Conservation Biology

Dependence of Europe's most threatened mammals on movement to adapt to climate change

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Abstract

Current rates of climate change and gloomy climate projections confront managers and conservation planners with the need to integrate climate change into already complex decision-making processes. Predicting and prioritizing climatically stable areas and the areas likely to facilitate adaptive species' range adjustments are important stages in maximizing conservation outcomes and rationalizing future land management. I determined, for the most threatened European terrestrial mammal species, the spatial adaptive trajectories (SATs) of highest expected persistence up to 2080. I devised simple spatial network indices for evaluation of species in those SATs: total persistence; proportion of SATs that offer in situ adaptation (i.e., stable refugia); number of SATs converging in a site; and relationship between SAT convergence and persistence and protected areas, the Natura 2000 and Emerald networks, and areas of low human disturbance. I compared the performance of high-persistence SATs with a scenario in which each species remained in the areas with the best climatic conditions in the baseline period. The 1000 most persistence SATs for each of the 39 species covered one fifth of Europe. The areas with the largest adaptive potential (i.e., high persistence, stability, and SAT convergence) did not always overlap for all the species. Predominantly, these regions were located in southwestern Europe, Central Europe, and Scandinavia, with some occurrences in Eastern Europe. For most species, persistence in the most climatically suitable areas during the baseline period was lower than within SATs, underscoring their reliance on adaptive movements. Importantly, conservation areas (particularly protected areas) covered only minor fractions of species persistence among SATs, and hubs of spatial climate adaptation (i.e., areas of high SAT convergence) were seriously underrepresented in most conservation areas. These results highlight the need to perform analyses on spatial species' dynamics under climate change.

KEYWORDS
30 by 30, adaptation, connectivity, conservation planning, optimization, protected areas, species distribution model, species range

INTRODUCTION

Climate change is a key driver of biodiversity loss and ecological dysfunction (Lovejoy & Hannah, 2019). If current change rates continue—leading to a 4.5°C temperature increase by 2050 relative to the preindustrial period—16% of species will be at a high risk of extinction, with some species groups being affected at even greater scales (IPCC, 2022; Urban, 2015). Even with a global temperature rise of 1.5°C relative to the preindustrial period, climate change is poised to become the leading driver of biodiversity loss (WWF, 2022).

Climate change affects ecological systems and hinders the effectiveness of conventional conservation practices (Hannah et al., 2002). For many species, local fitness is directly affected by climate change, making local conservation efforts to support species' robustness and resilience a top priority (Hällfors et al., 2016). Climate-induced changes in species' dynamics have the potential to disrupt established communities and create new ones. To address these changes, innovative management approaches will be required (Hobbs et al., 2009; Lindenmayer et al., 2008). This could lead to increased species turnover in protected areas and, consequently, decreased effectiveness of

such areas. Numerous species will shift their ranges in response to climate change, exposing them to hazards and emphasizing the need for conservation efforts outside formally protected zones (Krosby et al., 2010; McGuire et al., 2016). Furthermore, the dynamics of and unpredictability of changes in ecological systems under climate change will require substantial increases in conservation investments to facilitate habitat connectivity and expansion and redefinition of protected areas (Hoffmann et al., 2019).

To develop long-term land management policies that promote biodiversity, decision makers must anticipate how species will respond to climate change. In addition to areas with stable climates (i.e., climate refugia), attention should be given to regions where species are likely to adapt to climate change through habitat protection or restoration (D'Aloia et al., 2019). Some of these adaptive areas may benefit one or more species for extended periods, and others (transient areas) may provide benefits for shorter periods, typically for a single species or small group of species (Littlefield et al., 2019; McGuire et al., 2016). The differing values of adaptive areas means that distinct conservation strategies need to be implemented across the landscape (D'Aloia et al., 2019).

Although many researchers have studied the impacts of climate change at the level of species' ranges (e.g. Morrison et al., 2018; Pacifici et al., 2018, 2020), only a few have examined the potential adaptive routes of species as they follow climates most suitable to them (Alagador et al., 2014, 2021; Graham et al., 2010; Williams et al., 2005). Such assessments complement range-based studies by identifying the areas within changing species' ranges most likely to provide spatiotemporal climatic connectivity for species and the periods that offer high adaptive value. Those trajectories may be used as analytical conservation units because they catch the movement of a species through time (each trajectory defines a chain of time-ordered grid cells—with each grid cell referring to a particular period of time—which a species may use and whose persistence depends on local environmental suitability and the success of dispersal among grid cells).

Finding extensive sets of spatial adaptive trajectories (SATs) for one or multiple species may pinpoint critical areas for spatial adaptation, enhancing the conservation importance of these areas. If an area is predicted to be valued in the future, then its management needs to be planned in advance. Likewise, if the value of an area decreases substantially, then its release from conservation focus ought to be considered (although controversial in the light of the downgrading–downsizing debate) after careful analyses of the associated pros and cons (Fuller et al., 2010; Mascia & Pailler, 2011).

I sought to provide planners and decision makers at the national and EU levels with the necessary tools to perform strategic evaluations of landscape management, thereby supporting the natural or assisted adaptation of species to climate change. Such assessments are pivotal in aiding EU member states in achieving their pledge to conserve 30% of land within protected areas by 2030, with one third of these areas strictly managed for nature conservation. Additionally, I aimed to offer projections for extended time frames to ensure that forthcoming land-use policies integrate the mechanisms through which species can adapt to climate change.

I had 2 main objectives: first, to use SAT analysis as a framework for assessing a set of spatial network metrics designed to guide conservation area prioritization over the long term and, second, to apply these metrics to conduct a comprehensive analysis of how the most threatened European terrestrial mammal species are expected to adapt spatially to climate change up to 2080. By combining bioclimatic niche modeling and dispersal models with an algorithm that identifies persistence-optimized SATs, I aimed to pinpoint areas conferring the largest adaptive response for each species; areas where multiple SATs converge (at a species level and for the entire set of 39 threatened mammal species); and the proportions of SATs that represent local areas of adaptation (i.e., stable refugia). Furthermore, I assessed the relationship and overlap of SATs with current nationally designated protected areas, the Natura 2000 and Emerald networks, and levels of habitat disturbance (i.e., the human footprint index). I sought to emphasize the urgency of proactive planning to preserve the ecological value of areas crucial to climate adaption for the analyzed species.

METHODS

Species

I focused on terrestrial mammal species currently occurring in European countries (excluding Armenia, Azerbaijan, Georgia, and Russia) and listed as near threatened, vulnerable, endangered, and critically endangered on the European Red List of Species (https://www.eea.europa.eu/data-and-maps/data/european-red-lists-7). Global maps of current species' ranges were gathered from the International Union for Conservation of Nature (IUCN) website. I selected only range polygons classified as native, extant, and probably extant (https://www.iucnredlist.org/). From the initial set of species ($n = 47$), 8 were excluded because of their reduced range size, which limits the performance of bioclimatic models. Thirty-nine species were retained (Table 1). For 8 of these species, the most recent European Atlas of Mammal Species (https://www.european-mammals.org/emma2/) provided surplus range area. I merged this with IUCN's data and used it as input data in the bioclimatic modeling. I preferred to use data that might be inconsistent over missing polygon data. Appendix S1 contains a map of richness patterns of the analyzed species.

Bioclimatic modeling

I undertook an ensemble forecasting of bioclimatic models (Araújo & New, 2007) with 8 bioclimatic variables spanning a set of thermal and precipitation conditions considered important in limiting the distribution of mammal species (Pacifici et al., 2018): annual mean temperature, mean diurnal range, temperature seasonality, minimum temperature of coldest month, mean temperature of warmest quarter, total annual precipitation,

TABLE 1 Statistics on the species for which their spatial adaptive trajectories (SATs) under climate change were examined.

Species	Abbreviation	Threat status[a]	Range area (km²)	True skill statistic[b]	Body mass (g)	Dispersal (km/year)	Dispersal (km/20 years[c])	Dispersal (km/20 years[d])
Allactaga major	Ama	NT	4,946,688	0.85–0.97	350	1.5	30	45
Arvicola sapidus	Asa	VU	912,896	0.88–0.99	220	1.5	30	45
Barbastella barbastellus	Bba	VU	4,224,000	0.89–0.97	8.3	7.5	150	225
Bison bonasus	Bbo	NT	74,752[e]	0.91–0.97	610,000	30	600	900
Desmana moschata	Dmo	VU	1,536,000	0.91–0.99	333	1.5	30	45
Dinaromys bogdanovi	Dbo	VU	82,432[e]	0.87–0.99	100	1.5	30	45
Eliomys quercinus	Equ	LC	2,671,872	0.79–0.96	82	1.5	30	45
Galemys pyrenaicus	Gpy	EN	206,592[e]	0.86–0.99	80	1.5	30	45
Gulo gulo	Ggu	VU	39,500,800	0.84–0.95	25,000	30	600	900
Lepus castroviejoi	Lca	VU	21,760[e]	0.91–1.00	2800	15	300	450
Lepus corsicanus	Lco	VU	110,080	0.90–0.99	5000	15	300	450
Lutra lutra	Llu	NT	32,477,696	0.73–0.87	12,000	30	600	900
Lynx pardinus	Lpa	EN	141,568[e]	0.89–0.99	16,000	30	600	900
Mesocricetus newtoni	Mne	NT	71,424[e]	0.93–1.00	98	1.5	30	45
Microtus cabrerae	Mca	NT	119,552[e]	0.93–0.99	52	1.5	30	45
Miniopterus schreibersii	Msc	VU	1,965,312	0.87–0.97	14	7.5	150	225
Mustela lutreola	Mlu	CR	9,497,600	0.88–0.97	800	3	60	90
Myomimus roachi	Mro	EN	21,504	0.93–1.00	70	1.5	30	45
Myotis bechsteinii	Mbe	VU	2,872,320	0.91–0.98	10	7.5	150	225
Myotis blythii	Mbl	NT	6,006,016	0.73–0.92	23	7.5	150	225
Myotis capaccinii	Mcp	VU	1,206,016	0.89–0.97	8.2	7.5	150	225
Myotis dasycneme	Mda	NT	7,120,896	0.84–0.96	15	7.5	150	225
Myotis punicus	Mpu	NT	592,384	0.86–0.99	25	7.5	150	225
Oryctolagus cuniculus	Ocu	NT	620,032	0.92–0.99	2500	15	300	450
Plecotus kolombatovici	Pko	NT	909,312	0.91–0.98	12	7.5	150	225
Plecotus macrobullaris	Pma	NT	995,584	0.87–0.96	12	7.5[f]	150	225
Plecotus sardus	Psa	VU	23,040	0.92–1.00	10	7.5	150	225
Rhinolophus blasii	Rbl	VU	3,005,184	0.81–0.92	18	7.5	150	225
Rhinolophus euryale	Reu	VU	2,908,672	0.82–0.91	18	7.5	150	225
Rhinolophus ferrumequinum	Rfe	NT	9,132,800	0.79–0.92	23	7.5	150	225
Rhinolophus hipposideros	Rhi	NT	6,157,312	0.78–0.93	9	7.5	150	225
Rhinolophus mehelyi	Rme	VU	1,857,792	0.83–0.95	14	7.5	150	225
Sorex alpinus	Sal	NT	456,192	0.87–0.98	8	1.5	30	45
Spalax arenarius	Sar	EN	2304	0.92–1.00	660	3	60	90
Spalax graecus	Sgr	VU	54,272[e]	0.93–1.00	570	3	60	90
Spalax zemni	Sze	VU	192,000	0.90–0.99	550	3	60	90
Spermophilus citellus	Sci	EN	461,824	0.89–0.98	240	1.5	30	45
Spermophilus suslicus	Ssu	NT	961,280	0.87–0.97	250	1.5	30	45
Vormela peregusna	Vpe	VU	7,988,224	0.87–0.93	715	1.5	30	45

[a]From European Red List: NT, near threatened; VU, vulnerable; EN, endangered.

[b]Range obtained across all models.

[c]Maximum dispersal in a year and dispersal rates in 20 years' time for the most restrictive scenario.

[d]Maximum dispersal in a year and dispersal rates in 20 years' time for the less restrictive scenario (i.e., 50% more than the most restrictive scenario).

[e]Range size obtained by merging International Union for Conservation of Nature Red List polygon data with European Atlas Data.

[f]Data obtained from congeneric species.

precipitation seasonality, and precipitation of driest quarter. Climate data were obtained from the Worldclim platform (https://www.worldclim.org/) at 10-arc-minute (for model calibration) and 5-arc-minute (for model projection) resolutions from 3 CMIP6 global circulation models (GCMs: MIROC6, HadGEM3-GC31, CanESM5) with effective climate sensitivities (2.6 K for MIROC6 to 5.6 K for CanESM5) spanning the full spectra of sensitivities (1.8−5.6 K) across 27 CMIP6 models (Zelinka et al., 2020). Data were collected and averaged for 4 periods of 20 years (baseline, 2021–2040; 2040, range 2041–2060; 2060, 2061–2080; 2080, 2081–2100) for 2 CMIP6 shared socioeconomic pathways (SSP245 and SSP585) that define medium–low and high emissions scenarios, respectively (Eyring et al., 2016).

Current species' distribution polygons were gridded using the 10-arc-minute resolution (∼15 × 15 km) grid from baseline climate data as a template. Grid cells with more than 50% area encompassing distribution polygons for a species were considered occurrence grid cells. Grid resolution for model calibration was chosen to fit the coarser resolution of atlas data when compared with polygon data. Bioclimatic models were run using biomod2 (Thuiller et al., 2009), a package in CRAN-R (https://cran.r-project.org/), to fit 5 niche model types (artificial neural networks, generalized additive models, generalized linear models, random forests, and maximum entropy [i.e., Maxent]) for each species. The climatic predictors were standardized on a zero-one scale. Models were calibrated using 10 random samples made of 80% occurrence data and evaluated on the remaining 20% with the model-specific default parameters in biomod2. For each run, 5 random samples of pseudoabsences were obtained. The number of pseudoabsences was the lowest between 10 times the number of species' occurrences or 10,000. For each species and SSP 750, models were built: 5 model types × 3 GCMs × 10 data partition × 5 pseudoabsence selection. Models with true skill statistic (TSS) values <0.7 were discarded because values far from 1 reflect poor predictive ability (Allouche et al., 2006).

Once calibrated, models were projected to 5-arc-minute resolution (∼7.5 × 7.5 km) in each of the 4 periods, SSPs, and GCMs. The rescaling was performed to increase the resolution of the predictions, under the assumption that species–climate relationships among approximated calibration and projection scales are maintained. Projections were made with a TSS-weighted consensus map among the 5 modeling techniques. Final consensus outputs were obtained after averaging the TSS-weighted maps among the 3 GCMs. To remove effects of sample size when comparing models for species with distinct prevalence, I corrected suitability values with the favorability function (Acevedo & Real, 2012). Favorability corrects local suitability for a species from what is expected by its prevalence, thus making the scores comparable among species. As a result, favorability values >0.5 occurred where local conditions favored the presence of the species. Favorability corrections were made in CRAN-R. For convenience, the favorability scores obtained for each species were designated by suitability.

In the baseline period, where a species occurrence was not recorded (i.e., <50% polygon overlap), the corresponding suitability score was set to zero. For future periods, to overcome plausible situations of species being recorded in sink areas (i.e., areas of low fitness), I defined unsuitable areas as those 5 × 5-arc-minute grid cells (henceforth sites) with suitability projections lower than the 10th percentile score obtained in the baseline period among the sites with species records.

Dispersal models

A model of dispersal success (d_D^s) related to the geographic distance between a source and a colonizing site was built for each species with dispersal rate information from Jones et al. (2009) (Table 1):

$$\begin{cases} d_D^s = \exp\left(-\alpha . \dfrac{D}{D_{\max}^s}\right), & D \leq D_{\max}^s, \\ d_D^s = 0, & D > D_{\max}^s, \end{cases} \tag{1}$$

where d_D^s is dispersal success of species s moving between any pair of sites separated by a distance D. The $D_{\max}^s$ parameters are the maximum distance species s is able to disperse in 20 years. Alongside median dispersal rates, possible long-distance dispersal events were accounted for with $D's_{\max} = 1.5 \times D_{\max}^s$. For each of the 39 species, I used the same simplified exponential decaying function over geographic distance (Equation 1), assuming that habitat and suitable climates for the establishment, survival, and reproduction of populations will exist between the source and the receptor areas throughout the 20-year interval between time slices (i.e., the dispersal periods) and that populations will disperse directly to the closest suitable receptor site. The measure of dispersal success ranged from zero to one. I parameterized α to produce 2 settings of dispersal success corresponding to $d_{D\max}^s = 0.05$ and $d_{D\max}^s = 0.025$ (i.e., in 1000 dispersal events from a source to a receptor site distancing $D_{\max}^s$, only 50 and 25 events were presumed successful in fixing a population, respectively).

Spatial adaptive trajectories

The dispersal corridor concept originally proposed in Alagador et al. (2014) was used to represent the SATs of species (i.e., time-ordered chains of areas that a species may potentially inhabit through time). An SAT is an ordered set of sites (i_0, i_1, …, i_T), where each site corresponds to one period of time (Figure 1). An index of persistence for a species s in an SAT (P_{SAT}^s) was settled using 2 ecological descriptors that modulate the spatial responses of species to climate change (i.e., local climatic suitability and dispersal success):

$$P_{SAT}^s = o_{i_0}^s \times d_{D(i_0,i_1)}^s \times o_{i_1}^s \times d_{D(i_1,i_2)}^s \times \ldots \times d_{D(i_{T-1},i_T)}^s \times o_{i_T}^s, \tag{2}$$

where an SAT is made by the sites i_0, i_1, …, i_T referenced to the periods 0, 1, …, T, respectively; $o_{i_t}^s$ is the estimated suitability in site i for species s during period t (suitability increases from zero to one); $D(i,j)$ is the distance between
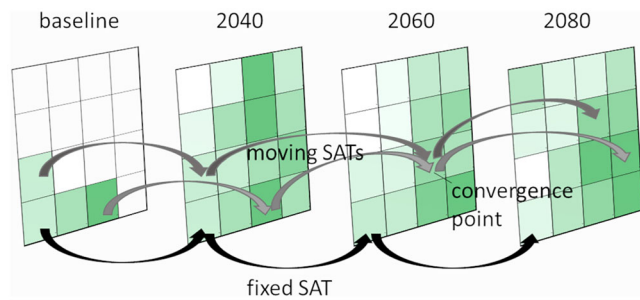
FIGURE 1 A set of 4 conservation planning units (SATs [spatial adaptive trajectories]) (gridded squares, a site at a certain period; green shading, suitability gradient [one per period]; black arrows, fixed SAT of a unique site selected for all periods; gray arrows, moving or dynamic SATs with >1 site; convergence point, 2 SATs converge when they cross the same site at the same period).

sites i and j (geographic distance herein); and $d_{D(i,j)}^s$ is the dispersal success of species s when moving from i to j (Equation 1). Although suitability scores estimated over time may be obtained from bioclimatic niche modeling or other predictive techniques, the quantification of dispersal processes may be settled using approaches with different data demand. General approaches, as the one here implemented, establish simple relationships between the geographic distance of dispersal events and colonization success, but functional connectivity models may be employed, but this implies large computational resources because local, idiosyncratic characteristics will determine dispersal movements.

An SAT may be a single site used throughout all the periods analyzed, thus mimicking a stable, in situ response (i.e., $i_0 = i_1 = \ldots = i_T$). In this case, $d_{D(i,i)}^s = 1$ (Equation 1). Potentially, P_{SAT}^s ranges from zero, when at least one of the factors in the product is zero, to one, when local suitability and dispersal success along the SAT are repetitively maximum (i.e., one). The persistence index P_{SAT}^s can be calculated using the information provided in the more commonly available data (i.e., local suitability predictions derived from the bioclimatic models and dispersal success obtained from empirical or experimental dispersal kernels), and if $o_{i_t}^s$ and d_D^s refer to true probabilities, P_{SAT}^s can be interpreted as the probability of success of a population of species s to persist along the SAT from a baseline period until T.

For each species, I identified the 1000 SATs with the largest persistence scores with the algorithm developed by Martins et al. (1999), where all existing SATs from a virtual source point (upstream the maps referring to the baseline period) to a virtual destination point (downstream the maps respecting the final period) are ranked on their persistence values. The identification of top persistence adaptive trajectories for each species was made for each of the 2 SSPs and the 4 dispersal assumptions (made by combining the 2 D_{max}^s with the 2 α parameterizations). Analyses were carried out with C++ programing in iC5 (Alagador & Cerdeira, 2020b).

The selection of 1000 SATs per species was made under the rationale that 1000 is a sufficient number of 5-arc-minute sites

to grasp most of SATs with positive persistence scores, so as to provide minimum guarantees of persistence for a species.

Protected areas, Natura 2000, and Emerald network

I assessed whether species' persistence along SATs relates to existing protected areas and high-level conservation areas in Europe made up of the Natura 2000 and the Emerald networks. The latter is a system of conservation areas in countries that are not part of the European Union but are members of the Council of Europe (i.e., Norway, Balkans, and eastern Europe countries) (Appendices S2 & S3).

Protected area boundaries were obtained from the Word Database on Protected Areas website (https://www.protectedplanet.net) on June 2023. Analyses were restricted to the I–IV protected area categories as these are the areas where biodiversity conservation goals are most enforced. Protected areas whose reference was limited to point data (i.e., encompassing a small number of protected areas with small sizes) were disregarded; those described by polygons were maintained. Protected area polygons were clipped using the European landform mask file (https://ec.europa.eu/eurostat/web/gisco) to remove marine protected areas and to keep the land fractions of mixed protected areas (i.e., occurring on land and coastal waters). The clipping procedure was undertaken with ArcGIS.

The Natura 2000 is a network of areas of conservation focus that, established under the principles of complementarity and redundancy, are at the scale of the European Union. I obtained the latest version of Natura 2000 distribution data from https://ec.europa.eu/environment/nature/natura2000/data/index_en.htm (revised in October 2022). Because this last version omits sites in the United Kingdom that are still maintained as conservation areas under UK national legislation, UK Natura 2000 sites were obtained from the 2017 version.

For Norway, the Balkans, and the easternmost countries, I used the Emerald Network areas—a precursor of Natura 2000 directives settled under the Council of Europe and based on premises of the Bern Convention. The location of these areas was downloaded from the European Environmental Agency repository on the Emerald Network (https://www.eea.europa.eu/en/datahub/datahubitem-view/4c4c8086-c940-400b-9064-29063143b2de). I used the ArcGIS join function to merge the 2 Natura 2000 data sets with the Emerald data set. The areas were clipped using the Europe landforms shapefile to keep only their terrestrial component. For simplicity, I refer to these merged data sets as Natura 2000 sites.

Protected areas and Natura 2000 polygons were transformed into 5-arc-minute grid sets by assessing the areal fraction of each site covered by each one of these area networks. Calculations were undertaken in ArcGIS by intersecting conservation area polygons with the 5-arc-minute grid.

Human footprint

The human footprint index (Venter et al., 2018) is a composite index made of 8 different sources of human-driven disturbance. Defined globally, it shows the levels of cumulative human pressure in 1-km^2 grid cells (40 × 40 arc seconds). The human footprint data were scaled up to match the 5-arc-minute sites by estimating the area-weighted average of the footprint index inside each 5-arc-minute site. Analyses were carried out in ArcGIS (Appendices S2 & S3).

Analyses

First, I identified the locations of the top 1000 SATs for each species under each of the 4 dispersal scenarios and the 2 SSPs (Appendix S4). I then calculated the average number of SATs from each species crossing each site across different dispersal scenarios (i.e., a measure of SAT convergence), the average persistence of those SATs, and the average number of time periods (i.e., one to 4) that a site was used in an SAT (i.e., to assess the stability value of each SAT site). The SAT convergence was transformed into a measure of SAT redundancy:

$$\text{redun } d_s = 1 - \frac{1}{\text{mxconv}_s}, \tag{3}$$

where mxconv$_s$ is the maximum theoretical level of convergence among the SAT sites of species s.

The 3 site-based SAT metrics above were measured alongside site coverage in protected areas and Natura 2000 and with the human footprint values. I used linear regression models as simple descriptors to outline the general relationship between SAT site properties and local conservation and disturbance statuses. A similar analysis was performed in which I merged the SATs of all species. In this case, I complemented the above-mentioned site metrics with one that counts for each site the number of species using it through an SAT. Regression analyses were carried out in R-CRAN with the lm function.

To measure at what levels the persistence of species in SATs relies on species movements, I compared the persistence scores associated with the 1000 optimized SATs with the persistence scores if a species remains fixed in the 1000 sites with the greatest suitability in the baseline period. For each species, the number of SATs depicting a stable, in situ response from the baseline period up to 2080 was also measured. Finally, I estimated the persistence of each species in SATs crossing sites with high density or large extents of protected areas and Natura 2000 (i.e., sites with over 50% conservation area coverage) and using sites with very low levels of human disturbance (i.e., human footprint index <5 [0–50 scale]) (Appendix S3).

RESULTS

The 1000 SATs highlighted for the each of the 39 analyzed species were well distributed throughout Europe. The total area
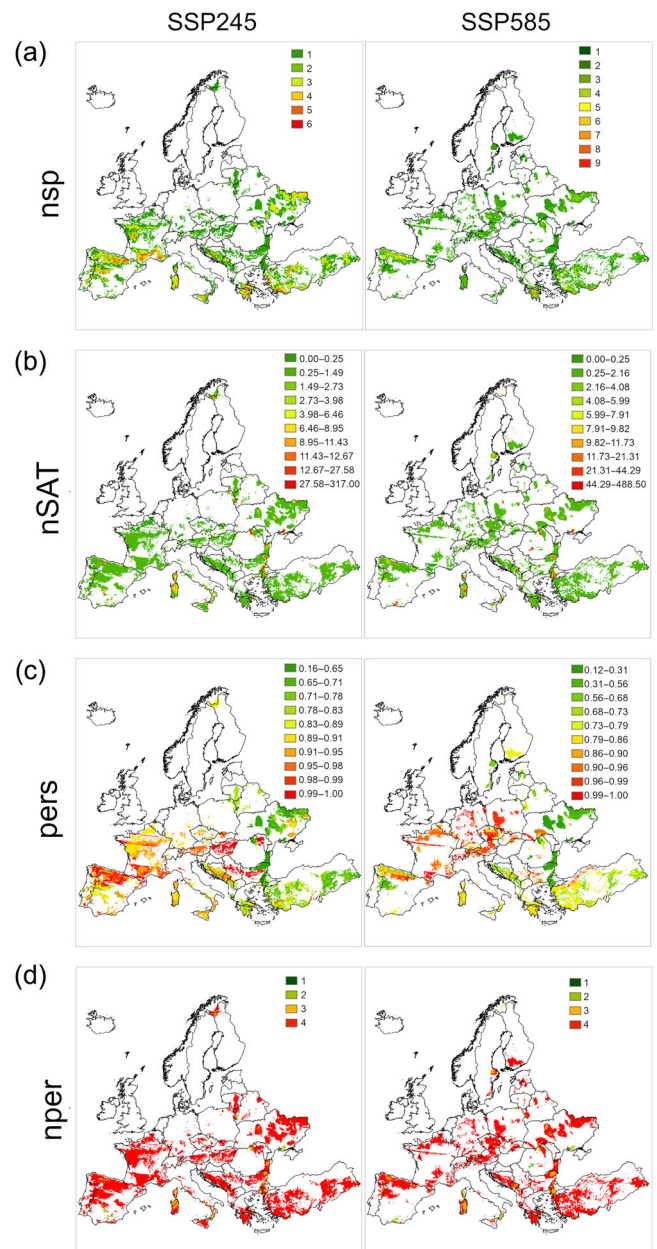

FIGURE 2 Distribution of spatial adaptive trajectories (SATs) for threatened European mammals based on climate change scenarios SSP245 and SSP585 and averaged among the 4 dispersal scenarios with different (a) numbers of species (nsp), (b) average numbers of SATs (nSAT), (c) average persistence scores among SATs (pers), and (d) average periods in a SAT (nper).

encompassed by SATs was larger with SSP245 (1,325,000 km^2: 19.9% of the focal area) than with SSP585 (1,112,000 km^2: 16.7% of the focal area). The regions with the highest average number of SATs per species were small and were located in northern Finland, north of the Iberian Peninsula, Corsica, Sardinia, Romania, Bulgaria, northwestern Turkey, Byelorussia, and southern Ukraine (Figure 2, ncor). For SSP585, a similar pattern emerged, but Scandinavia did not exhibit the same high SAT density per species. The maps showing the average number of SATs per species closely fit the maps illustrating the number

of species utilizing those SATs (Figure 2, nsp). In these maps, a longitudinal strip in the northern Iberian Peninsula, some areas in southern France, patches in Sardinia, eastern Ukraine, and southeastern Turkey were highlighted for SSP245 and SSP585, although in the latter scenario, more species (i.e., maximum 9 species) were expected to pass over SAT sites than with SSP245 (i.e., maximum 6 species). See Appendix S5 for maps illustrating SATs for each species.

When examining the average persistence along SATs, the largest clusters were observed in northern Iberian Peninsula, southern France, Hungary, Slovakia, Austria, Czech Republic, Bulgaria, Serbia, and Ukraine under the SSP245 scenario (Figure 2, pers). In contrast, for SSP585, high levels of SAT persistence were anticipated in a narrow region of northern Iberian Peninsula and various scattered areas across Central Europe (patterns obtained for each species in Appendix S6). Furthermore, assessments of SAT stability revealed certain areas where SAT turnover was high (i.e., sites used in one period) (Figure 2, nper). These areas occurred mainly in Central and southern Iberian Peninsula and some parts of Ukraine (for SSP245). Maps of SAT stability at a species level are in Appendix S7.

When considering individual species, the average persistence in the topmost SATs was in general higher in SSP245 than in SSP585. In the former, 6 species exhibited less than half the maximum theoretical persistence, whereas in the latter, this number increased to 10 species (Figure 3; Appendix S8). Under scenario SSP245, 7 species were projected to achieve more than 95% the maximum theoretical value, whereas under SSP585, only 3 species were expected to reach such high levels of persistence.

Under SSP245, two thirds of the species (*n* = 26) had their highest persistence SATs fixed in the same sites (i.e., in situ responses) from the baseline period until 2080 (Figure 3; Appendix S9). This value decreased to 18 under SSP585. Under this latter scenario of change, most of the species presented a higher dependency on moving SATs because fixed SATs tended to decrease substantially (e.g., *Gulo gulo* showed approximately half of SATs in fixed areas under SSP245 and only 5% of SATs in SSP885).

Comparing the total persistence of species in the optimized SATs with the total persistence in the sites featuring the most suitable climates in the baseline period, distinct responses among the analyzed species were observed (Figure 3; Appendix S10). Again, there was a reduced dependence of species persistence on baseline-fixed sites in SSP585 compared with SSP245. In SSP245, a substantial proportion of persistence was obtained from the most suitable areas in the baseline period, whereas in SSP585, SATs relied far less on those areas (Appendix S11).

On average, the overall species persistence within SATs was lower in nationally designated protected areas than in Natura 2000 and Emerald network sites, as well as in the less disturbed areas in Europe (Figure 3; Appendix S12). The SAT persistence in protected areas showed greater variability among dispersal scenarios and yielded different results depending on the SSP considered; species with the largest captured persistence in protected SATs differed in both scenarios. In general, a small set of species presented the highest SAT persistence representation, although they varied among the 3 area systems (i.e., protected areas: *G. gulo* and *Bison bonasus* for SSP245 and *Lepus castroviejoi* for SSP585; Natura 2000 sites: *L. castroviejoi*, *Lynx pardinus*, and *B. bonasus*; less disturbed areas in Europe: *G. gulo* and *L. castroviejoi*). Of concern is the finding that for a large number of species, SAT persistence in the 3 area systems was substantially low, jeopardizing the persistence expectancies of these species in areas with current conservation focus and in good-quality habitats. Results at the species level are in Appendices S14 and S15.

The 2 SSPs analyzed showed different relationships between SAT locations and the 3 area systems (Appendix S13). For example, under SSP245, the sites with the largest number of SATs for *B. bonasus* related significantly and positively with the density of both conservation area systems, but under SSP585, the trend was inverted with respect to protected areas. In this climate scenario, high levels of SAT convergence for *G. gulo* and *Plecotus sardus* related positively with Natura 2000 networks (Appendix S15). The SAT convergence related negatively with habitat disturbance for *L. pardinus*, *Spalax arenarius*, *L. corsicanus*, and *Plecotus sardus*. These patterns were not consistent in the comparison of the SAT stability and persistence in SATs against conservation area systems. In the latter case, statistically significant relationships with few positive relationships occurred when persistence and the human footprint index were compared. For a third of the species, the less disturbed areas encompassed the sites with the largest SAT persistence (Appendix S15, SSP585). Overall, linear relationships were mostly not statistically significant and even the significant ones exhibited weak correlations (Appendix S14).

DISCUSSION

Climate change puts conventional conservation measures to the test. There is a need to integrate the dynamics of change in spatial conservation actions and tools. I showed how the identification of SATs may go in that direction and be used to assist proactive decision-making for the management of and planning for conservation lands in the long term (up to 2080).

Although traditional assessments have typically focused on shifts in species' ranges (Fordham et al., 2013; Taheri et al., 2021; Thuiller et al., 2011), my framework introduces novel indices that rely on SATs and climate impact assessments and long-term conservation planning. These indices may serve a dual purpose: evaluating the effectiveness of current conservation areas and aiding in forward-looking conservation planning. The latter involves considering the timing of when specific areas are predicted to become critical for species persistence, as indicated by SATs (Alagador et al., 2014; Drechsler, 2005). To assess both the present and future conservation needs of species, I introduced quantitative indices obtained from the analysis of SATs (network analysis): overall species persistence in the set of SATs expected to provide the most viable pathways for species to adapt to climate change; proportion of SATs encompassing fixed sites (i.e., where species are found consistently for the entire time horizon of analysis under optimized climate
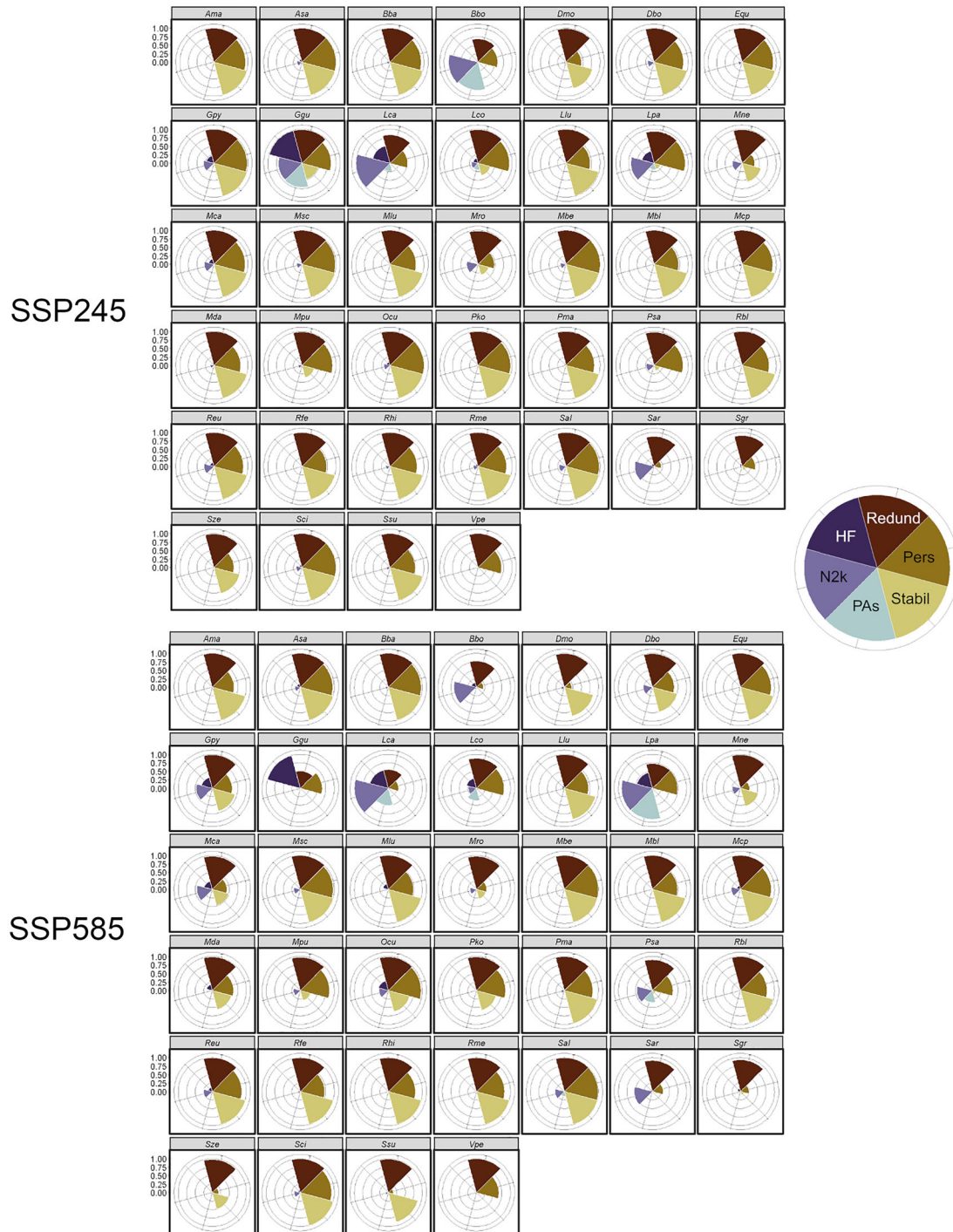
SSP245

SSP585

FIGURE 3 Summary of parameters assessed to evaluate the effectiveness of spatial adaptive trajectories (SATs) among different dimensions under 2 climate change scenarios (SSP245 and SSP585) (redund, index of SAT redundancy [inversely dependent on SAT convergence levels]; pers, fraction of maximum theoretical trajectory persistence relative to the 1000 most persistent SATs; stabil, fraction of SATs that rely on fixed sites from present time to 2080; PAs, fraction of total SAT persistence in protected areas; N2k, fraction of total SAT persistence within Natura 2000 and the Emerald networks; HF, fraction of total SAT persistence in the less disturbed areas in Europe [hf < 5]).

conditions); degree of spatial convergence among SATs (a measure of adaptive spatial autocorrelation); and extent to which existing conservation and undisturbed areas capture and relate to species persistence within SATs and the sites presenting the largest levels of SAT centrality.

As anticipated, the 2 climate change scenarios assessed had varying effects on species persistence scores within their highest ranked SATs (although this impact was variable among species). Higher rates of climate change (i.e., SSP585) generally lead to reduced species persistence along SATs, and there are no simple

management strategies to locally mitigate climate-driven effects (Meek et al., 2022; Peterson et al., 2019). Actionable, climate-smart conservation may imply the identification (at detailed spatial scales) of areas with low climatic variability over time (i.e., stable refugia) and the use of habitat restoration measures to attenuate temperature changes and water loss over extended periods (Shoo et al., 2013). By influencing the local climatic suitability characteristics, $o_{i_t}^s$, these actions might increase species persistence ideally in the areas where it is expected to be highest (i.e., SATs).

Levels of species persistence were highly dependent on the distance species needed to disperse, $d_{D(i,j)}^s$. Fixed areas presenting high climatic suitability through time are likely to provide higher persistence than a set of geographically dispersed areas with similar climatic suitability. Consequently, particular emphasis must be placed on those in situ adaptation grounds (Beaumont et al., 2019; Stralberg et al., 2020), especially for the species whose persistence is heavily reliant on them (about half of the mammal species assessed). Tailored conservation measures, such as the establishment of conservation areas and appropriate restoration measures, can prove effective in such cases (Lenoir et al., 2017; Michalak et al., 2018). Additionally, my results demonstrated that the sites deemed to be the most climate suitable for a species currently may not be the ideal locations to invest conservation resources in over the long term because climate change causes them to perform worse in the future even compared with other fixed SATs. However, moving SATs require innovative mechanisms in dynamic area protection (Hermoso et al., 2019; Rhodes et al., 2022; Williams & Johnson, 2013). Measures facilitating connectivity among SAT sites need to be enforced (i.e., acting over $d_{D(i,j)}^s$), and the sites perceived to be valued in short to medium terms must be carefully managed to provide adequate habitats for species when they cross them in the future. The transient value of some sites may be best accommodated by dynamic land management policies capable of regulating land use in sites that are perceived valuable in future times and whose natural value should be maintained or restored in the medium to long term (Lennox et al., 2017).

The results showed that the SATs of some species were largely convergent (i.e., use the same site). For simplicity, higher order convergence that would pinpoint not only the sites but also the exact time periods when multiple SATs converge was not considered. The importance of these adaptive hubs in conservation planning has been largely overlooked (Beger et al., 2022; Daigle et al., 2020). I assessed the extent to which conservation areas and undisturbed areas capture high-convergence areas at a species level. Results showed that relationships were far from linear and that only for a small number of species did SAT convergence relate positively with conservation areas (i.e., the larger the convergence of SATs, the larger the coverage on protected areas and Natura 2000 and Emerald networks) and negatively with areas disturbance (Appendix S15). In the latter case, conservation actions may be established to formally protect those sites or, as is being done under several European-wide programs, to develop rewilding strategies (Fernández et al., 2017; Perino et al., 2019; Svenning et al., 2016). Often, opportunity lands have guided the locations where rewilding takes place (e.g. abandoned farmlands) (Navarro & Pereira, 2012; Wang et al., 2023), but no study has conceptually guided rewilding locations based on climate change predictions to enhance the effectiveness of rewilding systems in the long term. The framework proposed here could contribute to conducting analyses along those lines. Some of the species I analyzed could be of interest in rewilding initiatives, in particular those involved in trophic rewilding (e.g., *B. bonasus*, *G. gulo*, *L. pardinus*) (see Figure 4 for the results obtained for *L. pardinus*).

Under both in situ and displacement adaptation settings, the persistence of most of the analyzed species in SATs crossing areas already protected (through protected areas, the Natura 2000 network, or the Emerald network) or with small human disturbance was considerably low. This is a worrying finding because overall the top 1000 adaptive areas for each of the 39 most threatened mammal species still covered a sizeable portion of Europe (i.e., 17–20%). Not all the areas I considered will maintain a steady conservation value over time. Although some areas will be continuously needed for species to adapt, others may lose or gain their importance at different points in the future. Once again, dynamic land management schemes are needed to embrace these complexities (Rhodes et al., 2022). For instance, regulations may be needed now to ensure that a site remains suitable in the future, either through habitat protection or restoration actions (Bullock et al., 2022; Millar et al., 2007).

I emphasized the importance of considering SAT convergence in conservation planning. Although the convergence of SATs can potentially lead to savings in area requirements (i.e., a single site may provide opportunities of success for several SATs), it is also crucial to recognize that the sites where multiple SATs for a particular species converge are central points for the successful adaptation of that species and therefore emerge as a top conservation priority. These sites function as essential hubs in climate-adaptive networks. They play a critical role in preserving the functionality of the entire network (Estrada & Bodin, 2008; Williams & Musolesi, 2016). Similarly, centrality can be extended to provide insights into the number of SATs for different species passing over a site or the number of species using a site in their adaptive movements (Figure 2). In this case, the protection or restoration of these sites favors the adaptability of many species. Unlike a species-centered centrality measure, multispecific centrality might not evidence critical areas for the preservation of the persistence capacity for a species. Nevertheless, these multispecies adaptive hubs hold instrumental value when minimizing conservation costs is a priority (Alagador et al., 2016). In light of centrality, I identified the northern Iberian Peninsula, the Hellenic Peninsula, and the westernmost regions of Turkey as relevant to climate-adaptive movements up to 2080 for 6–9 threatened mammal species.

The heavy reliance of species persistence on a few sites where multiple SATs converge makes those species highly vulnerable to the vagaries of threats within those areas (Anderson et al., 2023; Domínguez-García et al., 2019). To overcome this shortfall, an additional requirement could have been used in the identification of SATs, defining for each species a set of persistence-optimized SATs where no 2 SATs use the same
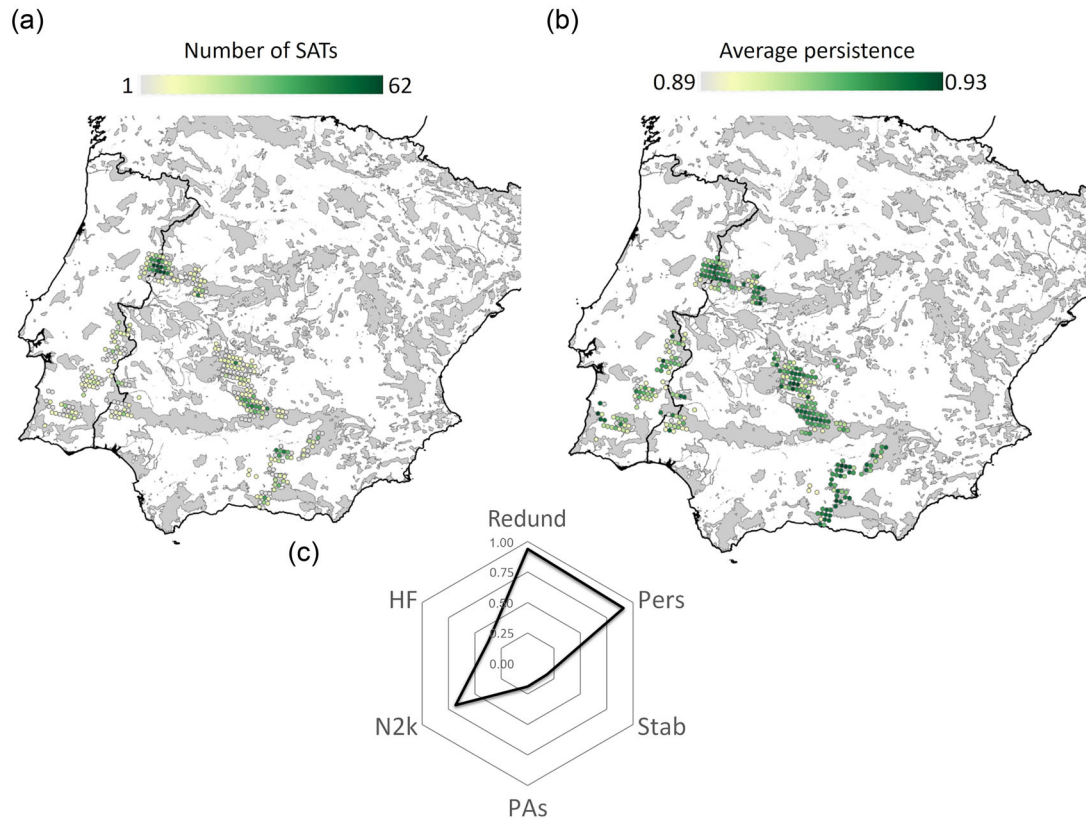
FIGURE 4 For the Iberian lynx (*L. pardinus*), (a) the number of spatial adaptive trajectories (SATs) converging in grid cells, (b) average persistence of SATs crossing each site under the SSP585 climate scenario (gray, locations of current protected areas and Natura 2000 sites), and (c) SAT persistence withing protected areas (PAs), Natura 2000 sites (N2k), and areas with the lowest levels of human footprint (HF) assessed by the index applied (redund, inverse relation with the maximum levels of SAT convergence; pers, fraction of the theoretical maximum persistence in SATs captured by the 1000 most persistence SATs; stab, faction of SATs defining stability trajectories).

place at the same time (i.e., an independent set of SATs). This constraint would replicate through time a conservation setting based on spatial targets, where a minimum area requirement is established for each species. Conservation networks designed in this manner incorporate redundancy, a critical feature in robust decision-making, especially in anticipative (uncertainty-prone) conservation planning (Alagador & Cerdeira, 2022). The identification of optimized independent sets presents computational challenges that can be overcome with efficient heuristic algorithms.

This framework may help establish priorities by differentiating those species able to cope locally with climate change from those whose persistence is largely reliant on the success of adaptive movements. It also identifies species that require active intervention either locally or along SATs over time (Probert et al., 2019). The versatility of the SAT framework allows its use in assisting policy makers in planning managed relocations of species (Brodie et al., 2021; Hällfors et al., 2017). For example, the areas with high climatic suitability in a given period and from which no SATs are defined forward in time can be considered adaptive bottlenecks. By simulating unlimited dispersal from these areas (i.e., assisted dispersal), planners can model their utility as source populations for the new colonizing areas

ahead in time, optimizing persistence expectations through the SAT identification algorithm.

I focused primarily on illustrating the usefulness of spatial network indices to inform the adaptive capacity of species, which rests upon several assumptions that require careful consideration. First, the analysis was limited to a small set of species that, although highly threatened and with conservation relevancy, will not be the sole focus of a conservation or restoration policy at the European scale. The commitments of European member states for 2030 and forward aim to target a much larger set of species, spanning a variety of taxonomic and habitat forms. To address this limitation, the next step is to replicate this assessment enlarging the number of species assessed while taking into consideration the minimization of the areas encompassed by the whole set of SATs. The optimization problems running with SATs settled by Alagador and Cerdeira (2020a) may deliver cost-effective solutions to plan conservation policies in the long term.

Second, the bioclimatic modeling I undertook relied on a limited set of variables considered influential in determining species' distributions. There is the possibility for further exploration by testing various combinations of variables tailored to individual species. Additionally, I incorporated only climate data

from 3 GCMs and 2 SSPs. In the context of practical application, analyses should encompass a wider range of scenarios, incorporating quantitative measures of uncertainty within the analytical phase (i.e., by considering the variability of site values and favoring sites with less variable scores) (Myers et al., 2021) or during decision-making stages (i.e., by designing resilient or robust networks using the principles of redundancy or portfolio theory) (Drechsler, 2020). Furthermore, the presence of appropriate habitats and land uses significantly influences the distribution of mammal species (Rondinini et al., 2011). Although there are models predicting the potential trends of these factors into the future (Baisero et al., 2020), they heavily depend on uncertain political choices, leading to a multitude of scenarios to analyze. To indirectly gauge the impact of land use on species, I examined the correlation between climate-adaptive regions for each species and the human footprint index. Initially pinpointing the areas with the highest long-term climatic suitability for the species, this approach targets specific regions and periods that need careful habitat management to safeguard the adaptive responses of species.

Third, the accurate estimation of species dispersal abilities is challenging and largely idiosyncratic on the properties of the landscapes. For each species, I used published data on dispersal and body mass relationships, and general rules were established to assess how dispersal distance may affect colonization success. Four general dispersal scenarios were defined to capture a range of potential species' responses. Due to computational constraints, the assessment focuses solely on the geographic distance between source and colonizing sites and not on the functionality of landscapes for each of the species (Anderson et al., 2023; Fung et al., 2017; Parks et al., 2020).

Fourth, recognizing the significance of intraspecific responses to climate change, this framework could potentially be applied at the level of species' populations. If genetic data are available, SATs for fully genetic entities can be traced, allowing for the identification of sites where SATs of distinct genetic lines converge in time and space. Such convergence may be particularly relevant for enhancing genetic diversity within species to bolster their resilience and local adaptive capacity under climate change conditions (Shoo et al., 2013).

Lastly, species do not exist in isolation within the ecological systems. They depend, either positively or negatively, on the occurrence of other species (i.e., species interactions) (Urban et al., 2013). Identifying the SATs that confer adaptive advantages for codependent species is an avenue of further investigation. This can be pursued in 2 ways: by incorporating a constraint on SAT identification, setting a maximum distance among the SATs designated for codependent species, or by employing area prioritization models (using SATs as selection units) that minimize the total covered area, thereby encouraging the convergence of SATs for different species across a maximum number of sites (Alagador & Cerdeira, 2020a).

This study underscores the importance of employing spatial network metrics to evaluate species' adaptability to climate change and leveraging this information to guide decisions in conservation planning. The results demonstrate that climate change could have significant impacts on the persistence of Europe's most threatened mammals. Approximately half of these species face a bleak future, especially when considering the more extreme changing scenario (i.e., SSP585). Although some species will find optimal persistence conditions in fixed sites up to 2080, many will depend heavily on adaptive movements and on the functionality of a few key sites where many SATs converge.

To meet the 2030 targets outlined in the European Union's Biodiversity Strategy and the global goals set in the Kunming–Montreal Global Biodiversity Framework, policy makers must carefully evaluate which areas to prioritize for intervention. These interventions should be aimed at ensuring long-term effectiveness and creating optimal ecological conditions for species persistence at long term. Shedding light on often-overlooked aspects of climate-adaptive planning, this study may offer new lines of analyses in the context of biodiversity research and effective policy making.

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SUPPORTING INFORMATION

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