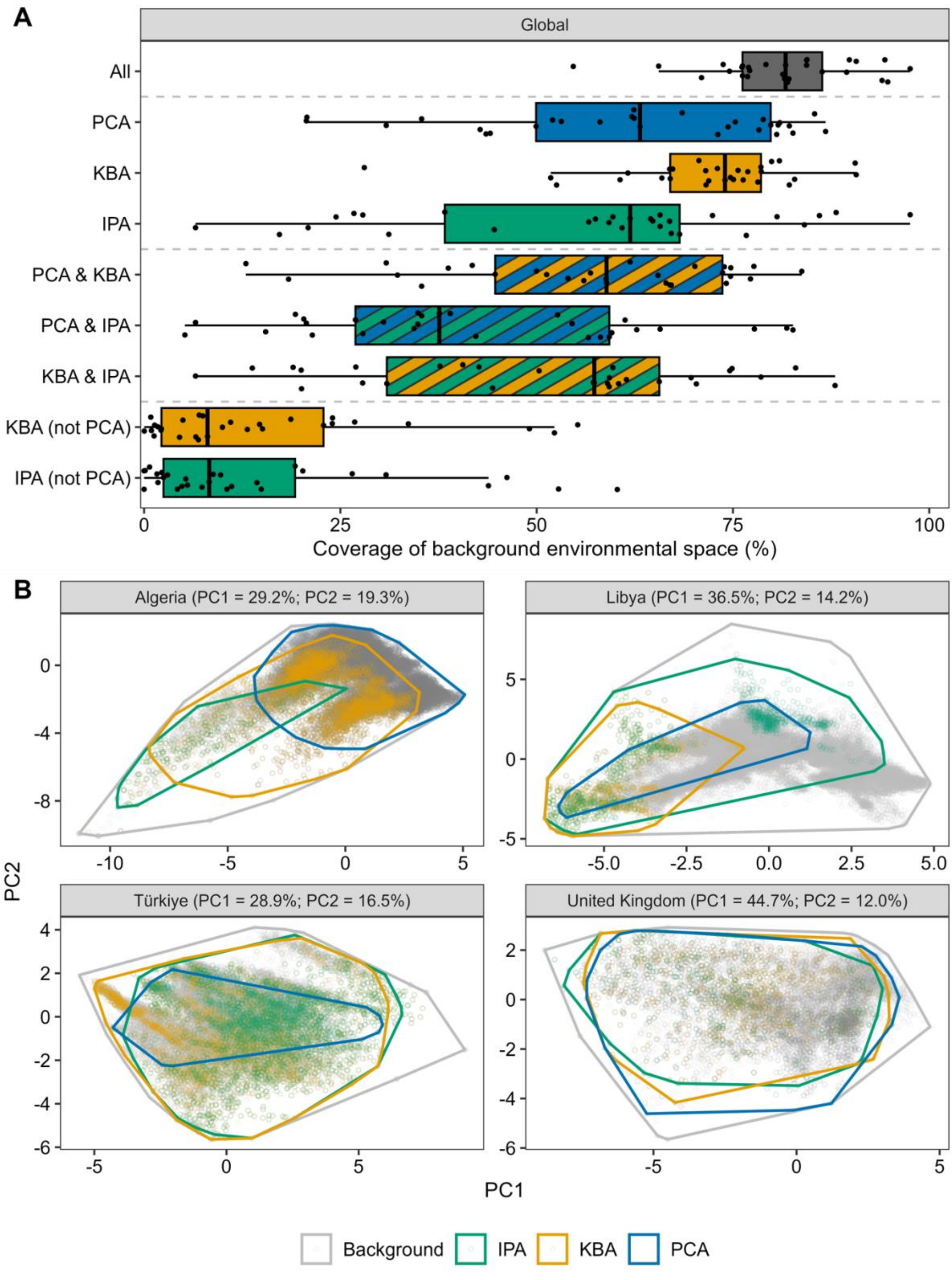


Figure 4. Current representation of environmental space by Protected and Conserved Areas (PCAs), Key Biodiversity Areas (KBAs) and Important Plant Areas (IPAs), based on principal component analysis of 13 environmental variables. (A) Boxplot summarising the median and variation of environmental coverage across all 28 studied countries. (B) Principal component analysis plots for four countries with different proportions and structure of environmental coverage across PCAs, KBAs and IPAs.

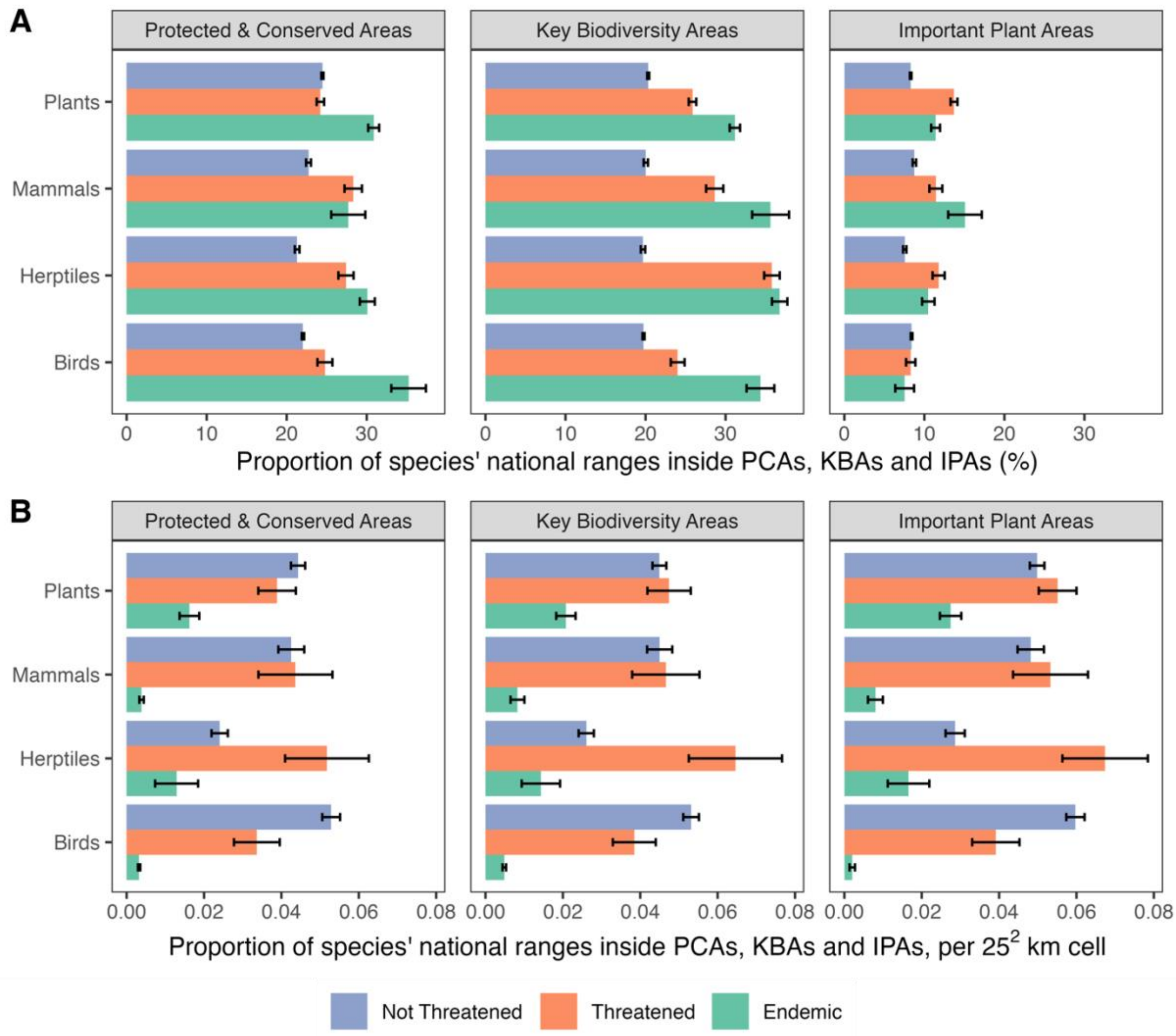


Figure 5. Current representation of threatened, not threatened and endemic plant, mammal, bird and herptile species' ranges by Protected and Conserved Areas (PCAs), Key Biodiversity Areas (KBAs) and Important Plant Areas (IPAs). (A) Mean proportion (%) of species' national ranges overlapping the country's PCAs, KBAs and IPA. Error bars indicate the standard error of the mean for each group. (B) The same overlap percentages as in (A) divided by the number of cells in the country's PCAs, KBAs and IPAs to account for national-level differences in network size.

Supporting Information

Appendix S1: Glossary of key terms and abbreviations used in this study.

Term	Abbreviation	Definition
Other effective area-based conservation measures	OECMs	Sites for in-situ biodiversity conservation outside of protected areas
Key Biodiversity Area	KBA	The most important sites globally for species and their habitats
Global Standard for the Identification of Key Biodiversity Areas	KBA Standard	A framework that builds on other important area programmes and sets out 11 criteria for identifying KBAs to support conservation and monitoring efforts
Important Plant Area	IPA	The most important sites for plants and their habitats, developed by Plantlife International and extended by RBG Kew
Important Bird and Biodiversity Area	IBA	Globally important sites for birds and other biodiversity, many of which are also now KBAs
Areas of particular importance for biodiversity	Important areas	Overarching term for the most important places for biodiversity on Earth, including KBAs, IPAs and IBAs
Protected and Conserved Areas	PCAs	Collective term for protected areas and OECMs
Global Biodiversity Framework	GBF	Agreement committing countries to halting and reversing nature loss, adopted in Montreal in 2022
Target 3 of the Global Biodiversity Framework	30-by-30	GBF's target of conserving 30% of Earth for nature by 2030
Minimum convex polygon	MCP	Smallest polygon drawn around a given dataset of points where all internal angles are <= 180 degrees
Permutational multivariate analysis of variance	PERMANOVA	Semi-parametric test for variance using a given distance matrix

Appendix S2: Selection of studied countries.

When referring to specific countries or territories in this study, we follow the IUCN Red List in using the standard names provided by the United Nations Statistics Division (UNSD, 2024). We extracted PCA data from the World Databases on Protected Areas (WDPA) and OECMs (WDOECM) (UNEP-WCMC & IUCN, 2024), KBAs and IBAs from the World Database on Key Biodiversity Areas (WDKBA) (BirdLife International, 2024a, 2024b) and IPAs from Plantlife International (2023), the Tropical Important Plant Areas Explorer portal (RBG Kew, 2024) and Kor & Diazgranados (2023). We retained the 28 countries with accessible polygon (rather than point) data for PCAs, KBAs and IPAs. IPAs were the limiting factor here, as we were only able to obtain polygon data for 27 countries from Plantlife International and through the TIPAs Explorer (although TIPA programmes are now also underway in New Guinea and Sierra Leone too) and for one further country from Kor & Diazgranados (2023). The latter provide polygon boundaries for IPAs from 10 sites in Colombia identified as the top priority areas nationally for plant conservation, although these sites are yet to be integrated into the main IPA or TIPA databases.

Appendix S3: List of countries included in this study and the absolute and proportional geographic coverage of their land area in 2024 by Protected and Conserved Areas (PCAs), Key Biodiversity Areas (KBAs) and Important Plant Areas (IPAs).

	PCAs		**KBAs**		**IPAs**	
Country	**Area coverage (km^2)**	**Coverage of total land area (%)**	**Area coverage (km^2)**	**Coverage of total land area (%)**	**Area coverage (km^2)**	**Coverage of total land area (%)**
Albania	6879	23.87	4832	16.76	3484	12.09
Algeria	1260965	54.41	215962	9.32	10941	0.47
Bhutan	19225	50.83	13236	35.00	2150	5.69
Bolivia ‡	328690	30.14	367323	33.68	87180	7.99
Cameroon	51842	11.07	40030	8.55	25499	5.44
China	910207	9.68	1098039	11.68	642975	6.84
Colombia	323600	28.25	147291	12.86	2552	0.22
Croatia	21554	38.14	18482	32.70	9407	16.64
Egypt	119635	12.13	31940	3.24	30185	3.06
Ethiopia	196506	17.29	144180	12.69	28593	2.52
Guinea	92628	37.88	6300	2.58	10949	4.48
India	154330	5.19	171238	5.75	10819	0.36
Israel	5340	25.63	7235	34.72	1319	6.33
Jordan	5083	5.69	8785	9.83	5773	6.46
Lebanon	584	5.70	3346	32.62	2461	23.99
Libya	1248	0.08	39187	2.41	40333	2.48
Montenegro	4565	32.87	1732	12.47	1454	10.47
Morocco	216414	52.11	39187	9.44	11801	2.84
Mozambique	233164	29.45	135896	17.17	22779	2.88
Nepal	34622	23.39	33119	22.38	34973	23.63
North Macedonia	7143	28.06	8479	33.31	6499	25.53
Pakistan	111161	14.05	34796	4.40	1709	0.22
Palestine, State of	772	12.36	1828	29.28	889	14.23
Syria †	1492	0.79	22617	11.98	9112	4.82
Tunisia	12273	7.89	11039	7.09	328	0.21
Türkiye	1909	0.24	153448	19.64	102336	13.10
United Kingdom	69106	28.32	23884	9.79	11161	4.57
Virgin Islands, British	15	9.80	57	37.30	69	45.24
Overall	4190953	16.63	2783490	11.05	1117732	4.44

‡ Plurinational State of Bolivia; † Syrian Arab Republic

Appendix S4: Preparation and filtering of PCA, KBA, IBA and IPA data.

We supplemented PCA data from the WDPA/WDOECM for India and China with protected area polygon data from OpenStreetMap using the R package osmdata (Padgham et al., 2017). We used the package's add_osm_features() function to select three feature types ("boundary" = "protected_area", "leisure" = "nature_reserve", "boundary" = "national_park") and the osmdata_sf() function to return a spatial object. While this approach enabled us to obtain more comprehensive PCA data for India and China than what we would have otherwise had from the WDPA/WDOECM alone, it meant we were unable to extract accurate or complete data on the year of PCA establishment for these countries. Therefore, we exclude India and China from our temporal analyses, i.e. the environmental representation through time principal component analysis and the chi-squared tests of association between cells inside important areas and cells inside PCAs. We were also unable to verify the accuracy of each polygon download from OpenStreetMap and acknowledge that these polygons are unlikely to precisely represent India and China's PCA networks.

Approximately 7.9% of PCAs (excluding those in India and China obtained from OpenStreetMap), 3.4% of KBAs, 2.4% of IBAs and 13.2% of IPAs across our studied countries were designated with points and not polygons. For PCAs, we removed sites that had point geometries and no reported area values but retained sites with reported area values. In those instances, we added a circular buffer equivalent to the site's reported area and then clipped this polygon by a boundary of its host country (following Visconti et al., 2013). Consequently, we only excluded 4.6% of PCAs for having point geometries. We considered protected areas of all IUCN categories, though we note previous concerns about the governance and effectiveness of certain categories of protected areas, particularly those in categories V-VI (Shafer, 2020). We excluded PCAs that were entirely marine and those categorised as "proposed", which are not yet legally designated sites (UNEP-WCMC, 2019). For KBAs, IBAs and IPAs, we excluded sites with only point based spatial information and, in the case of IPAs, included buffer zones in addition to the core zones. In instances where a given PCA, KBA, IBA or IPA had invalid geometry, we used the st_make_valid() function from the sf package to fix those geometries (Pebesma, 2018).

Appendix S5: Environmental variables extracted from each country's stratified sample of points, and their respective source and resolution. All variables were downloaded using the geodata package (Hijmans et al., 2024), using functions that provide aggregated data (to 30 arc-seconds). The 13 variables retained for analyses following correlation and variance inflation factor testing are emboldened.

Predictor variable	**Data source**	**Resolution**	**Further details**
Bioclimatic			
Annual mean temperature (BIO1)	WorldClim V2.1 (Fick & Hijmans, 2017)	30 arc-seconds (c. 1km)	Temperature variables (BIO1—BIO11) from WorldClim V2.1, downloaded using worldclim_global() function
Mean diurnal range (BIO2)			
Isothermality (BIO3)			
Temperature seasonality (BIO4)			
Max temperature of warmest month (BIO5)			
Max temperature of coldest month (BIO6)			
Temperature annual range (BIO7)			
Mean temperature of wettest quarter (BIO8)			
Mean temperature of driest quarter (BIO9)			
Mean temperature of warmest quarter (BIO10)			
Mean temperature of coldest quarter (BIO11)			
Annual precipitation (BIO12)			Precipitation variables (BIO12—BIO19) from WorldClim V2.1, downloaded using worldclim_global() function
Precipitation of wettest month (BIO13)			
Precipitation of driest month (BIO14)			
Precipitation seasonality (BIO15)			
Precipitation of wettest quarter (BIO16)			
Precipitation of driest quarter (BIO17)			
Precipitation of warmest quarter (BIO18)			
Precipitation of coldest quarter (BIO19)			
Topographic			
Elevation	Shuttle Radar Topography Mission (SRTM 90m) (Jarvis et al., n.d.),	30 arc-seconds (c. 1km)	Slope, roughness, aspect, TPI and TRI calculated from elevation layer using the terrain function in the R
Slope			
Roughness			
Aspect			

Topographic Position Index (TPI) Terrain Ruggedness Index (TRI)	supplemented with GTOPO30 data for high latitudes		package terra. Downloaded using elevation_global() function
Soil			
Soil organic carbon Water pH **Nitrogen content** **Clay content** Silt content **Sand content**	SoilGrids250m V2.0 (Poggio et al., 2021)	30 arc-seconds (c. 1km)	Data derived from prediction models based on soil profiles from WoSIS. Downloaded at a depth interval of 5-15 cm. Downloaded using soil_world() function

Appendix S6: An environmental space approach versus an ecoregions approach.

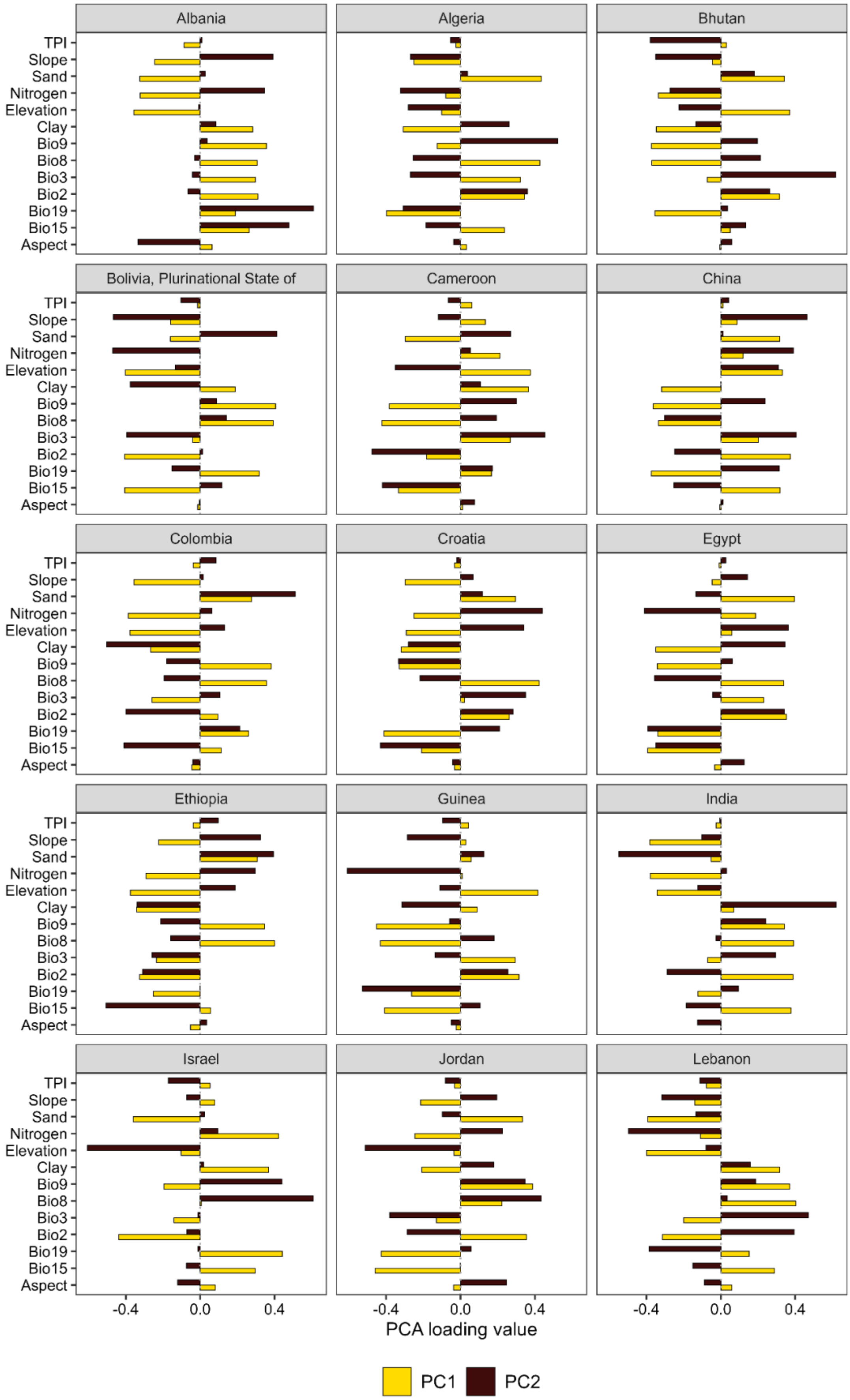
The classification of Earth's distinct ecological and environmental assemblages into spatially explicit Terrestrial Ecoregions of the World (TEOW; hereafter "ecoregions") has provided biologists with a tool for assessing and monitoring ecological representation and thus informing spatial conservation planning (Olson et al., 2001). There are more than 800 terrestrial ecoregions across 14 biomes and eight biogeographic realms (Olson et al., 2001). We recognise that an ecoregion-based approach can and has been effectively used to assess ecological representation in the context of area-based conservation targets (Dinerstein et al., 2017; Dobrowski et al., 2021; Jantke & Mohr, 2024). However, the number and types of ecoregions differs greatly between countries, making it challenging to accurately compare national-level progress towards building ecologically representative PCAs. Furthermore, while a key benefit of ecoregions is that it reduces ecological complexity and environmental multidimensionality into broadly recognised, well-understood and easily interpretable categories, this approach also risks obscuring finer scale environmental variation across geographic space.

For these reasons, we instead use a multidimensional environmental space approach to assess environmental representation by PCAs, KBAs and IPAs. Principal component analysis enables the reduction of multiple environmental variables into principal components, while retaining a continuous representation of environmental gradients. In using this method, we were able to then calculate the proportion of a given country's total environmental variation that was covered by each conservation area, enabling direct and standardised comparisons of environmental representation between countries, between area-based conservation designations, and through time. When calculating the coverage of total environmental space by each network we use only the first and second principal components to prevent overcomplicating these values unnecessarily. That said, we acknowledge that in all countries' principal component analysis, the third principal component has an eigenvalue > 1 (Figure S2) and thus explains more variance than a single variable in the original environmental dataset.

For some countries (e.g. Pakistan, Albania and Montenegro), the eigenvalue of PC3 only marginally exceeds 1, whereas for others (e.g. Israel, Morocco and Syrian Arab Republic) it nears or even, in the case of Israel, marginally exceeds 2.

Appendix S7: Minimum convex polygons to characterise environmental space.

To characterise each country's background environmental space, we calculate 100% minimum convex polygons (MCPs) to incorporate every point from the stratified sample and thus capture the country's total environmental variation. However, when characterising the environmental space covered by PCAs, KBAs and IPAs, we calculate 99% MCPs to prevent inflating environmental coverage values based on few outlier points. This represents a conservative approach to quantifying environmental coverage by PCAs and important areas, since the 99% MCPs capture the most typical environmental conditions in each area without incorporating rare environmental values that do not represent the core niche captured by each. We also experimented with 95% MCPs, which produced relatively similar results, albeit with slightly lower environmental coverage values. Therefore, while we settled on 99% MCPs, we acknowledge that the proportion of outliers to be excluded from computation will inevitably shape the precise environmental representation outputs.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Egypt
Ethiopia
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India
Israel
Jordan
Lebanon
TPI
Slope
Sand
Nitrogen
Elevation
Clay
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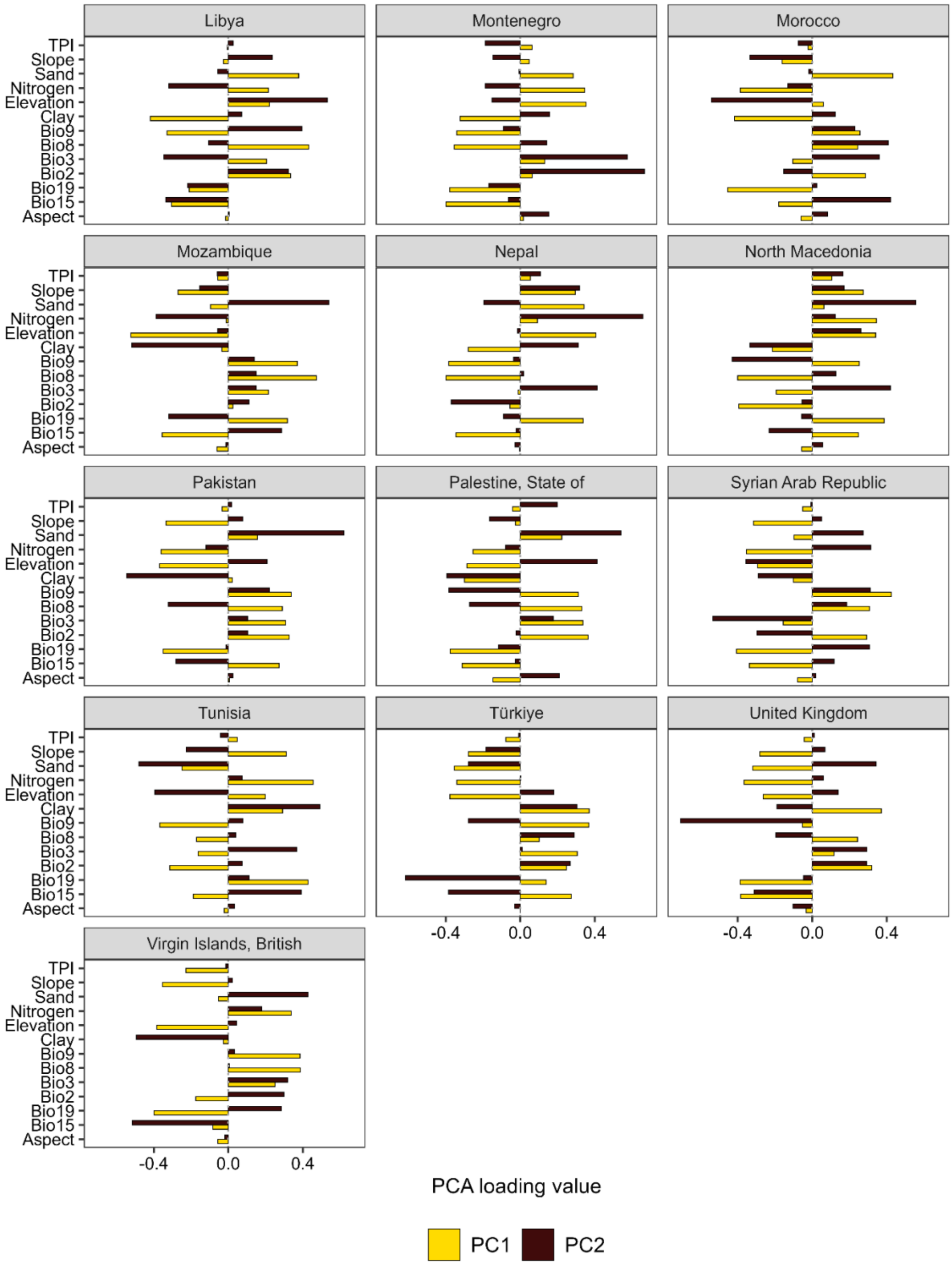
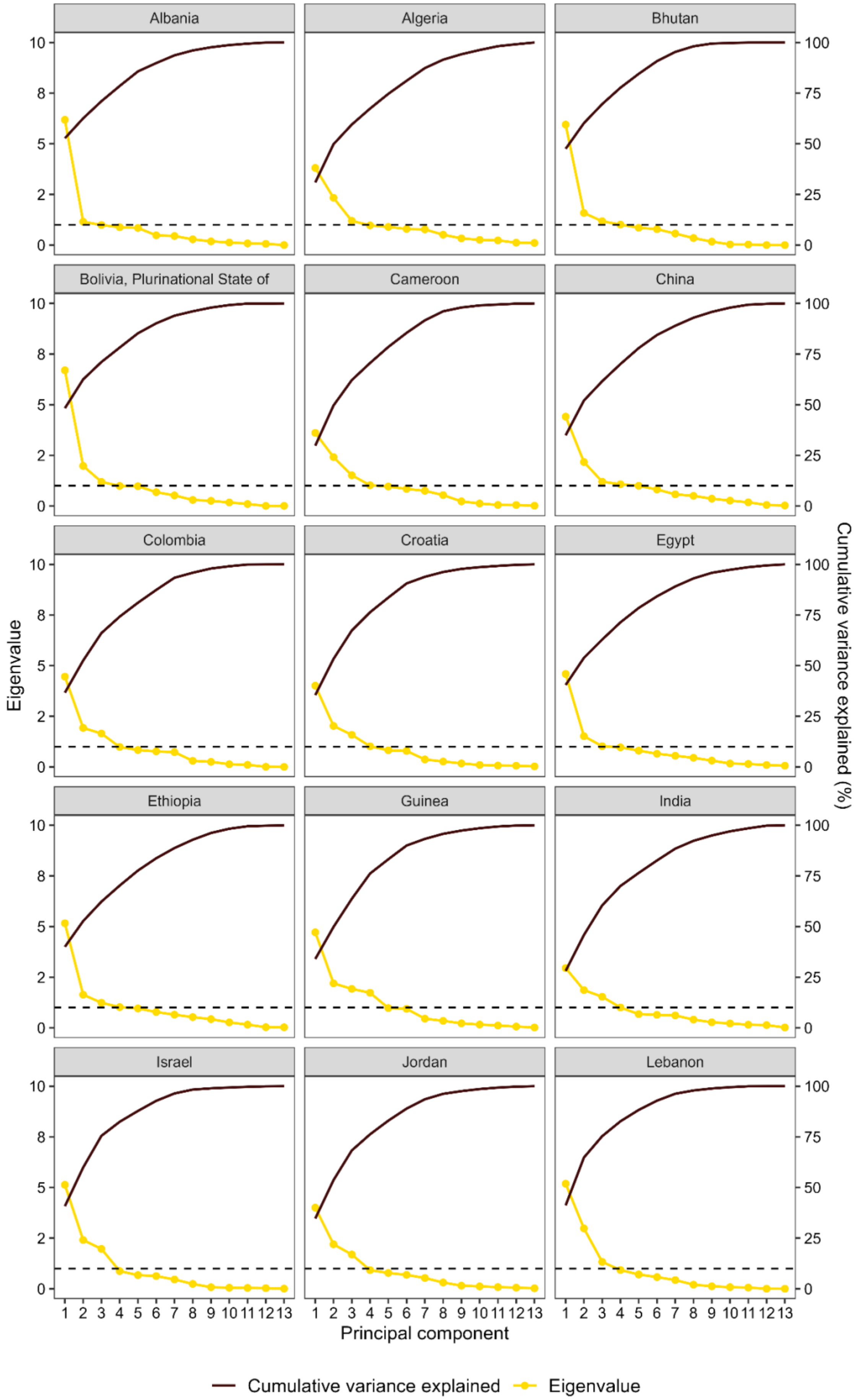
PC1
PC2



Appendix S8: Loadings of each environmental variable onto the first and second principal components in the principal component analysis of environmental representation by Protected and Conserved Areas (PCAs), Key Biodiversity Areas (KBAs) and Important Plant Areas (IPAs).



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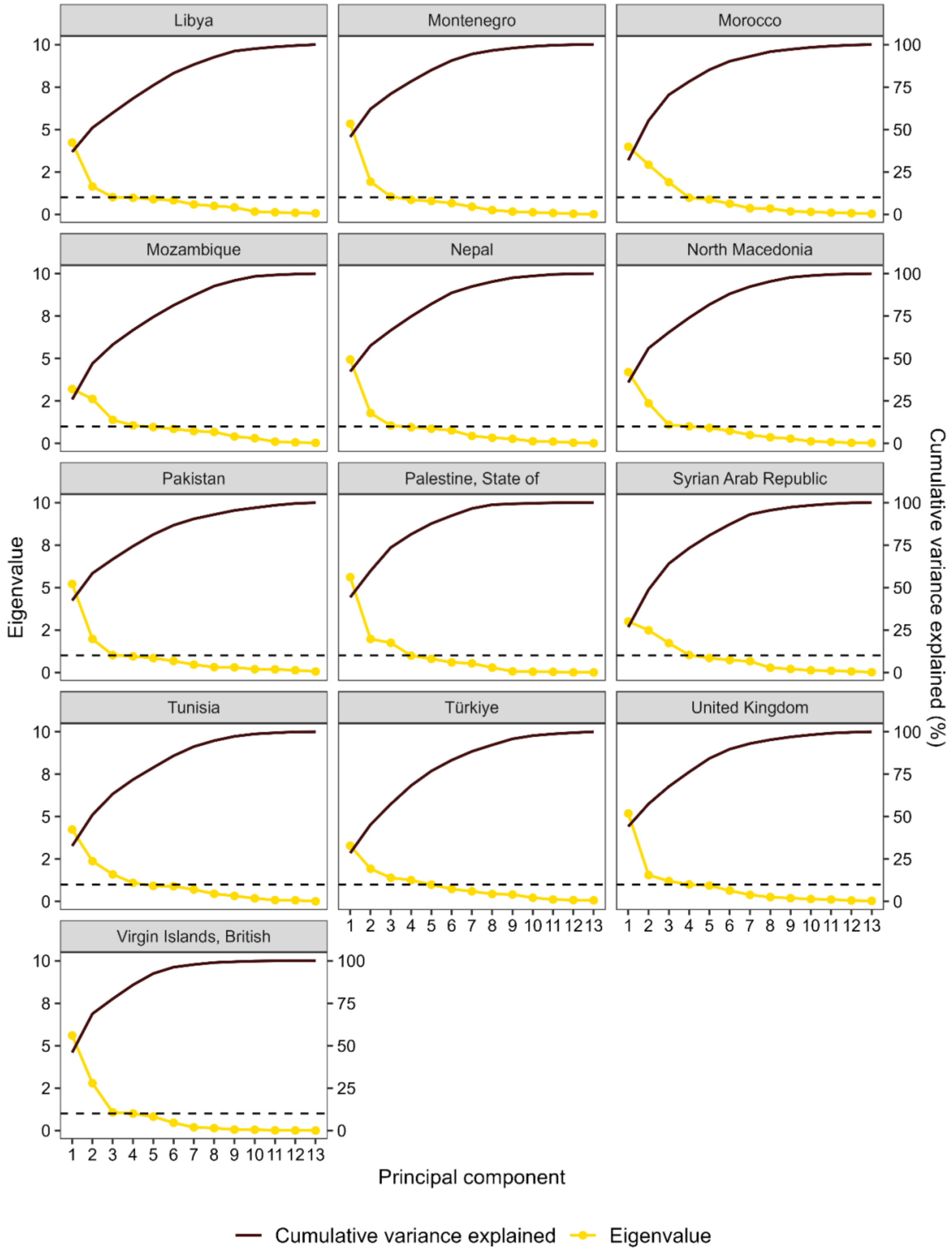
Bolivia, Plurinational State of
Cameroon
China
Colombia
Croatia
Egypt
Ethiopia
Guinea
India
Israel
Jordan
Lebanon
Eigenvalue
Cumulative variance explained (%)
Principal component
0
2
5
8
10
25
50
75
100
1 2 3 4 5 6 7 8 9 10 11 12 13
Cumulative variance explained
Eigenvalue



Appendix S9: Scree plots for the principal component analysis of environmental representation by Protected and Conserved Areas (PCAs), Key Biodiversity Areas (KBAs) and Important Plant Areas (IPAs), showing eigenvalues and cumulative variance explained across principal components. Dashed horizontal line, where eigenvalue = 1, represents the threshold above which principal components explain more variance than a single, original variable.

Appendix S10: Spatial thinning on stratified sample of points.

Spatial autocorrelation violates the independence assumption underlying many statistical tests. Therefore, while we retained the entire stratified sample of points (and their respective environmental extractions) for the principal component analysis, we undertook a process of spatial thinning prior to conducting PERMANOVA for each country to reduce the number of sampled points and thus mitigate spatial autocorrelation and artificially inflating our statistical power. We did this by applying a function in R that randomly selects a specific point in geographic space, adds a 10 km buffer around that point and removes all points within that given distance (Roberts, 2015). We ran 5 iterations for every country and retained the output with the largest number of points for each. We then conducted PERMANOVA on this reduced sample to test for significant differences in environmental coverage between PCAs, KBAs and IPAs in each country. When running the PERMANOVA for all 28 countries together, we instead used a subset of 10,000 points from the entire stratified sample, wherein we maintained the proportion of points between countries and conservation areas. We also used a subset of 10,000 points when conducting the Kruskal-Wallis tests on each environmental variable.

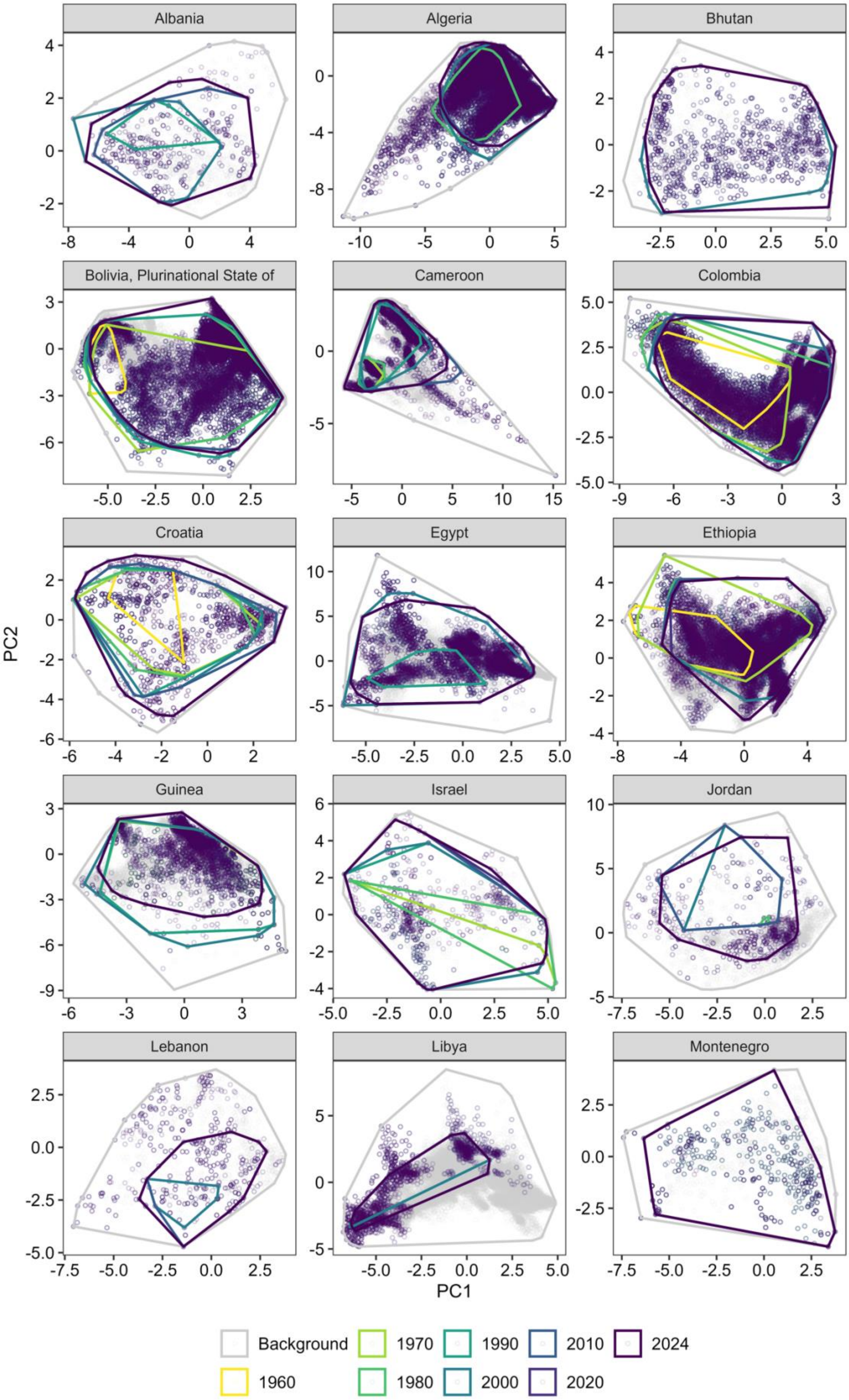
Appendix S11: Number of threatened and not threatened bird, herptile, mammal and plant species with ranges overlapping each of the studied countries.

	Not Threatened				Threatened			
Country	**Bird**	**Herp.**	**Mam.**	**Plant**	**Bird**	**Herp.**	**Mam.**	**Plant**
Albania	271	45	84	356	11	11	9	8
Algeria	291	91	85	353	18	14	12	28
Bhutan	636	143	126	378	27	22	31	68
Bolivia	1373	485	335	2606	44	50	25	153
Cameroon	881	366	294	1575	31	85	49	481
China	1216	628	473	1976	83	182	80	270
Colombia	1775	844	374	4727	82	278	66	815
Croatia	275	47	94	385	13	11	7	9
Egypt	321	89	89	211	17	11	11	11
Ethiopia	794	231	226	1148	37	13	40	154
Guinea	668	220	218	1033	28	19	31	180
India	1109	587	279	1161	82	215	89	296
Israel	313	79	86	188	15	10	13	21
Jordan	278	92	71	162	15	5	7	13
Lebanon	254	47	66	179	12	7	6	89
Libya	222	64	59	154	11	6	9	8
Montenegro	258	37	81	317	10	11	6	6
Morocco	310	86	98	339	21	16	15	53
Mozambique	674	269	233	1315	30	18	19	251
Nepal	763	161	159	378	34	22	29	35
North Macedonia	254	40	73	332	9	4	6	6
Pakistan	601	156	174	227	29	15	19	14
Palestine	283	63	64	158	14	6	7	10
Syria	311	87	88	213	16	12	10	55
Tunisia	277	62	68	265	14	7	8	15
Türkiye	352	129	137	436	15	31	16	122
United Kingdom	232	13	62	276	10	4	6	31
Virgin Islands, British	138	11	24	212	2	17	4	24
Global	5089	3274	1717	11460	338	894	335	2849

Appendix S12: Proportion of each country's total environmental space covered by Protected and Conserved Areas (PCAs) through time, at decadal intervals since 1960. We exclude India and China as we were unable to extract accurate or comprehensive data on the year of PCA establishment for those countries. Environmental coverage by PCAs derived from 99% MCPs.

	Percentage of country's total environmental space covered by PCAs							
Country	**1960**	**1970**	**1980**	**1990**	**2000**	**2010**	**2020**	**2024**
North Macedonia	16.93	16.93	23.84	42.37	51.81	53.97	76.98	86.80
Croatia	15.42	48.36	51.68	60.51	61.04	66.63	85.40	85.40
Virgin Islands, British	0.00	0.00	1.07	1.07	82.65	82.65	82.65	82.65
Bhutan	0.00	0.00	0.00	0.00	77.50	82.18	82.18	82.18
United Kingdom	60.05	72.14	78.96	80.35	80.33	80.96	80.96	80.96
Israel	0.00	14.45	27.08	72.85	74.20	78.42	79.58	80.76
Montenegro	0.00	0.00	80.57	80.57	80.57	80.57	80.57	80.57
Colombia	28.25	48.32	69.01	71.55	73.35	79.67	80.63	79.81
Morocco	17.96	17.96	53.91	53.91	71.63	80.03	81.18	78.85
Bolivia ‡	6.79	60.74	68.78	74.06	76.32	75.17	75.30	75.30
Pakistan	0.00	11.72	35.81	50.85	69.01	69.73	69.80	74.39
Tunisia	11.57	11.63	39.31	52.33	41.00	73.07	73.07	73.07
Nepal	0.00	0.00	42.05	53.66	68.30	68.48	68.53	68.53
Palestine, State of	0.00	0.00	0.00	41.39	40.16	41.39	44.99	63.16
Albania	0.00	0.00	11.95	11.95	40.91	53.83	62.41	62.41
Egypt	0.00	0.00	0.00	12.08	62.94	62.13	62.13	62.13
Ethiopia	18.89	47.93	54.77	54.66	54.66	58.63	57.06	58.06
Jordan	0.00	0.00	0.15	24.56	24.56	34.10	52.02	52.02
Guinea	60.19	60.19	60.26	60.76	68.14	49.94	49.94	49.93
Algeria	0.00	0.00	26.87	45.15	45.30	43.46	44.08	44.08
Cameroon	0.00	3.80	4.60	22.12	27.20	46.24	43.55	43.55
Mozambique	28.37	28.37	27.86	27.86	28.89	42.78	42.80	42.80
Lebanon	0.00	0.00	0.00	0.00	8.72	33.63	35.35	35.35
Türkiye	0.00	0.00	0.00	0.05	13.80	30.84	30.84	30.84
Syria †	0.00	0.00	0.00	0.08	3.52	16.42	16.45	20.73
Libya	0.00	0.00	15.95	15.95	15.95	20.66	20.66	20.66
Mean	10.17	17.02	29.79	38.87	51.63	57.91	60.73	62.12

‡ Plurinational State of Bolivia; † Syrian Arab Republic


Albania
Algeria
Bhutan
Bolivia, Plurinational State of
Cameroon
Colombia
Croatia
Egypt
Ethiopia
Guinea
Israel
Jordan
Lebanon
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Montenegro
PC1
PC2
Background
1960
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1980
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2000
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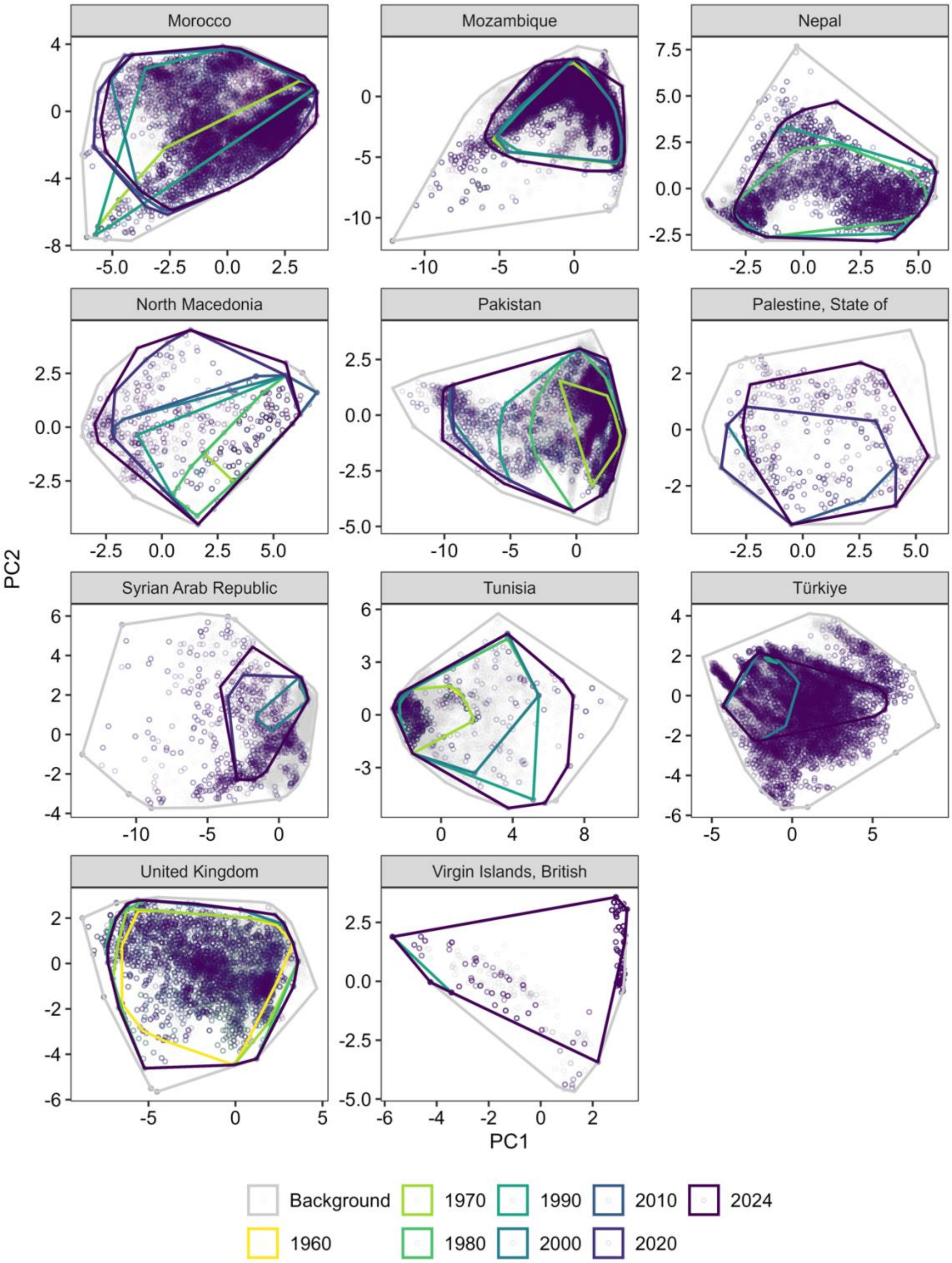
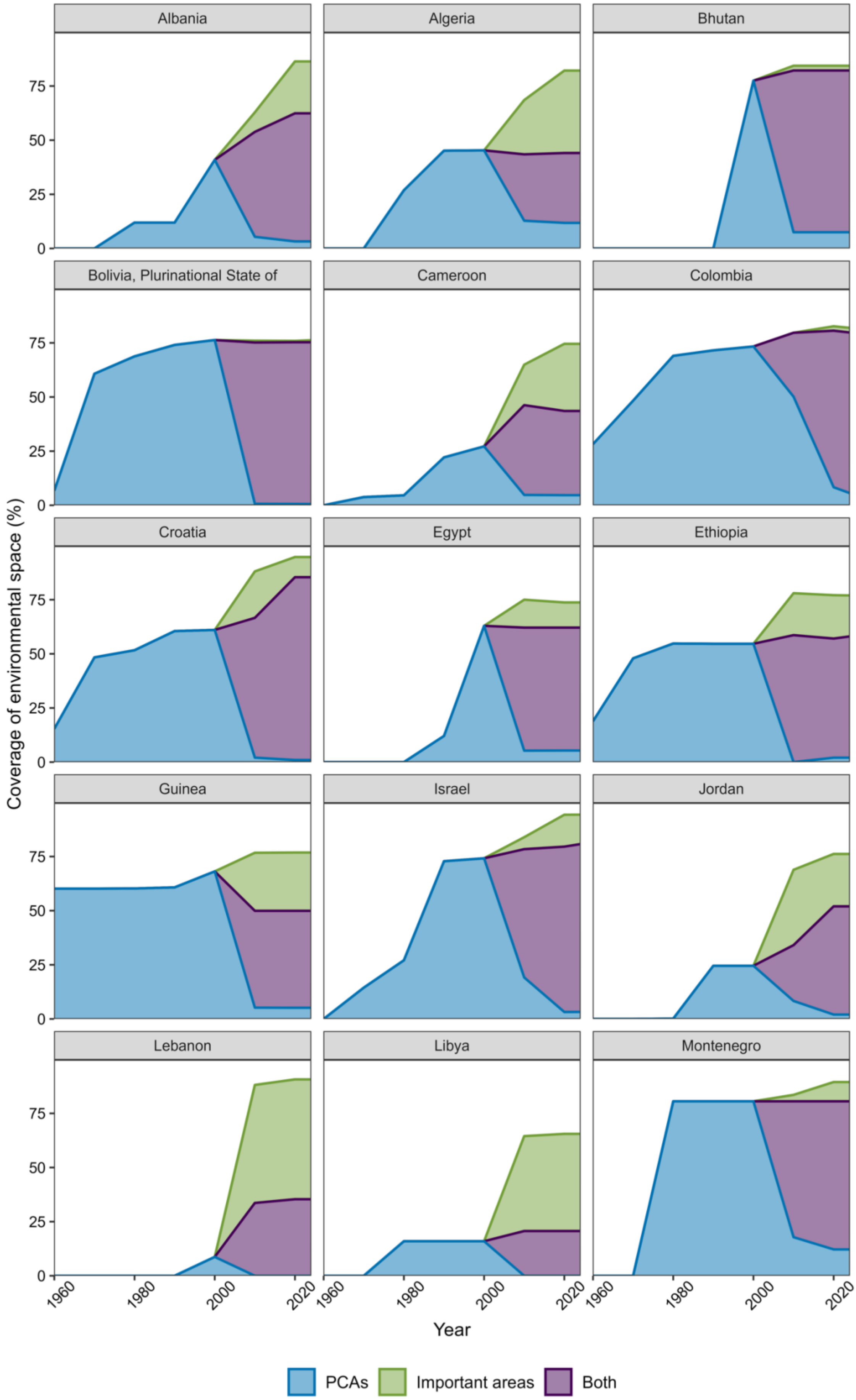
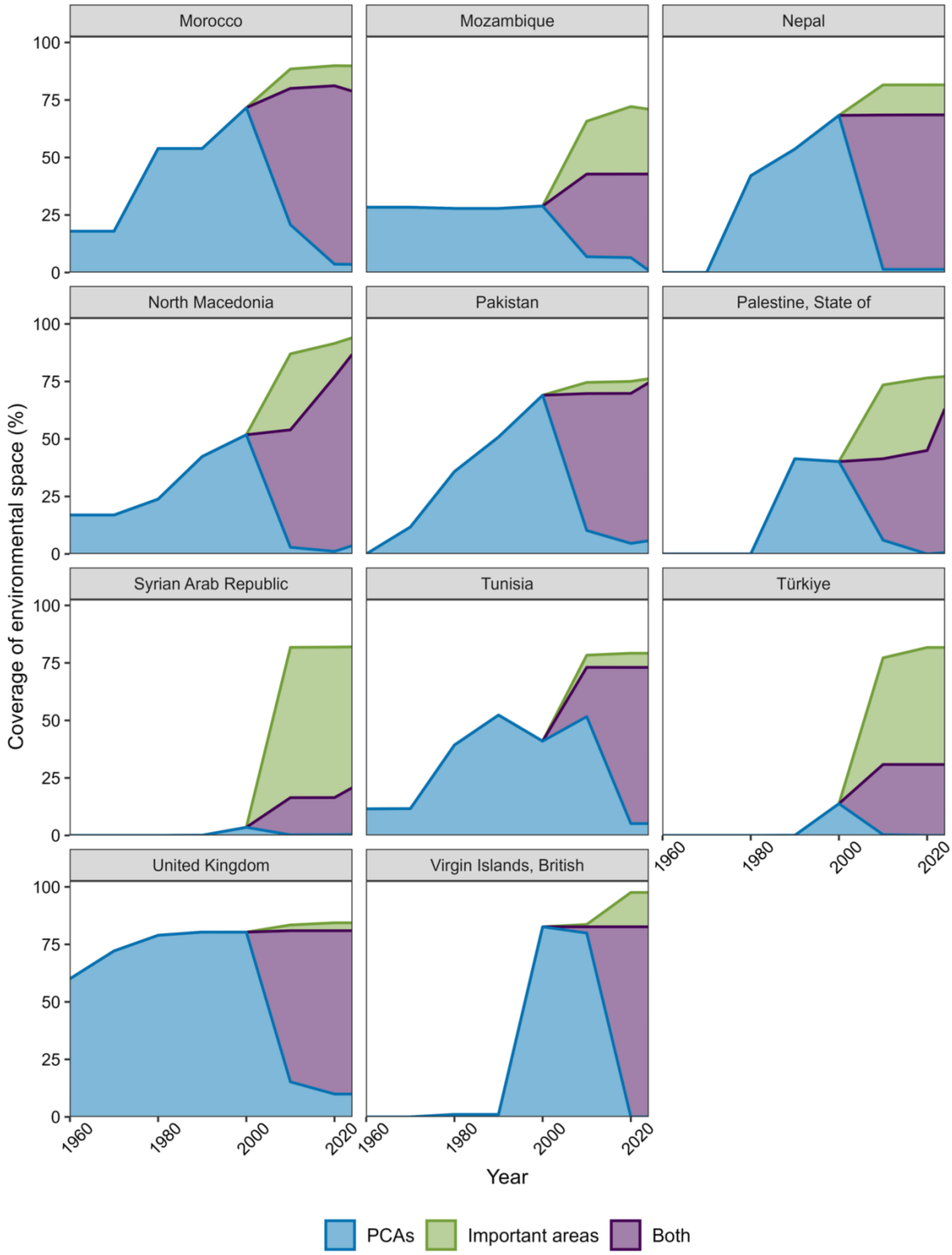
2024



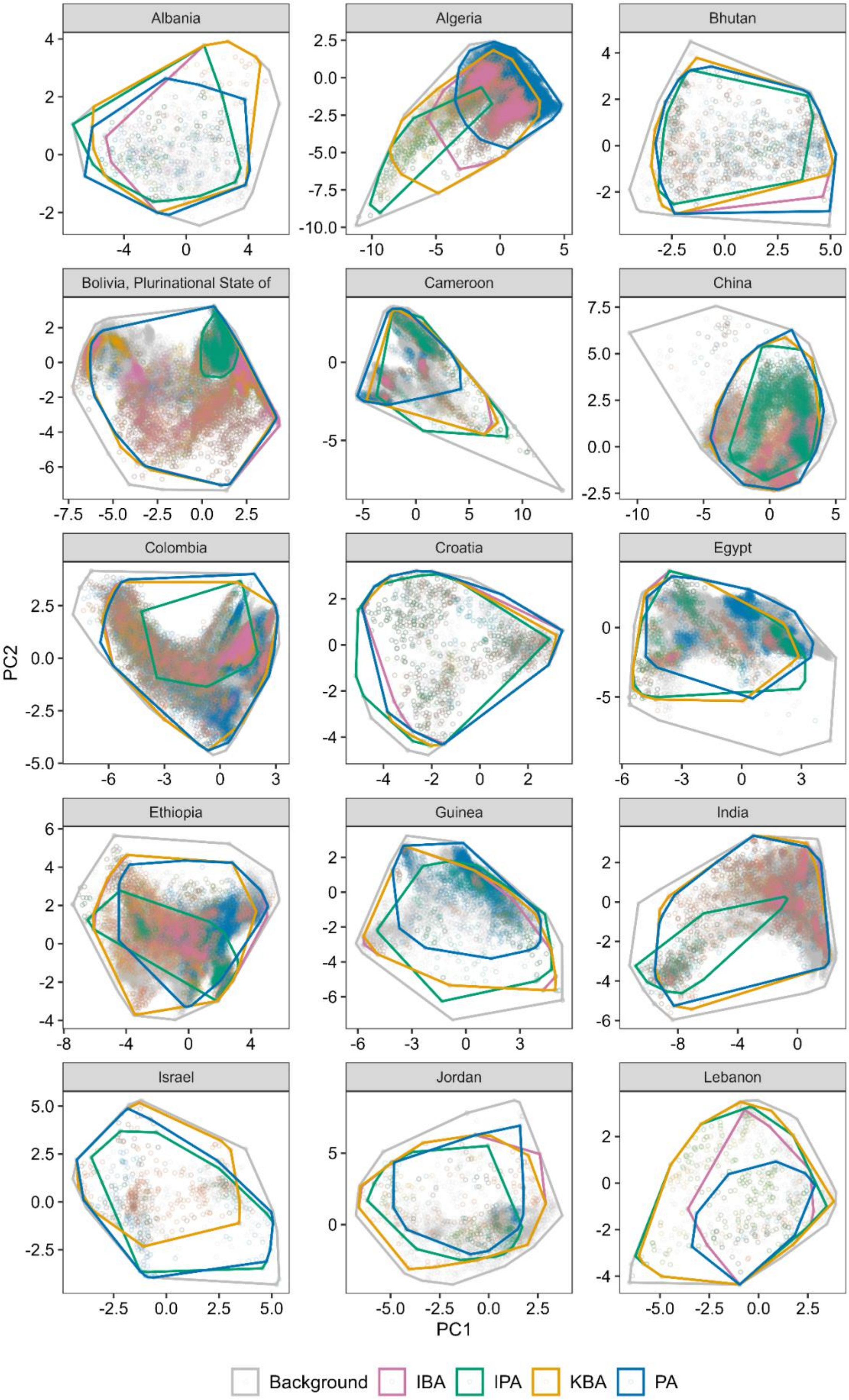
Appendix S13: Coverage of environmental space by Protected and Conserved Areas (PCAs) through time, based on principal component analysis of 13 environmental variables. PCA expansion is displayed at ten-year intervals from 1960 onwards. Points in environmental space are bounded by 99% minimum convex polygons (MCPs) for each time period and a 100% MCP for the background environmental space. The number of points sampled in each country was proportional to its geographic area.



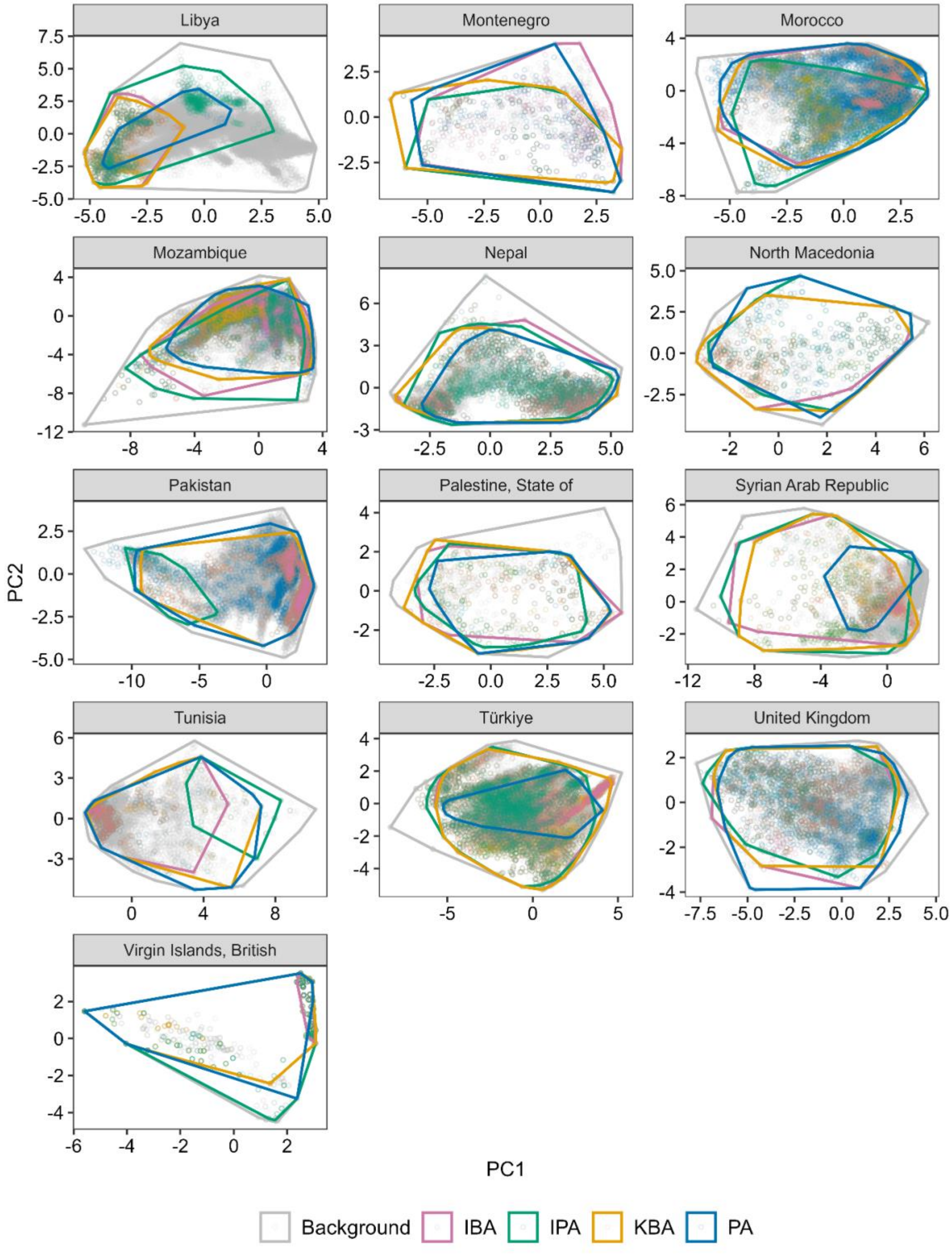
Albania
Algeria
Bhutan
Bolivia, Plurinational State of
Cameroon
Colombia
Croatia
Egypt
Ethiopia
Guinea
Israel
Jordan
Lebanon
Libya
Montenegro
0
25
50
75
1960
1980
2000
2020
Coverage of environmental space (%)
Year
PCAs
Important areas
Both



Appendix S14: Cumulative coverage of environmental space by Protected and Conserved Areas (PCAs) and areas of particular importance for biodiversity (important areas) through time, based on principal component analysis of 13 environmental variables. Area plots displayed separately for each of the studied countries.



Albania
Algeria
Bhutan
Bolivia, Plurinational State of
Cameroon
China
Colombia
Croatia
Egypt
Ethiopia
Guinea
India
Israel
Jordan
Lebanon
PC2
PC1
Background
IBA
IPA
KBA
PA



Appendix S15: Coverage of countries' background environmental space by Protected and Conserved Areas (PCAs), Key Biodiversity Areas (KBAs), Important Bird and Biodiversity Areas (IBAs), and Important Plant Areas (IPAs), based on principal component analysis of 13 environmental variables. Points in environmental space are bounded by 99% minimum convex polygons (MCPs) for each area and a 100% MCP for the background environmental space. The number of points sampled in each country was proportional to its geographic area.

Appendix S16: Comparisons of environmental coverage by Protected and Conserved Areas (PCAs), Key Biodiversity Areas (KBAs) and Important Plant Areas (IPAs), based on permutational multivariate analysis of variance (PERMANOVA) with pairwise post-hoc comparisons and post-hoc comparisons using Bonferroni correction. PERMANOVA results are displayed for each country separately and for all 28 countries combined. Significant values are emboldened.

	PERMANOVA		**Post-hoc pairwise comparisons**					
	PCA/KBA/IPA		**PCA/KBA**		**PCA/IPA**		**KBA/IPA**	
Country	**F**	**p-value**	**F**	**p-value**	**F**	**p-value**	**F**	**p-value**
Albania	1.32	0.231	NA	NA	NA	NA	NA	NA
Algeria	362.46	**0.001**	449.77	**0.003**	328.14	**0.003**	119.44	**0.003**
Bhutan	3.22	**0.007**	2.76	0.117	4.91	**0.018**	2.01	0.288
Bolivia ‡	45.81	**0.001**	2.32	0.135	84.59	**0.003**	87.27	**0.003**
Cameroon	22.25	**0.001**	21.53	**0.003**	36.86	**0.003**	5.83	**0.003**
China	180.31	**0.001**	78.06	**0.003**	285.68	**0.003**	192.20	**0.003**
Colombia	13.10	**0.001**	22.30	**0.003**	3.86	**0.018**	4.08	**0.021**
Croatia	1.14	0.326	NA	NA	NA	NA	NA	NA
Egypt	37.81	**0.001**	69.23	**0.003**	27.18	**0.003**	6.59	**0.003**
Ethiopia	77.91	**0.001**	117.89	**0.003**	47.08	**0.003**	39.88	**0.003**
Guinea	13.98	**0.001**	10.55	**0.003**	20.30	**0.003**	4.70	**0.006**
India	56.86	**0.001**	2.06	0.168	108.40	**0.003**	107.34	**0.003**
Israel	2.64	**0.005**	4.01	**0.009**	1.61	0.447	1.52	0.504
Jordan	4.14	**0.001**	6.20	**0.003**	5.30	**0.003**	1.65	0.399
Lebanon	0.94	0.468	NA	NA	NA	NA	NA	NA
Libya	19.51	**0.001**	10.55	**0.003**	1.28	0.726	35.10	**0.003**
Montenegro	1.10	0.342	NA	NA	NA	NA	NA	NA
Morocco	18.55	**0.001**	18.83	**0.003**	22.08	**0.003**	5.17	**0.003**
Mozambique	13.58	**0.001**	0.92	1.000	25.39	**0.003**	21.54	**0.003**
Nepal	11.13	**0.001**	5.60	**0.006**	21.66	**0.003**	6.91	**0.003**
North Macedonia	3.15	**0.003**	3.69	**0.042**	0.30	1.000	5.19	**0.012**
Pakistan	37.59	**0.001**	14.19	**0.003**	59.41	**0.003**	62.44	**0.003**
Palestine, State of	1.51	0.167	NA	NA	NA	NA	NA	NA
Syria †	3.22	**0.003**	1.64	0.441	2.80	0.069	4.43	**0.006**
Tunisia	9.04	**0.002**	3.51	**0.024**	18.53	**0.003**	10.78	**0.018**
Türkiye	11.86	**0.001**	1.34	0.663	2.27	0.096	22.23	**0.003**
United Kingdom	5.77	**0.001**	8.74	**0.003**	4.83	**0.018**	0.71	1.000
Virgin Islands, British	5.06	**0.009**	NA	NA	5.27	0.144	5.27	0.130
Global	61.72	**0.001**	69.12	**0.003**	81.63	**0.003**	25.42	**0.003**

‡ Plurinational State of Bolivia; † Syrian Arab Republic

Appendix S17: Environmental differentiation, for each retained variable, between Protected and Conserved Areas (PCAs), Key Biodiversity Areas (KBAs) and Important Plant Areas (IPAs), based on Kruskal-Wallis tests and post-hoc Dunn's tests with Bonferroni correction. We run each test on all 28 countries together, using a sub-sample of 10,000 points, wherein we retain the original data structure of points per country and per area. Significant values are emboldened.

	Kruskal-Wallis test		Dunn's test with Bonferroni correction						Median of raw values		
	PCA/KBA/IPA		KBA vs PCA		IPA vs PCA		IPA vs KBA		PCA	KBA	IPA
Variable	**H**	**p-value**	**z**	**p-value**	**z**	**p-value**	**z**	**p-value**			
Aspect	3.30	0.19	NA	NA	NA	NA	NA	NA	176.51	173.55	177.67
Clay	229.07	**< 0.01**	-15.13	**< 0.01**	-4.09	**< 0.01**	5.77	**< 0.01**	24.54	26.69	25.51
Nitrogen	566.74	**< 0.01**	-18.25	**< 0.01**	-19.37	**< 0.01**	-6.71	**< 0.01**	1.29	1.61	1.96
Sand	509.27	**< 0.01**	21.01	**< 0.01**	13.24	**< 0.01**	-0.84	1.00	47.29	41.03	40.30
Slope	449.48	**< 0.01**	-13.58	**< 0.01**	-19.16	**< 0.01**	-9.49	**< 0.01**	0.60	1.22	2.62
TPI	1.37	0.50	NA	NA	NA	NA	NA	NA	-0.24	-0.21	-0.17
Bio15	60.63	**< 0.01**	-7.35	**< 0.01**	-4.32	**< 0.01**	0.59	1.00	61.41	66.8	69.96
Bio19	433.58	**< 0.01**	-19.03	**< 0.01**	-12.94	**< 0.01**	-0.13	1.00	35.77	101.57	112.86
Bio2	495.98	**< 0.01**	17.41	**< 0.01**	17.80	**< 0.01**	5.76	**< 0.01**	12.93	11.53	11.18
Bio3	122.54	**< 0.01**	-1.34	0.54	10.30	**< 0.01**	10.61	**< 0.01**	47.65	58.37	42.97
Bio8	374.32	**< 0.01**	13.01	**< 0.01**	17.12	**< 0.01**	7.92	**< 0.01**	24.53	21.62	15.29
Bio9	356.06	**< 0.01**	14.82	**< 0.01**	15.02	**< 0.01**	4.78	**< 0.01**	23.55	22.26	21.47
Elevation	91.20	**< 0.01**	-5.65	**< 0.01**	-8.87	**< 0.01**	-4.80	**< 0.01**	490.02	618.02	735.45

Appendix S18: Contingency table used to analyse (using a chi-squared test of independence) the association between the number of threatened species from each taxonomic group with ranges overlapping each conservation network (Protected & Conserved Areas, Key Biodiversity Areas and Important Areas).

	PCA	KBA	IPA
Birds	318	331	167
Herptiles	650	772	252
Mammals	292	317	186
Plants	2305	2503	1607

Appendix S19. Number of additional species with ranges overlapping Important Plant Areas (IPAs) and/or Key Biodiversity Areas (KBAs), but not overlapping Protected and Conserved Areas (PCAs) in any of the studied countries.

	Threatened			Not Threatened		Endemic	
Taxon	**CR**	**EN**	**VU**	**NT**	**LC**	**Threatened**	**Not Threatened**
Birds	3	6	6	9	25	10	2
Herptiles	41	83	34	30	85	120	45
Mammals	7	14	7	2	30	17	3
Plants	165	146	63	22	141	286	56

Appendix S20: Contingency table used to analyse (using a chi-squared test of independence) the association between cells outside PCAs and inside important areas in 2010 and the same cells in 2024 that were either still outside PCAs or now inside PCAs. We excluded India and China as we were unable to extract accurate or comprehensive data on the year of PCA establishment for those countries.

	Outside PCA in 2024	Inside PCA in 2024	**Total**
Outside Important Area in 2010	357,065	14,868	371,933
Inside Important Area in 2010	18,040	3,313	21,353
Total	375,105	18,181	393,286

Appendix S21: Chi-squared test results for each country and across all 28 countries together, showing the association between cells outside PCAs and inside important areas in 2010 and the same cells in 2024 that were either still outside PCAs or now inside PCAs (Appendix S20). We exclude India and China as we were unable to extract accurate or comprehensive data on the year of PCA establishment for those countries. We report the chi-squared values, p values and Cramer's V values. Where values are NA, the given country did not have >= 1 cell in one or more components of contingency table. Significant values are emboldened.

Country	**X^2**	**p**	**Cramer's V**
Albania	22.34	**< 0.01**	0.18
Algeria	1038.37	**< 0.01**	0.16
Bhutan	8.22	**< 0.01**	0.11
Bolivia, Plurinational State of	409.08	**< 0.01**	0.11
Cameroon	122.39	**< 0.01**	0.09
Colombia	7465.52	**< 0.01**	0.46
Croatia	847.27	**< 0.01**	0.68
Egypt	4777.33	**< 0.01**	0.37
Ethiopia	7.68	**0.01**	0.01
Guinea	< 0.01	1.00	0.00
Israel	7.13	**0.01**	0.16
Jordan	61.67	**< 0.01**	0.14
Lebanon	0.30	0.58	0.09
Libya	NA	NA	NA
Montenegro	NA	NA	NA
Morocco	121.85	**< 0.01**	0.10
Mozambique	3438.07	**< 0.01**	0.40
Nepal	0.01	0.90	0.01
North Macedonia	246.24	**< 0.01**	0.55
Pakistan	1.33	0.25	0.01
Palestine, State of	32.15	**< 0.01**	0.43
Syrian Arab Republic	0.08	0.78	0.01
Tunisia	< 0.01	1.00	0.00
Türkiye	5.31	**0.02**	0.02
United Kingdom	< 0.01	1.00	0.00
Virgin Islands, British	NA	NA	NA
Global	6073.24	**< 0.01**	0.12

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