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Climate change drives functional transitions in conservation priority areas

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Abstract

Climate change is reshaping biodiversity, challenging conservation planning based on contemporary distributions and static priorities. Whether areas that remain spatially important under future climates will require different conservation responses remains unclear. Using ensemble species distribution models for 242 waterbird species across the East Asian–Australasian Flyway, we projected suitable habitat under three SSP scenarios for 2100 and quantified changes in species richness and community composition. We then developed a framework distinguishing three conservation functions, represented by persistence, intervention and emerging priorities. With increasing climate forcing, the proportion of species projected to lose suitable habitat rose from 56% to 69%. Strong community reassembly affected 33.8–73.1% of the analysis domain, exceeding the 17.6–32.3% experiencing significant richness change. Although 87.2% of each scenario-specific top 30% priority portfolio was shared across all scenarios, its functional composition changed markedly: persistence priorities declined from 74.8% to 34.9%, whereas intervention and emerging priorities together increased from 25.2% to 65.2%. Existing conservation areas covered only 12.3–12.9% of these portfolios. These findings show that spatial persistence of conservation priorities does not necessarily imply stability in their management needs. Climate-adaptive planning should therefore address both where priorities occur and how conservation responses must change.

Introduction

Climate change is reshaping the spatial organization of global biodiversity at an unprecedented rate[1,2]. Continuing changes in temperature, precipitation and climate extremes are driving contractions, expansions and geographical shifts in species ranges, with consequent changes in local species richness and community composition[1,2,3]. These dynamics challenge conventional conservation-planning approaches based on contemporary species distributions and biodiversity hotspots[4,5,6]. At the same time, the Kunming–Montreal Global Biodiversity Framework calls for the effective conservation and management of at least 30% of terrestrial, inland-water, marine and coastal areas by 2030—the 30×30 target[7]. Yet, as species distributions are reorganized, increasing the extent of protected land and water alone may not represent future biodiversity needs; conservation outcomes will depend strongly on where new areas are located, which ecological features they represent and how effectively they are managed[8,9]. Because protected-area boundaries are typically static and are often designed around current distribution patterns, existing conservation systems may implicitly assume that areas of high present-day value will remain similarly important in the future. Under a changing climate, however, some contemporary hotspots may undergo sustained species losses, whereas areas of limited current value may become centres of biodiversity as species redistribute[4,6]. The conservation challenge posed by climate change therefore concerns not only where priority areas will occur, but also which functions different areas will need to perform.

Areas may assume markedly different conservation roles under climate change, requiring climate-adaptive planning to move beyond the identification of a single set of future hotspots. Here, we define conservation function as the principal role that an area is expected to serve within a climate-adaptive conservation strategy. Within this framework, areas that retain high biodiversity and relatively stable community composition through time can be identified as persistence priorities, representing potential climatic refuges that require long-term maintenance[6,10]. Areas of high current conservation value that face substantial habitat loss or community reassembly may instead constitute intervention priorities, where habitat restoration, connectivity maintenance and adaptive management are needed to reduce future risk[4,11]. Conversely, areas that are not currently core hotspots may gain conservation value rapidly as species redistribute and new species arrive, creating emerging priorities for which space should be secured in advance[6,12]. Previous studies have proposed climate-adaptation strategies for protected areas and key sites and have identified spatial shifts between present and future priorities[6,11,12]. Most, however, have treated existing protected areas or predefined key sites as the analytical units and matched adaptation strategies to individual sites. The relative composition of different conservation functions across entire landscapes, and how these functions change systematically with increasing climate forcing, remain poorly quantified. Identifying a shift in conservation demand from maintaining persistence to active intervention and anticipatory action is therefore a prerequisite for building dynamic, future-oriented conservation networks.

Waterbirds provide a tractable system for examining how climate-driven redistribution alters conservation functions across large spatial scales. Their distributions are closely constrained by climate, hydrology and wetland availability[11,13], while their annual cycles link geographically distant breeding, stopover and wintering habitats. Consequently, changes occurring in one part of a migratory system may alter conservation requirements across multiple regions and jurisdictions. The East Asian–Australasian Flyway (EAAF) provides a particularly informative test system because it spans Arctic, temperate and tropical climate zones, encompasses diverse wetland ecosystems and supports more than 50 million migratory waterbirds from over 270 populations[14]. At the same time, many of its wetlands are exposed to rapid land-use change, habitat degradation and climate pressures[15,16], making the EAAF one of the most threatened of the world's eight recognized flyways[16,17]. Climate-driven redistribution may therefore not only reorganize existing patterns of waterbird diversity across the EAAF, but also create new spatial and functional mismatches between the current conservation network and future conservation needs.

Here, using a comprehensive dataset covering 242 of the 289 waterbird species initially compiled across the EAAF, we tested whether climate-driven biodiversity redistribution produces systematic transitions in the functions of conservation priority areas. We first quantified changes in suitable habitat, species richness and community composition to determine whether net richness change captures the full spatial extent of biodiversity reorganization. We then developed a climate-adaptive prioritization framework that distinguishes persistence priorities, intervention priorities and emerging priorities, and tested whether their relative contributions change consistently with increasing climate forcing. Finally, we assessed whether existing protected areas and 30×30-oriented expansion adequately represent these changing

functions. By linking species redistribution and community reassembly to changes in conservation function, our framework provides a transferable basis for evaluating climate adaptation needs in other dynamic conservation systems.

Results

Climate change drives pronounced latitudinal redistribution of waterbird diversity

Present-day species richness was spatially heterogeneous, with major concentrations along eastern China, the middle and lower Yangtze River basin and other wetland-rich regions of East and Southeast Asia (Fig. 1a). As climate forcing increased, the proportion of species projected to lose suitable-habitat area rose from 56% under SSP1–2.6 to 69% under SSP5–8.5 (Fig. S1). Among species with projected contractions, the mean loss increased from 19.1% to 40.9% and the median loss from 13.2% to 37.0% (Fig. S1; Supplementary Data 1). Among species with projected expansions, the mean gain increased from 21.0% to 55.0%, whereas the median ranged from 9.9% to 27.5% (Fig. S1; Supplementary Data 1). For migratory species with complete annual-cycle information, breeding and migration-stage habitats showed comparatively high risks of suitable-habitat loss (Fig. S2).

These species-level responses produced a pronounced latitudinal redistribution of waterbird diversity. Present-day diversity was concentrated at low to mid-latitudes, forming a continuous band of high richness at approximately 25°–35° N (Fig. S3). This band encompasses wetland-rich regions in northern South China, the southeastern coast and the middle and lower Yangtze River basin, where coastal tidal flats, river and lake floodplains, shallow lakes and artificial wetlands collectively support waterbirds during breeding, migration and wintering[18,19,20]. All three future scenarios projected declines in richness at lower latitudes and gains at middle to high latitudes, with the magnitude of change increasing with climate forcing (Fig. 1b–e). This pattern indicates an overall redistribution of EAAF waterbird diversity towards higher latitudes, consistent with the widespread poleward shifts expected under climate warming [21,22,23]. The largest decline occurred near 18.5° N and increased from 12 species under SSP1–2.6 to 27 species under SSP5–8.5; the largest gain occurred near 57.5° N and increased from 20 to 39 species (Fig. 1b). Climate change is therefore projected to alter not only the overall richness of suitable habitat for EAAF waterbirds, but also its latitudinal distribution.

Community reassembly is more widespread than significant changes in species richness

Concurrent species gains and losses indicated that net changes in richness can conceal substantial species replacement. By partitioning species retained, gained and lost between present-day and future scenarios, we found that local assemblage change commonly involved both gains and losses, and that their relative contributions shifted with increasing climate forcing (Fig. 2a–d). Under SSP1–2.6, gains

and losses totalled 5.28 million and 5.27 million species–grid-cell occurrences, respectively, and were therefore nearly balanced. Under SSP2–4.5 and SSP5–8.5, losses increasingly exceeded gains, yielding net changes of − 1.31 million and − 4.13 million species–grid-cell occurrences, respectively (Table S1a). The magnitude and relative contribution of gains and losses varied spatially; parts of northern Russia, Alaska and northwestern Australia, for example, experienced high levels of both (Fig. 2a–c), and their balance also showed a pronounced latitudinal pattern (Fig. 2d). Thus, as climate forcing increased, species losses contributed increasingly to flyway-wide assemblage change, while widespread gains and losses partly offset one another numerically.

Community reassembly covered a substantially greater area than changes in species richness. Within the pairwise domain defined by the union of present-day and future distributions for each scenario, the proportion of area undergoing a significant richness change after false-discovery-rate correction increased from 17.6% under SSP1–2.6 to 24.3% under SSP2–4.5 and 32.3% under SSP5–8.5 (Fig. S4; Table S1b); significant richness declines accounted for 8.8%, 14.4% and 21.4%, respectively. By contrast, mean Jaccard dissimilarity between present-day and future waterbird assemblages increased from 0.45 to 0.56 and 0.69, while the proportion of area undergoing strong community reassembly (Jaccard dissimilarity > 0.5) expanded from 33.8% to 49.6% and 73.1% (Fig. 2e–h; Table S1b). Strong reassembly was more extensive than significant richness change under every scenario and, under SSP5–8.5, covered approximately 2.3 times as much area (73.1% versus 32.3%). Assessments based only on net richness change would therefore substantially underestimate the spatial extent of climate impacts on waterbird assemblages.

Spatial overlays further revealed how significant richness change and strong community reassembly became increasingly coupled with climate forcing, while retaining distinct latitudinal patterns (Fig. 2i–l). Among areas with significant richness change, the proportion also undergoing strong reassembly increased from 34.8% under SSP1–2.6 to 47.9% under SSP2–4.5 and 67.4% under SSP5–8.5 (Fig. 2i–k; Table S1c). Overlap was consistently greater in areas of significant richness gain than in areas of significant richness loss: strong reassembly occurred in 49.3%, 69.8% and 91.3% of significant-gain areas across the three scenarios, compared with 20.4%, 32.9% and 55.2% of significant-loss areas. Particularly under stronger climate forcing, local richness gains therefore reflected the net outcome of extensive species gains and losses rather than the persistence or simple accumulation of the existing assemblage.

Climate forcing reconfigures the functions of spatially stable conservation priorities

Climate-adaptive conservation priorities showed strong spatial consistency across climate scenarios but underwent marked functional reconfiguration (Figs. 3a–c and 4a–c). Approximately 87.2% of the area within each scenario-specific Top 30% portfolio was consistently selected under all three scenarios (Fig. 4a–c). Despite this spatial stability, the functional composition of these priority areas changed

substantially with increasing climate forcing. Persistence priorities declined from 74.8% under SSP1–2.6 to 34.9% under SSP5–8.5, whereas intervention priorities increased from 4.4% to 35.9% (Fig. 3a–c). Emerging priorities also increased from 20.8% to 29.3% (Table S2a). Consequently, the combined contribution of intervention and emerging priorities increased from 25.2% under SSP1–2.6 to 65.2% under SSP5–8.5 (Table S2a). Thus, stronger climate forcing altered the functions required within priority areas more markedly than their broad spatial configuration. Future conservation demand therefore shifted from predominantly maintaining areas of high current value towards a greater dependence on active intervention and the anticipatory identification of future high-value areas.

Functional reconfiguration was accompanied by increasing overlap among conservation roles. Using a relative-contribution threshold of ≥ 30%, the proportion of dual-function areas increased from 56.5% under SSP1–2.6 to 74.0% under SSP5–8.5 (Fig. 3d–f; Table S2c). This increase was driven primarily by areas jointly supporting persistence and intervention functions, whose proportion rose from 24.9% to 53.4% (Table S2b). These patterns indicate that areas retaining substantial biodiversity value increasingly also face habitat loss or community reassembly, requiring long-term protection to be combined with active management rather than treated as mutually exclusive conservation strategies.

The functional transition was robust to alternative parameterizations and model structures. Across all 27 combinations of importance weights, risk weights and priority-area extents, persistence priorities consistently declined and intervention priorities consistently increased with stronger climate forcing (27 of 27 parameterizations; Fig. 3g–i; Table S3a-e; Supplementary Data 2). When only component weights were varied, continuous priority rankings remained highly correlated with the baseline parameterization (Spearman's $\rho > 0.998$), and area-weighted Jaccard overlap among the corresponding Top 30% portfolios exceeded 0.984. Alternative within-function operators and approaches for aggregating the three conservation functions produced the same overall direction of functional change (Fig. S5; Table S3a-e; Supplementary Data 2). Together, these analyses show that the shift from persistence-dominated priorities towards a greater contribution of intervention and emerging priorities was not an artefact of a particular weighting scheme, spatial threshold or aggregation rule.

The existing conservation network represented only 12.3–12.9% of the scenario-specific Top 30% priorities (Fig. S6). To determine whether the existing conservation network preferentially represented the highest-value areas, we divided each Top 30% portfolio into three mutually exclusive tiers (Top 0–10%, Top 10–20% and Top 20–30%). The highest-ranked Top 0–10% core areas were not better represented, with only approximately 10% currently protected, compared with 15–16% of the Top 20–30% tier (Fig. 4d–f). Protection gaps were also spatially and functionally uneven. The proportion of emerging priorities located outside present-day Top 30% species-richness hotspots increased from 30.3% under SSP1–2.6 to 37.2% under SSP2–4.5 and 49.7% under SSP5–8.5 (Fig. S7), while only 3.6% of intervention priorities that were robust across scenarios were represented within the existing conservation network, markedly less than the corresponding coverage of persistence and emerging priorities (Fig. S8). Retaining the existing network, we applied a common expansion budget of approximately 4.47 million km² under each scenario, bringing the total conservation portfolio to 30% of

the effective analysis domain (Fig. 4g–i). Priority additions were concentrated in currently under-represented but potentially high-value regions, including the eastern Mongolian Plateau, central and eastern China, the Korean Peninsula, Japan and coastal Southeast Asia. Nevertheless, even after reaching the 30% area target, approximately 42% of the climate-adaptive Top 30% priorities remained outside the final portfolio across all three scenarios, indicating that area-based expansion alone would not fully represent future spatial and functional conservation needs under climate change.

Discussion

Our results reveal two forms of change that may be overlooked in conservation planning based on species richness and the spatial location of priority areas. First, limited net changes in species richness can conceal extensive community reassembly. Second, conservation priority areas that remain spatially important across future climate scenarios can undergo functional transitions, meaning that the principal conservation role required at the same location shifts from maintaining persistence towards active intervention or anticipatory protection. Together, these findings suggest that climate-adaptive conservation requires attention not only to where biodiversity and priority areas are located, but also to how community composition and associated conservation needs differ under alternative climate futures.

Climate impacts on EAAF waterbirds were not expressed as a simple, spatially uniform decline in species richness; instead, they involved pronounced redistribution and extensive community reassembly. This finding demonstrates the limitations of using species richness alone to evaluate future conservation value. Biodiversity priorities are commonly identified from contemporary species distributions, richness or hotspot patterns[24,25], but richness does not reveal whether assemblage identity and composition remain stable[26,27]. An area may retain a similar number of species while undergoing substantial replacement, with consequences for ecological function, resource requirements and the identities of conservation targets[1,28]. Conservation planning based only on richness change may therefore underestimate the effects of climate change on regional biodiversity and should also account for changes in community composition and conservation targets.

Projected increases in species richness at middle and high latitudes should not be interpreted as ecological benefits of climate change. Local gains may arise primarily through the arrival of warm-affiliated species and may coincide with the loss of cold-affiliated species, population declines and biotic homogenization[29,30]. These regions may therefore become recipient areas for redistributed species, expanding their conservation function from maintaining existing assemblages to accommodating future biodiversity reorganization. Moreover, the emergence of climatically suitable space does not ensure that species will reach it or establish viable populations. Colonization is jointly constrained by dispersal capacity, wetland-network connectivity, migratory routes, land-use change and human disturbance[1,31,32]. The future suitable areas identified here should consequently be interpreted as potential climatic space,

whose realized conservation value will depend on habitat availability, spatial connectivity and accessibility to species.

The redistribution of richness and reassembly of communities ultimately produced a systematic shift in the functional composition of conservation priorities. With increasing climate forcing, high-priority areas shifted from dominance by persistence priorities towards a larger contribution from intervention and emerging priorities. Persistence priorities declined from 74.8% under SSP1–2.6 to 34.9% under SSP5–8.5, whereas intervention priorities increased from 4.4% to 35.9% and emerging priorities also became more prominent. As forcing intensified, a growing share of areas with high persistence value simultaneously faced species loss and community reassembly, making single, static functional classifications increasingly inadequate. Assessing where conservation is needed should therefore be complemented by an assessment of what conservation response is needed there.

Empirical evidence indicates that protected areas can perform multiple, dynamic functions as species redistribute. Compared with unprotected areas, protected areas support higher colonization rates and lower local extinction rates in waterbirds and are associated with smaller community-level climatic debts[30]. Studies of other taxa likewise show that colonization by range-expanding species occurs disproportionately within protected areas, which may serve as important establishment sites even when they were not originally designated for incoming species[33]. When climate risk coincides with habitat loss, wetland degradation or human disturbance, however, legal boundaries alone may be insufficient to maintain ecological function. The Yellow Sea intertidal zone, for example, is a critical stopover region for migratory shorebirds in the EAAF, and 20 years of monitoring have documented marked declines among species strongly dependent on these habitats[34]. Existing conservation instruments already provide partial foundations for these responses, including long-term site designation[35,36], invasive-species control[37], wetland restoration[38] and environmental-flow allocation[39], as illustrated by initiatives in the Yellow Sea–Bohai Gulf and the Murray–Darling Basin.

By comparison, anticipatory protection of future emerging priorities remains limited. Although the EAAFP Flyway Site Network has established a process for nominating new sites, its current criteria are based mainly on the occurrence of threatened species, observed waterbird abundance, proportions of populations, migratory aggregations and the importance of a site during critical annual-cycle stages[14,16]. These criteria can identify wetlands with demonstrated present-day conservation value, but do not explicitly incorporate future climatic suitability, projected community reassembly or the potential to receive redistributed species. Including such forward-looking indicators in Flyway Site Network nominations, protected-area expansion and the identification of other effective area-based conservation measures could secure space before emerging areas become future diversity centres and reduce the risk that land-use change forecloses future conservation options.

These results expose a structural limitation of area-based conservation targets. Global assessments show that the expansion of protected areas since 2010 has produced limited improvements in the representation of threatened species, Key Biodiversity Areas and ecoregions, while shortfalls in

ecological representation and management effectiveness remain widespread[8]. If new conservation areas are placed primarily where opportunity costs, development pressure or political resistance are low, high-risk areas and future recipient regions may remain under-represented even when the 30×30 target is met[40,41]. This tendency has been described as residual conservation: area coverage increases, but the additional reduction in threats or biodiversity loss remains small. Implementation of 30×30 should therefore account not only for area, but also for ecological representation, climate robustness and functional complementarity within conservation portfolios[8,42]. For the EAAF, a highly transboundary system connecting different annual-cycle stages, conservation action must also extend beyond national jurisdictions and static site boundaries to coordinate contemporary core areas, high-risk areas requiring active management and potential future recipient regions at the flyway scale[43].

More broadly, our findings suggest that climate adaptation should treat conservation priorities as dynamic functional portfolios rather than fixed spatial categories. Areas that remain spatially important may require substantially different management objectives as communities reorganize, while locations of limited current value may need protection before their future importance becomes evident. Integrating persistence priorities, intervention priorities and emerging priorities within a common framework can therefore help move conservation planning from static representation towards anticipatory management under climate change.

Methods

Species occurrence data and ensemble species distribution models

We compiled occurrence records for 289 waterbird species reported from the East Asian–Australasian Flyway (EAAF) between 2015 and 2023 from the China Bird Report and the Global Biodiversity Information Facility (GBIF), with the aim of characterizing their present-day distributions. Species taxonomy, migratory status and seasonal distributions were verified using eBird, Birds of the World and Guide to the Birds of China[44]. Occurrence records underwent three quality-control steps. First, duplicate records within the same 5 × 5 km grid cell were removed to reduce pseudo-replication and sampling bias. Second, range consistency was assessed by comparing records with distribution maps from the China Bird Report and BirdLife International; records outside these ranges were treated as potentially erroneous and excluded. Third, the coordinates and habitat plausibility of retained records were visually checked against Google Earth imagery and land-cover data, with particular attention to reversed coordinates, major positional errors and locations clearly inconsistent with species-specific habitat requirements. Records containing obvious errors that could not be corrected reliably were excluded[45]. To ensure sufficient data for model calibration, species represented by fewer than 15 occurrence records after quality control were not modelled. The final dataset comprised 242 species, representing 84% of the initial 289-species pool, and included 85% (183 of 216) of the migratory waterbird species listed by the EAAFP (Supplementary Data 1).

Because migratory waterbirds occupy different areas and have distinct environmental requirements across the annual cycle, we fitted stage-specific species distribution models for breeding, migration and wintering; non-migratory species were modelled using year-round distributions. Annual-cycle stages and their geographical extents were determined from seasonal distribution information in the sources described above and used to assign occurrence records to stages. To avoid constraining future projections artificially to present-day stage-specific boundaries, we buffered the known range of each stage by 500 km, following previous studies[11,46,47], and used the buffered area for model calibration and future projection. Bioclimatic and land-use variables were used as environmental predictors. Candidate climate predictors were drawn from the 19 WorldClim bioclimatic variables. Present-day climate was represented by the WorldClim baseline for 1970–2000, whereas future climate conditions centred on 2100 were represented by 20-year climatological averages for 2081–2100 under SSP1–2.6, SSP2–4.5 and SSP5–8.5. For each scenario, future climate layers were averaged across seven CMIP6 global climate models: UKESM1–0-LL, MRI-ESM2–0, MPI-ESM1–2-HR, MIROC6, IPSL-CM6A-LR, HadGEM3-GC31-LL and EC-Earth3-Veg. Scenario- and year-specific land-use projections were obtained from the original dataset and matched to the corresponding SSP and target period. Species–environment relationships were fitted under present-day environmental conditions and projected to SSP1–2.6, SSP2–4.5 and SSP5–8.5 in 2100. All environmental predictors and subsequent spatial datasets were harmonized to a resolution of 5 × 5 km. Pairwise Pearson correlations confirmed that no predictor pair exceeded $|r| = 0.70$, reducing the risk of unreliable inference caused by collinearity [48].

Ensemble species distribution models were fitted with the R package biomod2 using six algorithms: generalized additive models (GAM), generalized linear models (GLM), multivariate adaptive regression splines (MARS), maximum entropy (MAXENT), random forests (RF) and extreme gradient boosting (XGBOOST). For each species–stage combination, we generated two random sets of pseudo-absences, with the number of pseudo-absences equal to the number of presences or set to 100 when fewer than 100 presences were available. Each dataset was randomly partitioned five times, with 75% used for model training and 25% for evaluation[45]. Model performance was assessed using the area under the receiver operating characteristic curve (AUC) and the true skill statistic (TSS), which respectively quantify overall discrimination and threshold-dependent classification performance. AUC ranges from 0 to 1 and TSS from − 1 to 1, with larger values indicating better performance. Because subsequent analyses of community composition and species richness used binary distributions, TSS was used to screen and weight ensemble components. Models with TSS < 0.60 were excluded, and retained models were averaged using weights proportional to their TSS values[45]. Based on mean performance across ten replicate evaluations for each species–stage model, the median AUC across models was 0.938 (s.d. = 0.045) and the median TSS was 0.753 (s.d. = 0.105) (Fig. S9), indicating good overall discriminatory performance. Continuous suitability predictions for present-day and future conditions were converted to binary suitable–unsuitable maps using the threshold that maximized TSS during model calibration. Full model settings and workflows are provided in the code repository.

Species-richness redistribution and community-reassembly analyses

Using binary suitable-habitat maps for each species under the present-day baseline and future scenarios (SSP1–2.6, SSP2–4.5 and SSP5–8.5), we assessed species richness, species-level habitat change and community reassembly across EAAF waterbirds. Local richness was calculated by stacking suitable-habitat maps across all species for each period, and richness change was expressed as future minus present-day richness. For each future scenario, analyses were restricted to the pairwise domain defined by the union of grid cells containing at least one species under baseline or the corresponding SSP. Significant richness change was identified by applying an exact McNemar test to species gains and losses in each grid cell[49], followed by Benjamini–Hochberg false-discovery-rate correction within each future scenario[50]; grid cells with $q < 0.05$ were considered significant. The direction of change was determined from the difference between the numbers of gained and lost species. Latitudinal patterns of local richness and richness change were summarized within 1° latitude bands. To quantify climate-driven community reassembly, we compared species composition under present-day and future conditions in each grid cell and counted retained, lost and gained species. Jaccard dissimilarity was then used to quantify compositional differences between present-day and future assemblages[51], with larger values indicating stronger reassembly.

Identification of climate-adaptive conservation priorities

Using present-day and future species richness, species loss, species gain and Jaccard community dissimilarity across all study species—denoted R_c, R_f, L, G and J, respectively—we developed a climate-adaptive conservation-prioritization framework. After rescaling each metric to 0–1, we calculated biodiversity importance, persistence and climate risk as follows:

$$Importance = 0.5R_c + 0.5R_f$$

1

$$Persistence = \sqrt{R_c R_f}$$

2

$$Risk = 0.5L + 0.5J$$

3

Here, Importance integrates present-day and future biodiversity value, Persistence emphasizes areas that retain high richness in both periods, and Risk represents the combined climate risk arising from species loss and community reassembly.

We then defined three complementary conservation functions:

$$Persistence\ priority = \sqrt{Persistence(1 - J)}$$

4

$$Intervention\ priority = \sqrt{Importance \times\ Risk}$$

5

$$Emerging\ priority = \sqrt{R_f G}$$

6

These functions identify persistence priorities that maintain high biodiversity and relatively stable assemblages, intervention priorities with high biodiversity value but substantial climate risk, and emerging priorities characterized by high future richness and pronounced species gains. For each scenario, the integrated conservation-priority score was defined as the maximum of the three functional scores. All conservation-prioritization analyses were conducted within a common effective biodiversity analysis domain, defined as the union of 5-km grid cells containing suitable habitat for at least one waterbird species under present-day conditions or any of the three future climate scenarios. The same spatial mask was held constant across SSP1–2.6, SSP2–4.5 and SSP5–8.5. Within this domain, grid cells were ranked in descending order of their scenario-specific integrated priority scores and accumulated according to their actual areas, with the highest-ranking 30% designated as the scenario-specific priority portfolio.

Within each scenario-specific Top 30% portfolio, we calculated the relative contributions of persistence priorities, intervention priorities and emerging priorities and represented functional composition using continuous ternary colour mixtures. We treated a contribution of ≥ 30% as evidence that a function made a substantive contribution within a grid cell and classified cells as single-, dual- or three-function areas to quantify multifunctional overlap in conservation demand. Emerging priorities were also compared with present-day Top 30% species-richness hotspots to identify future emerging areas outside current hotspots. Finally, we overlaid priority areas with the existing conservation network, defined here as the combined spatial coverage of protected areas (PAs) and other effective area-based conservation measures (OECMs), to quantify current representation and conservation gaps for scenario-specific, robust and function-specific priorities. Hereafter, we refer to this combined network as the PA network. Starting from the existing PA network, we retained all currently conserved areas within the common effective analysis domain and added currently unprotected grid-cell fractions in descending order of their scenario-specific climate-adaptive priority scores. Addition continued until the combined area of the existing network and newly selected areas reached 30% of the domain.

To test whether the identified conservation functions depended on particular weights, integration rules or priority-area thresholds, we varied the relative weights assigned to present-day versus future importance, species loss versus Jaccard dissimilarity, and the spatial extent of priority areas, and recalculated functional and integrated priority scores using alternative mathematical operators. The core sensitivity analysis comprised 27 parameter combinations. We additionally compared geometric mean, arithmetic mean and minimum operators for combining indicators within functions, and maximum, arithmetic mean and geometric mean operators for aggregating the three functional scores. Multifunctional classifications were tested using contribution thresholds of 25%, 30% and 33%. Robustness was evaluated by comparing the area represented by each dominant function and its trajectory across climate scenarios under alternative parameterizations and structures. Spearman rank correlations and area-weighted Jaccard indices quantified, respectively, the consistency of continuous priority rankings and the spatial overlap of Top 30% portfolios with the baseline. Full procedures are described in the Supplementary Methods.

Data availability

All datasets used in this study are publicly available subject to their respective licence conditions. Species occurrence data were obtained from the China Bird Report (http://www.birdreport.cn/) and GBIF (http://www.gbif.org/); bioclimatic data from WorldClim (https://www.worldclim.org/); land-use data from Figshare (https://doi.org/10.6084/m9.figshare.12967760); and protected-area and OECM data from the June 2026 Protected Planet release (WDPA_Jun2026_Public_shp; accessed 25 June 2026; https://www.protectedplanet.net/).

Code availability

All custom R code used for ensemble species distribution modelling, climate-scenario projections, community-reassembly analyses and climate-adaptive conservation prioritization is provided: https://doi.org/10.6084/m9.figshare.34883142

Declarations

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Ethics declarations

Competing interests: The authors declare no competing interests.

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Figures

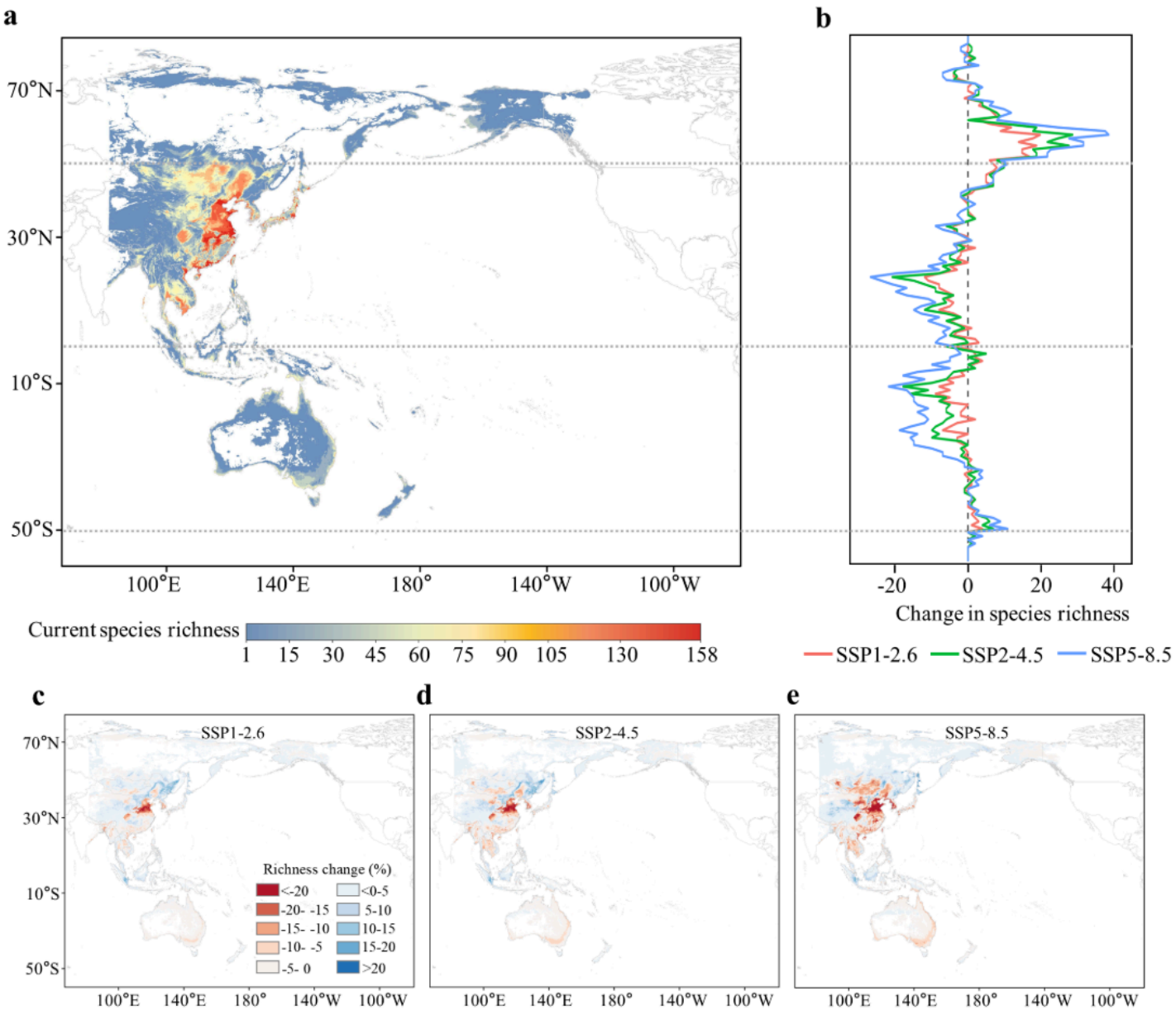


Figure 1

Projected spatial and latitudinal redistribution of suitable-habitat species richness in EAAF waterbirds under climate change.

a, Current spatial distribution of local suitable-habitat species richness under the baseline scenario, with warmer colours indicating higher richness. **b**, Latitudinal profiles of absolute changes in species richness under SSP1–2.6, SSP2–4.5 and SSP5–8.5 relative to baseline scenario. The vertical dashed line denotes no net change, whereas positive and negative values indicate richness gains and losses, respectively. **c–e**, Spatial distributions of percentage changes in local species richness under SSP1–2.6 (**c**), SSP2–4.5 (**d**) and SSP5–8.5 (**e**) relative to baseline scenario. Red shades indicate richness losses and blue shades indicate richness gains, with darker colours representing larger magnitudes of change. White areas

indicate grid cells outside the effective analytical domain or cells for which percentage change could not be calculated.

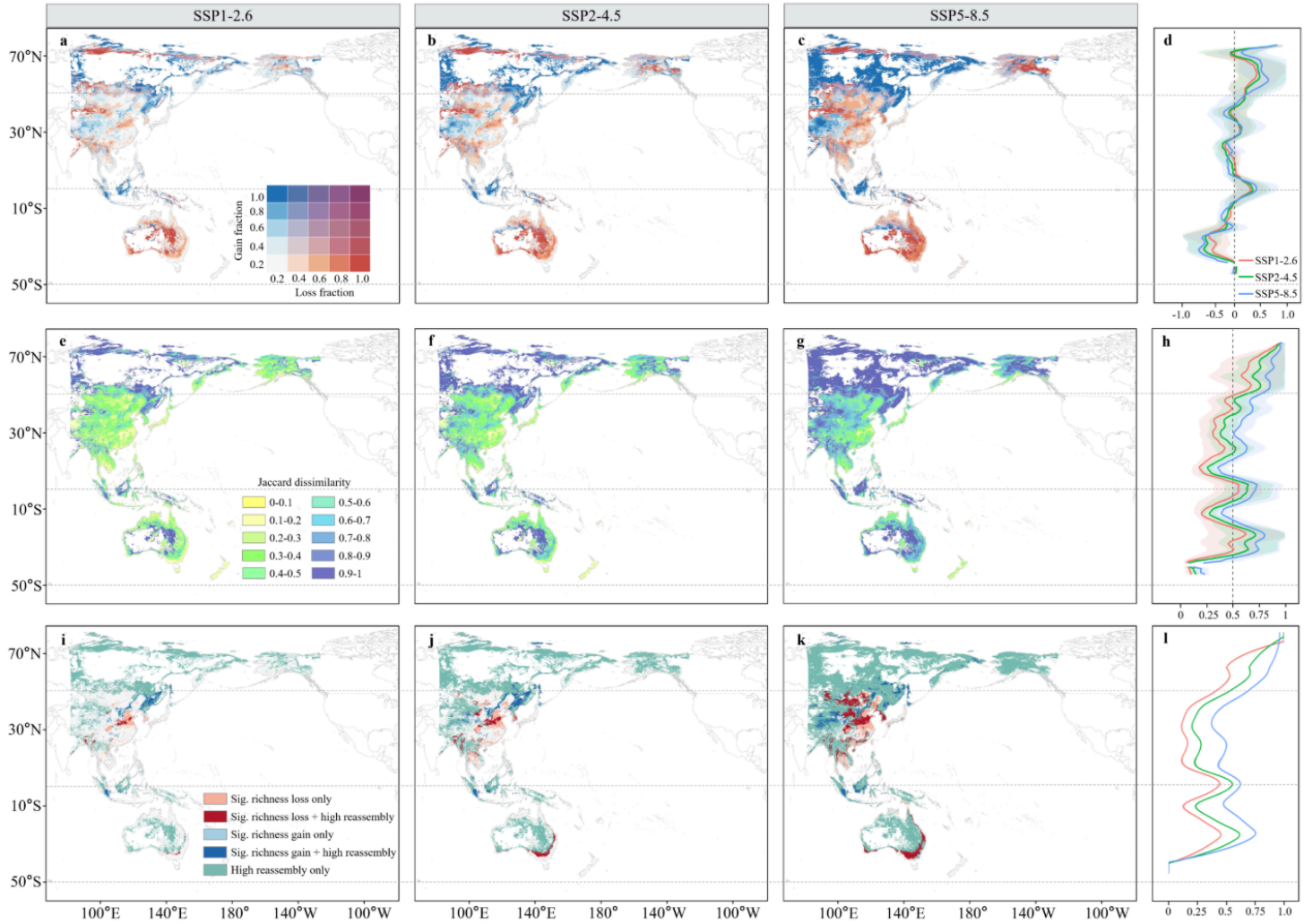


Figure 2

Projected community reassembly and its spatial decoupling from changes in species richness across EAAF waterbirds.

Columns correspond to SSP1–2.6, SSP2–4.5 and SSP5–8.5. **a–c,** Spatial patterns of community change represented by the bivariate combination of the fractions of species lost and gained relative to the present-day baseline. Blue shades indicate gain-dominated change, red shades indicate loss-dominated change and purple shades indicate concurrent high levels of species gain and loss. **d,** Latitudinal profiles of gain–loss balance, calculated as the fraction of gained species minus the fraction of lost species. Positive values indicate gain-dominated change, negative values indicate loss-dominated change and the vertical dashed line denotes equal contributions of gains and losses. **e–g,** Jaccard dissimilarity between present-day and future waterbird assemblages, with larger values indicating stronger compositional reassembly. **h,** Latitudinal profiles of Jaccard dissimilarity; the vertical dashed line marks the threshold for strong community reassembly (Jaccard dissimilarity > 0.5). In **d**and **h**, solid lines show

latitudinal means and shaded areas show the 25th–75th percentile ranges across grid cells. **i–k,** Spatial overlap between statistically significant changes in local species richness and strong community reassembly. Statistical significance was assessed using exact McNemar tests with false-discovery-rate correction. **l,** Latitudinal variation in the proportion of grid cells undergoing strong community reassembly without a statistically significant change in species richness.

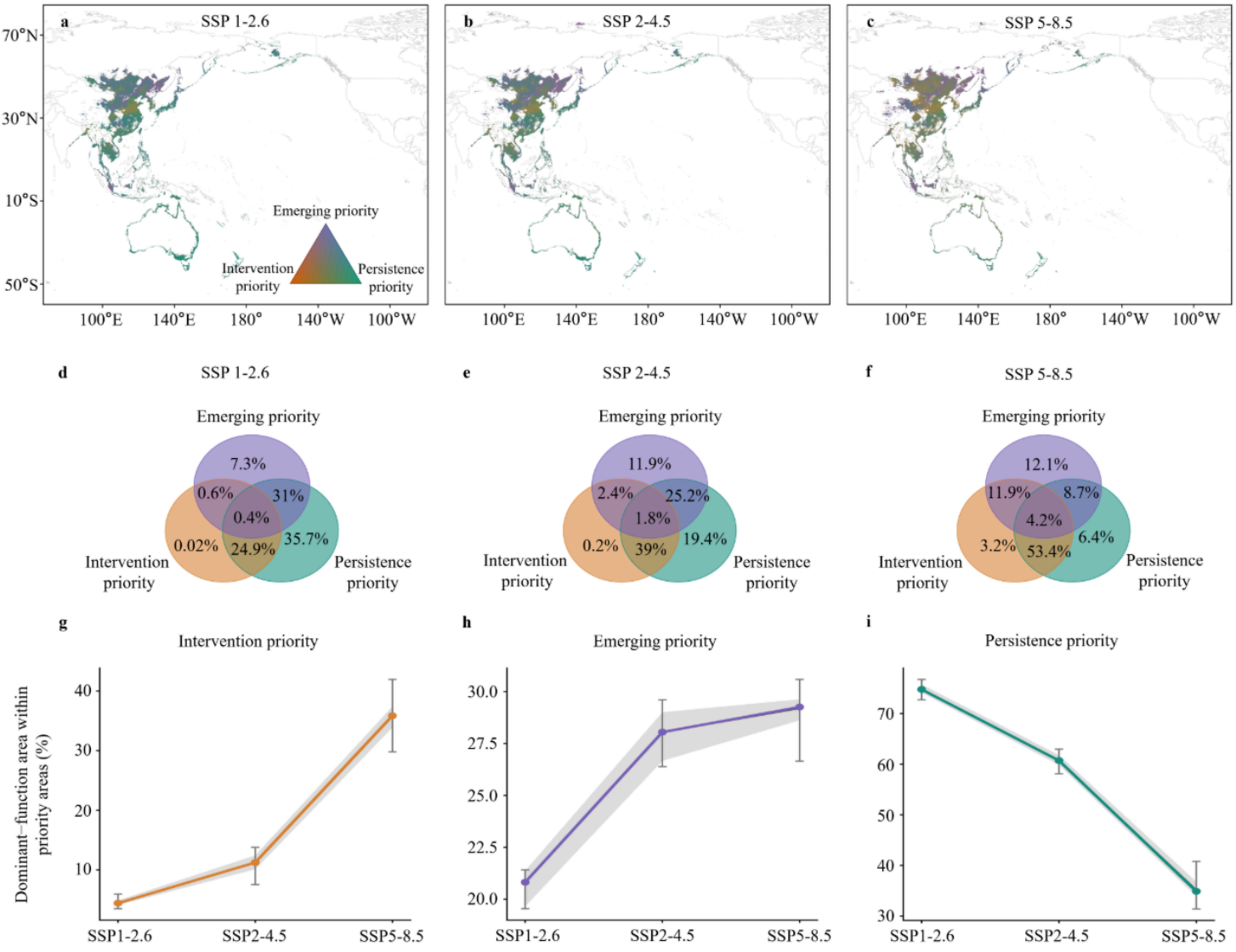


Figure 3

Climate forcing shifts climate-adaptive conservation from persistence priorities towards intervention and emerging priorities.

a–c, Spatial composition of conservation functions within the scenario-specific Top 30% climate-adaptive priority areas under SSP1–2.6 (**a**), SSP2–4.5 (**b**) and SSP5–8.5 (**c**). Ternary colours represent the relative contributions of persistence priorities, intervention priorities and emerging priorities in each grid cell, with colours approaching a vertex indicating a larger contribution of the corresponding function. **d–f,** Functional combinations within the Top 30% priority areas under SSP1–2.6 (**d**), SSP2–4.5

(**e**) and SSP5–8.5 (**f**). A function was considered represented when its relative contribution was ≥30%; non-overlapping sectors indicate single-function areas, whereas intersections indicate dual- or three-function combinations. Values denote the percentage of the scenario-specific Top 30% area assigned to each combination. **g–i,** Sensitivity of the proportions of priority areas dominated by intervention priorities (**g**), emerging priorities (**h**) and persistence priorities (**i**) across future climate scenarios. The dominant function was defined as that with the largest relative contribution. Sensitivity analyses jointly varied the weights assigned to present-day versus future species richness in the importance metric (0.4:0.6, 0.5:0.5 and 0.6:0.4), the weights assigned to species loss versus Jaccard community dissimilarity in the risk metric (0.4:0.6, 0.5:0.5 and 0.6:0.4), and the spatial extent of priority areas (Top 20%, Top 30% and Top 40%), yielding 27 parameterizations. Vertical error bars show the minimum–maximum range, grey bands show the interquartile range, and coloured lines and points show the baseline parameterization using equal weights and a Top 30% priority extent.

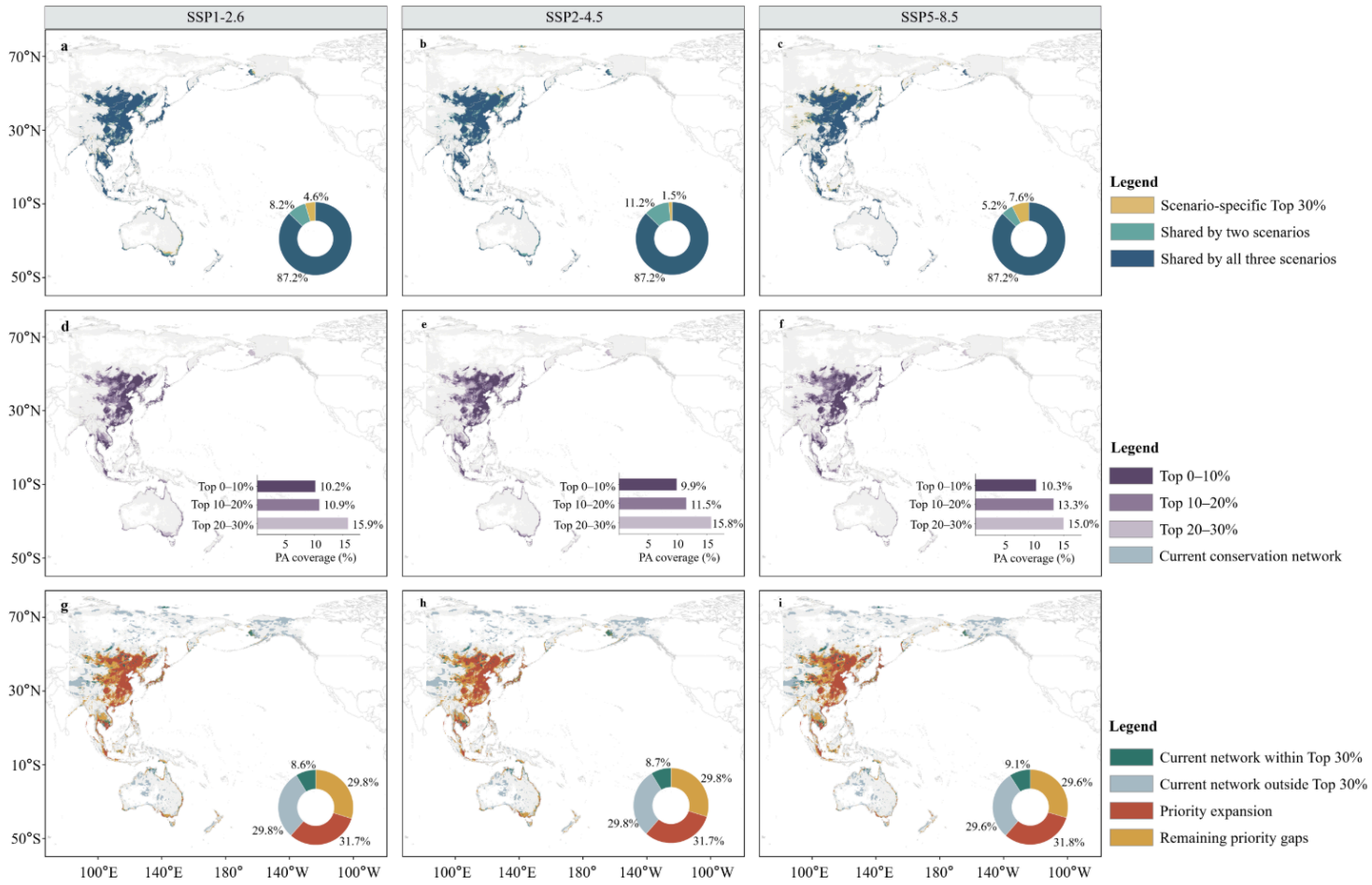


Figure 4

Existing protection and 30×30 expansion leave substantial gaps in climate-adaptive conservation priorities.

Columns correspond to SSP1–2.6, SSP2–4.5 and SSP5–8.5. **a–c,** Cross-scenario consistency of scenario-specific Top 30% climate-adaptive conservation-priority areas. Grid cells are classified as

unique to one scenario, shared by two scenarios or shared by all three scenarios. Donut charts show the areal proportions of these consistency classes within each scenario-specific Top 30% portfolio. **d–f,** Representation of priority tiers within the existing conservation network, comprising protected areas (PAs) and other effective area-based conservation measures (OECMs). Each scenario-specific Top 30% portfolio was divided into three mutually exclusive tiers—Top 0–10%, Top 10–20% and Top 20–30%—according to the climate-adaptive priority score. Insets show the proportion of each tier currently covered by the network. **g–i,**Priority-based expansion of the existing conservation network towards the 30×30 target. All areas within the existing network were retained, and unprotected grid cells were added in descending order of climate-adaptive priority until the combined network reached 30% of the effective biodiversity analysis domain. Maps distinguish the existing network within Top 30% priorities, the existing network outside the Top 30%, priority areas added during expansion and high-priority areas remaining outside the expanded portfolio. Donut charts show the area-weighted proportions of these four mutually exclusive spatial classes within the union of the existing conservation network and the scenario-specific Top 30% priority portfolio.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SupplementaryData2.xlsx
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- SupplementaryInformation.docx
- ReportingSummary.pdf