Assessing vulnerability of reptile hotspots through temporal trends of global change factors in the Iberian Peninsula

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HIGHLIGHTS

- Temperature and EVI increased in 43 % and 16 % of the reptile hotspots, respectively.
- Twenty two percent of the hotspots experienced temporal increments in both temperature and EVI.
- The degree of temporal change in EVI and temperature was positively related.
- Temporal increments in EVI were also related to changes in shrub and forest cover.
- Natura 2000 network offers moderate protection to reptiles under global change.

GRAPHICAL ABSTRACT

Which are the drivers of temporal change in primary productivity within reptile hotspots of the Iberian Peninsula?
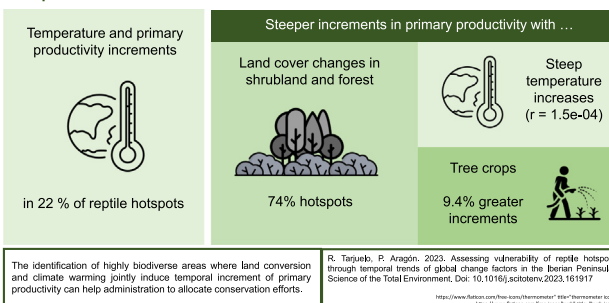
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ABSTRACT

Habitat degradation and climate change are major threats to the long-term persistence of reptile populations. However, their roles on primary productivity instability remain unclear at certain scales. Besides, the design of protected areas has often overlooked reptiles or assumed that their ecological requirements are represented under the umbrella of more charismatic species. Here, we assess the vulnerability of areas of high diversity of reptiles in the Iberian Peninsula to global change using data from satellite imagery. We focused on primary productivity, climate and land-use change because they are indicators of environmental variability that might impair ecosystem functioning and alter wildlife communities. We used linear regressions to detect monotonic temporal trends in primary productivity (through the enhanced vegetation index, EVI) and climate (mean temperature and accumulated precipitation) at two spatial resolutions (10-km^2 UTM squares and CORINE land-cover polygon level) over the period 2000–2020. We also determined how the strength of land-use and climate change affected the intensity of change in primary productivity at both spatial scales with multivariate linear regressions. We identified 339 hotspots (10-km^2 UTM squares) and monotonic increments of temperature, EVI or both occurred in 43 %, 16 % and 22 % of them, respectively. Positive trends of the EVI were related to increasing temperatures and changes in shrubland and forest cover. Within the hotspots with monotonic increments in EVI and temperature, EVI increments occurred in 65 % of the CORINE polygons that did not change their land-cover type, with stronger increases in tree crops. Finally, the Natura 2000 network provides only moderate protection to reptile hotspots, being most of the vegetation types relatively underrepresented. The proportion of forest and shrubland protected by the Natura 2000 network was higher in hotspots where EVI changed. Our procedures are relevant to prioritize hotspots requiring ground monitoring that allows economic and time savings.

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1. Introduction

Biodiversity is globally threatened by the pervasive effects of human activity (IPBES, 2019; Kennedy et al., 2019). Extinction rates have sped up for most taxa (Alroy, 2015; Ceballos et al., 2015), with habitat alteration, over-exploitation and climate change identified as primary drivers of population declines and species loss (IPBES, 2019; Maxwell et al., 2016; Mantyka-pringle et al., 2012). Implementing conservation measures is most required to mitigate the loss of biodiversity and the erosion of multiple ecosystems services that sustain our human welfare state (Cardinale et al., 2012).

The identification of conservation priorities on which governments should implement cost-effective strategies, such as the creation of protected areas, is mostly linked to high levels of endemic taxonomic diversity, presence of highly endangered or rare species, or critical habitats (Brooks et al., 2006; Gauthier et al., 2010; Rosso et al., 2018). Vulnerability to global change is another central concept to be considered when allocating conservation efforts (Margules and Pressey, 2000; Brooks et al., 2006). Yet, the evaluation of abiotic and biotic factors that can alter environmental conditions over time within protected sites, and consequently occupancy and abundance patterns of species, has been overlooked into systematic conservation planning (Pressey et al., 2007; Bellard et al., 2014), though it can provide a more realistic picture of dynamic biological systems and improve the schedule and performance of conservation initiatives in the mid- or long-term (Bellard et al., 2014).

Satellite remote sensing is a fast-evolving field with an enormous applicability in the assessment and monitoring of conservation targets (Pettorelli et al., 2014; Rose et al., 2014). Remote sensing can provide data on descriptors reflecting species distributions (e.g., Fitze et al., 2011; Sillero et al., 2009) and ecosystem properties that offer a more integrative picture of the functional response of the system to drivers of anthropogenic global change (Alcaraz-Segura et al., 2017; Knapp and Smith, 2001; Nemani et al., 2003; Pettorelli et al., 2005). Primary productivity, the amount of carbon assimilated by autotrophs, is a key descriptor of ecosystem functioning because it informs about the transfer of energy to heterotrophic organisms, thus linking the physical environment with different levels of the trophic web (Haberl et al., 2007). Primary productivity affects several aspects linked to animal fitness such as habitat use, migration, or body condition, that ultimately determine population dynamics and biodiversity patterns (Lewin et al., 2016; Pettorelli et al., 2005; Qian et al., 2007). Primary productivity is changing globally because of the effects of human activities on climate, land cover, quantity of available carbon in the atmosphere, or soil nutrient content among others (Eastman et al., 2013; Mao et al., 2012; Nemani et al., 2003). However, understanding the processes underlying spatiotemporal trends of ecosystem properties such as primary productivity is complex since global change factors can act directly, or through interactions or even complex feedback loops between them. The increasing availability and resolution of remotely sensed data can contribute to conservation actions through the identification of sites where animal populations face changes in ecosystem functioning that might alter biological communities and through the study of the underlying drivers.

Reptiles are among the vertebrates most threatened by the effects of human activity (Alroy, 2015; Böhm et al., 2013; IPBES, 2019). According to IUCN, reptiles are the third group of vertebrates with more proportion of endangered species (21 %; IUCN, 2022). Habitat degradation, climate change, harvesting, and displacement or predation from invasive species are major threats to reptile diversity (Böhm et al., 2013; Falaschi et al., 2019; Todd et al., 2010). These factors can also act indirectly on reptile populations by altering primary productivity. Variation in primary productivity has been linked to differences in performance traits such as body size (Aragón and Fitze, 2014), signaling glands (Jara et al., 2018), or clutch size (Meiri et al., 2020). Primary productivity also influences population abundance and species richness, but the effects vary between studies. Buckley et al. (2008) showed in a global study that population abundance of lizard species increased with primary productivity, probably because of greater food abundance. However, primary productivity was negatively related to the local abundance of three lizard species because increased

primary productivity was associated with habitat destruction (Romano et al., 2022). Similarly, species richness of reptiles increased with primary productivity but only in some regions (Qian et al., 2007; Tejero-Cicuéndez et al., 2022). Therefore, temporal variation in primary productivity that follows a monotonic trend can be used as a warning signal to monitor population- or community-level effects in reptiles due to changing ecosystem conditions in the mid- or long-term.

The Iberian Peninsula is a crucial region for the conservation of European reptiles because it has the highest number of European endemic and threatened species (Cox and Temple, 2009). It hosts about one third of the 151 reptile species, of which 42 % present declining trends (Cox and Temple, 2009). Several designations for preserving areas of high-nature value exist within European countries, and the Natural 2000 network is the most ambitious conservation figure to ensure the long-term persistence of European endemic species (https://www.eea.europa.eu/). Despite the paramount relevance of protected areas for biodiversity conservation (Chape et al., 2005), they have been criticized due to knowledge gaps or poor performance for the protection of groups other than mammals, birds, and plants (Abellán and Sánchez-Fernández, 2015; Araújo et al., 2007; López-López et al., 2011; Maiorano et al., 2015; Orlikowska et al., 2016). The alarming low conservation status of reptiles and their multiple functional roles within natural communities urge to assess how reptile diversity is protected by the Natura 2000 network under the context of high vulnerability to global change that characterizes the Mediterranean basin (Bellard et al., 2014; Brooks et al., 2006; Underwood et al., 2009).

Here, we aim at assessing the vulnerability of areas of high biodiversity of reptiles in the Iberian Peninsula to global change using satellite imagery and meteorological data, which help improve the allocation of conservation and research efforts by identifying sites where in situ studies of population dynamics are urgently needed. We first identify the areas of highest species richness and then measure their degree of vulnerability by determining which of them experienced temporal patterns of monotonic change in climate (temperature and precipitation) and/or primary productivity over two decades since 2000. Monotonic trends are used as indicators of more pervasive temporal changes, and hence, with higher potential of causing stronger and faster impacts in animal communities (Aragón et al., 2019). Therefore, hotspots of reptile biodiversity are considered vulnerable when they experience positive or negative monotonic trends in primary productivity or climate. For those hotspots where primary productivity changed over time, we further explore whether the strength of variation in primary productivity can be caused by three factors related to human activity: i) the intensity of change in temperature or precipitation regimens under a recent-past scenario of climate warming, ii) conversion of land-uses, iii) alteration in the functioning of unchanged land-uses. Finally, we assess the degree of environmental protection of reptile biodiversity within hotspots under the Natura 2000 network while considering temporal trends of primary productivity and land cover types.

2. Methods

2.1. Study area

This study covers the Iberian Peninsula, which has high levels of reptile biodiversity within the European context (Cox and Temple, 2009). Located in southern Europe (Fig. 1a), the Iberian Peninsula presents two major regions according to climatic features: the northern area is characterized by an Oceanic climate with mild temperatures and abundant precipitation throughout the year; the southern area has a Mediterranean climate with more extreme temperatures (cold winters and hot summers) and dry summers (http://koeppen-geiger.vu-wien.ac.at/). Yet, the Iberian Peninsula is climatically diverse and several sub-zones with climatic variations can be found, likely contributing to the high richness of reptile communities.

2.2. Identification of hotspot of reptile taxonomic diversity

To identify hotspots of reptile taxonomic diversity, we created a map of species richness at a resolution of 10-km^2 UTM squares (for a similar
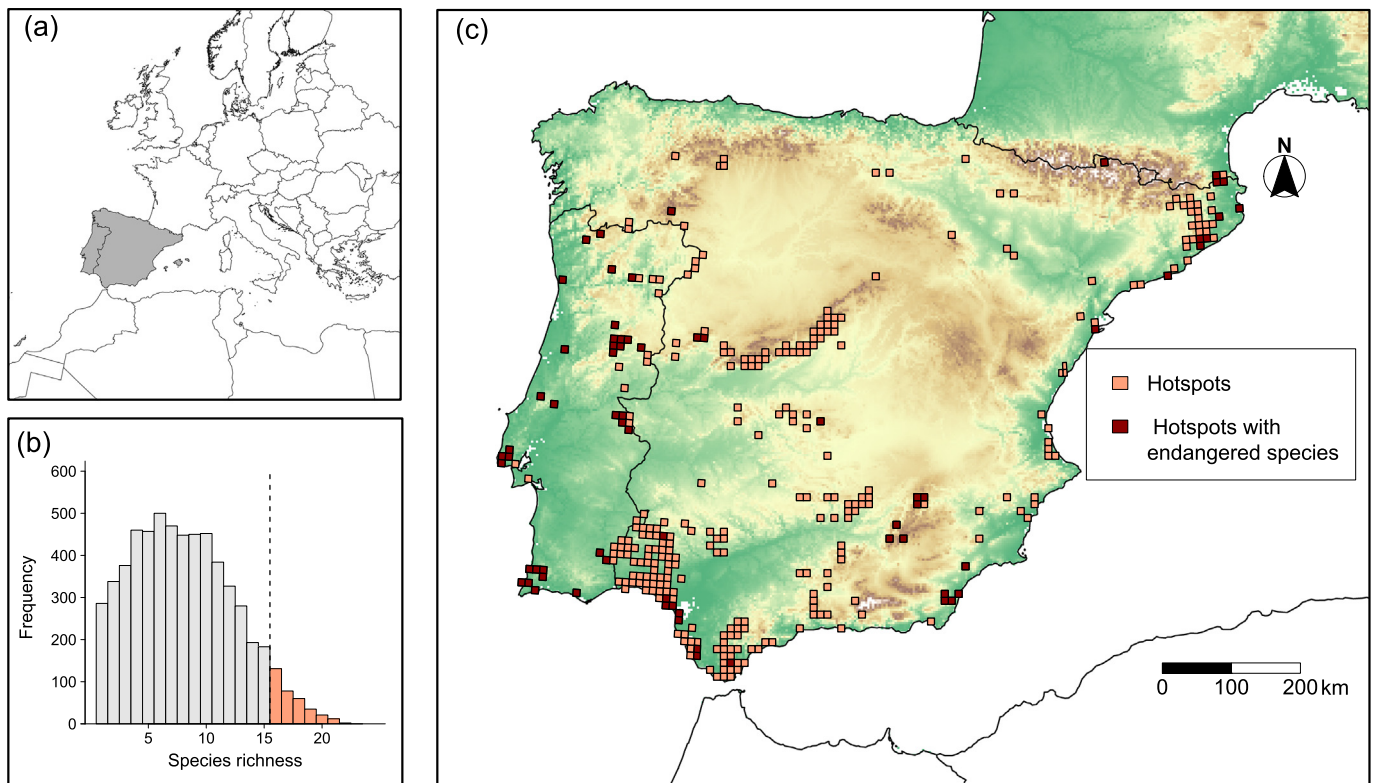
Fig. 1. Map (a) shows the location of the Iberian Peninsula and graph (b) displays the frequency distribution of the species richness per 10-km² UTM square, with orange bars indicating the species richness values for UTM squares considered as hotspots. Map (c) shows the distribution of hotspots of reptile biodiversity in the Iberian Peninsula (n = 339), with red squares indicating the presence of species classified as vulnerable or endangered in the Red Lists of Spain and Portugal.

procedure see Rosso et al., 2018). Data on the geographical distribution of reptile species were obtained from free-access databases from Spain and Portugal. We used the Spanish Inventory of Terrestrial Vertebrate Species of the Ministry for Ecological Transition and the Demographic Challenge (https://www.miteco.gob.es/es/biodiversidad/temas/inventarios-nacionales/inventario-especies-terrestres/default.aspx; accessed March 2021) to determine the spatial distribution of reptile species within the Spanish territory. For Portugal, we used distributional data available on the Atlas of reptiles and amphibians from The Instituto da Conservacão da Natureza e das Florestas (https://geocatalogo.icnf.pt; accessed March 2021). All data from both inventories were integrated in a single occurrence database. We excluded all records of exotic species.

We calculated the species richness for each UTM square to delimit the set of 10-km² UTM squares of highest reptile diversity (Fig. A.1). We defined a species richness threshold above which the UTM square was identified as a hotspot. That threshold was the number of species at the 95th percentile of the frequency distribution of the species richness of all UTM squares within the Iberian Peninsula with at least 1 reptile species recorded (Fig. 1b). Besides, we determined the presence of threatened species within the hotspots according to the Red List of each country (Portugal: seven reptile species listed as endangered or vulnerable in the continent; Spain: nine species listed as critically endangered or vulnerable in the continent).

2.3. Environmental variables

We rely on five environmental factors to assess the vulnerability of hotspots of reptile diversity to anthropogenic global change: primary productivity, climate, land conversion, variations in the vegetation functioning of land-uses that were not subject to land conversion over the study period, and degree of environmental protection. The analyses for identifying drivers of primary productivity change were done at two spatial scales: the 10-km² UTM square level and the land-cover polygon level of the

CORINE land cover inventory (spatial resolution of 25 ha; https://land.copernicus.eu/; see more details in Subsection 2.3.3). We determined the effects of land conversion on primary productivity trends at the 10-km² UTM square level (i.e., hotspot scale) whereas we addressed whether temporal trends in primary productivity could be driven by changes in the functioning of land-uses that remained unchanged over the study period at the smaller spatial scale of CORINE land-cover polygon level (hereafter landscape level). The effects of climate change were explored at both spatial scales. We processed environmental and spatial data with QGIS (QGIS.org, 2022) and the R software (R Core Team, 2021).

2.3.1. Primary productivity

We used the enhanced vegetation index (EVI) as a proxy of primary productivity (Huete et al., 2002; Pettorelli et al., 2005). The EVI is an index that overcomes some of the contamination problems associated with the NDVI (normalized difference vegetation index) and informs about canopy structural variations (Pettorelli et al., 2005). EVI values for the temporal series 2000–2020 were obtained from MODIS satellite images available on NASA's digital platform NASA-LP DAAC (MOD13A3, https://lpdaac.usgs.gov/). Because we obtained EVI values at a monthly temporal resolution and 1-km² spatial resolution (https://lpdaac.usgs.gov/products/mod13a3v006/), we calculated year values by averaging monthly values and 1-km² pixels to match the 10-km² resolution of the hotspot layer.

We also obtained year values of EVI at the landscape scale for those CORINE polygons not experiencing a change in land-cover type during the study period and within the hotspots displaying temporal trends in the EVI. We did so to evaluate whether variation in primary productivity can be also caused by more subtle changes in the functioning of unchanged land-cover types, compared to drastic vegetation shifts associated with land conversion. We computed the average EVI value at the polygon level by first increasing the resolution of the MODIS raster by a 25-fold factor (0.04 km²) to improve the spatial resolution match between EVI and

CORINE land-cover. When small-size CORINE polygons fall in a few MODIS cells, the average EVI value can be rough if it does not reflect the different cover of each MODIS cell. By increasing MODIS resolution, we can reduce this bias and obtain more precise average values for small-size CORINE polygons.

2.3.2. Climatic data

Climatic data were collected from the WorldClim2 database. WorldClim2 data comes from the spatial interpolation of monthly climatic data from weather stations (Fick and Hijmans, 2017) and is the most used climatic database in ecological studies due to its free access and high spatial resolution for global climate data (Cerasoli et al., 2022). We downloaded WorldClim2 data on monthly minimum and maximum temperatures as well as accumulated precipitation for the time series 2000–2018 (https://www.worldclim.org/data/monthlywth.html). We computed the mean annual temperature – as the average of maximum and minimum temperatures – and the annual accumulated precipitation for each year at the two spatial scales, i.e., in the hotspots and in the landscape level.

2.3.3. Land-cover data

Data on land conversion within hotspots (10-km² UTM squares) of reptile biodiversity in the Iberian Peninsula for the study period were obtained from the CORINE land cover inventory. Specifically, we used the databases of land cover change available for the periods 2000–2006, 2006–2012, and 2012–2018 (spatial resolution = 5 ha; https://land.copernicus.eu/pan-european/corine-land-cover). We checked that no changes in land cover were due to technical modifications. We reclassified the CORINE land-cover types using a functional approach based on grouping land-cover categories according to broad vegetation characteristics. Thus, we defined the following six vegetation categories: 1) forest, 2) shrubland, 3) grassland, 4) tree crops, 5) mixed areas, and 6) scarce or no vegetated areas (hereafter unvegetated areas; for a detailed description see Table A.1). For each hotspot, we calculated the proportion of each vegetation category that changed in each of the three periods. We subtracted the area of each vegetation type at the start of the period from the area at the end of the period and divided it by the hotspot area. Next, we summed the three proportions to obtain the net proportional change of each vegetation category in 2000–2018. Positive values of net change indicate expansions of the vegetation type and negative values indicate land cover reductions.

We applied a principal component analysis (PCA) on the net proportional change of the six vegetation categories. This procedure allows not only to summarize variation of the data on a few orthogonal axes, which can be interpreted as ecological gradients of land-use change, but also to avoid the correlation effects associated with a set of proportional variables that sum one. We retain for statistical analysis the two first axes that explained 83 % of the variance (Table A.2). The first axis was negatively associated with the proportion of change in shrubland and positively associated with the proportion of change in forest (Table A.2). In the hotspots, shrubland cover showed increments or small reductions over 2000–2018 (Fig. A.2; particularly transitional woodland-shrub, see Fig. B.1) whereas forest cover mainly decreased (Fig. A.2; particularly coniferous and mixed forests, see Fig. B.1). Therefore, PC1 can be interpreted as a gradient of forest loss and shrubland expansion. The second axis was positively related to the proportion of change of tree crops and unvegetated areas and negatively to the change in grassland cover (mainly natural grasslands, Figs. B.1, A.2), thus indicating a gradient of land conversion toward anthropogenic land-uses (urbanization and agriculture; Table A.2).

We extracted the CORINE land-cover type of 2018 (spatial resolution = 25 ha) of those polygons that did not change in the period 2000–2018 and within the hotspots with a temporal trend in the EVI and climate. We reclassified their land-cover type into one of the six vegetation categories.

2.3.4. Natura 2000 network

To assess the degree of protection of important areas for reptile biodiversity, we used the vector map of the Natura 2000 network (downloaded from www.eea.europa.eu/, version Natura2000End2019). The Natura

2000 is a network across all EU countries aiming at protecting rare and threatened species and habitats listed under the Birds Directive (Directive 2009/147/EC of the European Parliament and of the Council) and the Habitats Directive (Directive 92/43/EEC Council). For each reptile hotspot, we calculated the proportion of the hotspot area falling within the boundaries of the Natura 2000 network. To evaluate whether vegetation types have different degrees of environmental protection, we also calculated the proportion of each vegetation type (using the 2018 CORINE-land cover map) within the Natura 2000 network per hotspot. We merged this information with that of temporal trends of primary productivity to evaluate potential differences in the degree of environmental protection between hotspots with and without variation in primary productivity.

2.4. Statistical analysis

2.4.1. Temporal trends in primary productivity and climate in reptile hotspots

All statistical analyses were performed with the R software (R Core Team, 2021). We used univariate linear regressions to determine monotonic trends in primary productivity and climate in the hotspots (10-km² UTM squares) of high reptile diversity over the study period. For each hotspot, we ran three regression models using as response variables: i) the mean annual EVI, ii) mean annual temperature, and iii) annual accumulated precipitation. Year was used as the explanatory variable to detect temporal changes. The slope of these regressions (hereafter referred to as r coefficient or coefficient of change) indicated the direction and intensity of monotonic patterns of temporal change (for a similar procedure see Aragón et al., 2019). We checked for spatial autocorrelation of the r coefficients of the EVI, temperature, and precipitation to detect any spatial structure among the data given the proximity between many of the hotspots. We tested for spatial autocorrelation with correlograms of Moran's Index (I) and Bonferroni correction using the R package 'spdep' (Bivand et al., 2013). Moran's Index was calculated based on a configuration of the net of neighbors where all hotspots were connected at least to another one. Statistical significance ($p < 0.05$) in any distance class indicated the lack of spatial independence in the temporal trends of the environmental variable. We also checked for spatial autocorrelation in the number of reptile species to determine similarity in the richness of reptile assemblages as a function of the distance among hotspots.

2.4.2. Effects of land conversion and climate change on temporal trends of primary productivity

We first explored the effects of climate and land-cover change on the temporal trends of the EVI at the hotspot scale (10-km² UTM squares) with multivariate general linear models (GLMs). This analysis was applied only on those hotspots where the EVI presented a statistically significant temporal change over the study period (N = 129). We used the r coefficient of the EVI (hereafter r-EVI) as the response variable as it indicates the direction and intensity of variation in primary productivity over the temporal window. The full initial model was:

$$r\text{-EVI} = r\text{-temp} + r\text{-prec} + PC1 + PC2 + temp.sig + temp.sig \times r\text{-temp} + temp.sig \times PC1 + temp.sig \times PC2$$

where 'r-temp' and 'r-prec' are the r coefficients of change of temperature and precipitation, respectively; 'PC1' and 'PC2' are the axes of the PCA reflecting land conversion processes in 2000–2018; 'temp.sig' is a binary variable indicating whether the temperature variable experienced a significant monotonic change (or not) in the hotspot; the interaction temp.sig × r-temp indicates whether the EVI temporal trend is concomitant with that of temperature; and temp.sig × PC1/PC2 indicates whether the EVI trend is associated with land-cover change depending on the temperature trend. The binary variable for precipitation was not included in the model because we did not find significant temporal trends in the previous univariate linear regressions (see Results). All explanatory variables were standardized and tested for lack of strong collinearity (all Pearson's correlation $\rho < 0.6$) before model building. When model residuals of the full initial model showed

spatial autocorrelation, we computed spatial eigenvectors with the function 'mem' of the R package 'adespatial' (Dray et al., 2022) and included into the full model the set of eigenvectors showing significant ($p < 0.01$ or $p < 0.05$) correlations with model residuals to remove spatial autocorrelation. Then, we performed a backward stepwise model selection by AIC using the function 'stepAIC' of the R package 'MASS' (Venables and Ripley, 2002) to re-

tain most significant predictive variables in the final model, including the spatial eigenvectors when required. We evaluated model assumptions by inspection of the final model residuals and corroborate spatial independence of the residuals with a correlogram of Moran's I (see Figs. A.3–A.4).

2.4.3. Effects of variation in vegetation functioning and climate change on temporal trends of primary productivity

We ran a second set of analyses at the landscape (CORINE-polygon) scale to investigate if temporal variation in EVI could be also caused by more subtle variation in the vegetation functioning of unchanged land-uses than that caused by land conversion. We first ran a regression model with the mean annual EVI against year for the polygons falling within hotspots with significant temporal trends in the EVI. We restricted the subsequent analyses to data from polygons with a significant regression slope (the r coefficient of change), which indicates a monotonic change in primary productivity, and within hotspots with monotonic trends in EVI and temperature (N = 3415). We evaluated how vegetation types differed in primary productivity by means of an ANOVA and a post-hoc Tukey HSD test on EVI values of the year 2000. Then, we built a GLM to determine the main effects of unchanged vegetation types and variation in mean temperature and accumulated precipitation on EVI temporal changes. The full initial model was:

$$r\text{-EVI} = r\text{-temp} + r\text{-prec} + \text{vegetation type}$$

where r-EVI is the r coefficient of change of EVI in polygons not experiencing land conversion in the period 2000–2018; 'r-temp' and 'r-prec' are the r coefficients of change of temperature and precipitation of the CORINE polygons, respectively; and vegetation type is a categorical predictor with six levels. The continuous explanatory variables ('r-temp' and 'r-prec') were standardized and tested for lack of strong multicollinearity (Pearson's correlation $\rho < 0.6$). The full initial regression model also incorporated the set of spatial eigenvectors showing significant ($p < 0.05$) correlations with model residuals to control for the spatial autocorrelation. The final regression model was selected using backward stepwise model selection as described for the GLM at the hotspot scale. We evaluated model assumptions by inspection of the final model residuals and checked for spatial independence of the residuals with a correlogram of Moran's I (see Figs. A.5–A.6). Finally, we conducted a post-hoc Tukey HSD test on the final regression model to determine whether vegetation types differed in the r coefficient of EVI.

3. Results

The number of species found per 10-km² UTM square in the Iberian Peninsula ranged between 0 and 22 (Fig. 1b). The species richness threshold used to identify hotspots was set at 16 species according to the 95th percentile of the frequency distribution of species richness (Fig. 1b). This yielded 339 hotspots (279 in Spain, 41 in Portugal, and 19 in the boundary of both countries) located in different ecosystem types, from mountain systems to coastal areas and lowlands (Fig. 1c). Many hotspots were highly aggregated while others were found in isolation (the largest distance between the centroids of neighboring isolated hotpots was 114 km). Species richness in the hotspots was spatially autocorrelated, being more similar at the shortest distance classes (Fig. B.2). The spatial distribution of hotspots
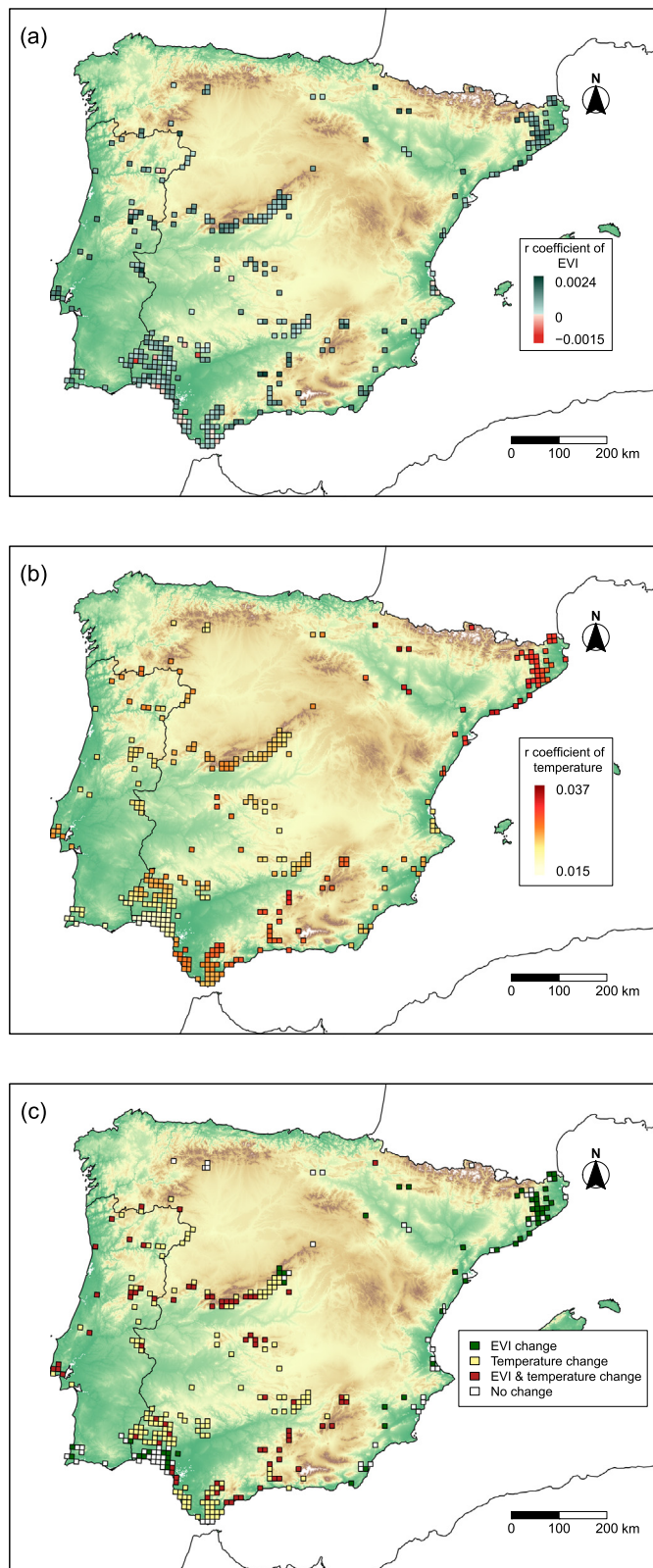
Fig. 2. Maps showing the temporal trends in primary productivity and climate within the hotspots of reptile biodiversity in the Iberian Peninsula. Map (a) indicates the direction and intensity of temporal change in primary productivity (using the EVI as a proxy). Map (b) displays the tendency and intensity of temporal change in mean annual temperature. Map (c) integrates the temporal trends of EVI and mean annual temperature of the hotspots, with color indicating whether significant temporal changes occurred: (i) only in primary productivity (EVI values; green), (ii) only in mean annual temperature (yellow), (iii) in both primary productivity and temperature (red), or (iv) no change neither in EVI nor temperature (white).

revealed several important areas for the conservation of reptile biodiversity, mostly in the Mediterranean region: the Central System, Parque Natural da Serra da Estrela, Serra de São Mamede, the west of the Tajo's estuary, Parque Natural do Sudoeste Alentejano, Western Andévalo, Doñana National Park and its surroundings, the Ecological Corridor and marshland of the rivers Tinto and Odiel, Sierra de Aracena y Picos de Aroche, Sierra Norte de Sevilla, the bay of Cádiz, Sierra de Grazalema, Parque Natural de los Alcornocales, Basin of Rumblar, Guadalén y Guadalmena, Montes de Toledo, Cordillera Costera and Cordillera Transversal in Catalonia, and coastal areas in the east of the Iberian Peninsula (Figs. 1c and B.3). 83 % of Portugal's hotspots harbor at least one of the seven threatened species of the Portugal's Red List. In Spain, six out of the nine species of the Red List occurred within the reptile hotspots. 12 % of the hotspots presented at least one threatened species and were in the bay of Cádiz and south of Doñana National Park, Parque Natural de las Sierras de Cazorla, Segura and Las Villas, Sierra de Alcazar, Segura y cañones del Mundo, Sierra de Cabrera y de Bédar, and Cordillera Costera in Catalonia (Figs. 1c and B.3).

3.1. Temporal trends of primary productivity and climate in reptile hotspots

We found 130 hotspots (38 %) with a significant ($p < 0.05$) temporal change in EVI over the 21-year period. All of them showed a positive r coefficient (EVI increased over time) except one (Fig. 2a; Table B.1). Because we only detected one hotspot with a significant negative trend in the EVI, we removed it from the statistical analyses to avoid any confounding effect. The explained variation (adjusted r^2) of the linear regressions between the EVI and year ranged from 15 % to 76 % (Table B.1). The proportion of hotspots showing a temporal trend in the EVI was slightly greater in Spain (38 %) than in Portugal (33 %). According to the correlogram of Moran's I, there was spatial autocorrelation in the r coefficient of the relationship between the EVI and year for the shortest distance class (Fig. B.4).

WorldClim2 data showed that mean temperature significantly increased ($p < 0.05$) over time in about 63 % of the hotspots (n = 215, Fig. 2b, Table B.1). The correlogram of Moran's I revealed a spatial correlation structure in which temperature was more similar at the shortest distance classes and differed as distance increased (Fig. B.5). For annual accumulated precipitation, we did not find significant temporal variation for any of the hotspots (Table B.1), but r coefficients were spatially autocorrelated, being similar at the shortest distance classes but differed with increasing distance (Fig. B.6). Integrating temporal trends, EVI and mean annual temperature significantly changed over time in 22 % of the hotspots whereas 43 % of the hotspots experienced temporal variation only in temperature and 16 % only in EVI (Fig. 2c).

3.2. Effects of land conversion and climate change on temporal trends of primary productivity

The final GLM exploring the effects of land conversion and climate change on temporal variation of the EVI at the hotspot scale (10-km² UTM square) presented a significant interaction between PC1 and

Table 1

Results of the final GLMs testing the effects of climate change and land conversion on the EVI temporal trends using climatic data from WorldClim2 (N = 129). The r coefficient of the EVI was used as the response variable. The r coefficients of mean temperature (r-temp) and accumulated precipitation (r-prec) and the two first PCA axes were included as explanatory variables in the full initial models. The model also included the interactions between a binary variable indicating whether temperature experienced a significant temporal change over time in the hotspot (temp.sig) and its interaction with its r coefficient and the PC axes (see Methods for more details).

Explanatory variables	F	df	p
PC1	0.97	1	0.328
r-temp	0.31	1	0.580
temp.sig	0.08	1	0.774
PC1 × temp.sig	7.09	1	0.009
r-temp × temp.sig	6.24	1	0.014

significant temperature change (Table 1). PC1 negatively affected the r coefficient of EVI in the hotspots where temperature significantly increased over time ($\beta = -1.4e\text{-}04$, $p < 0.001$), but had no effect in hotspots where temperature did not show a significant trend ($\beta = 6.5e\text{-}05$, $p = 0.239$). Thus, the EVI showed steeper increases over the years with increasing cover of shrubland or decreasing forest area. The final model also presented a significant interaction between the r coefficient of mean temperature and significant temperature change (Table 1). The positive effect of the r coefficient of mean temperature on the r coefficient of EVI was only significant in hotspots where temperature significantly increased over time ($\beta = 1.5e\text{-}04$, $p < 0.001$) but not in hotspots where temperature did not increase ($\beta = 2.29e\text{-}05$, $p = 0.418$). Therefore, the EVI increased with increasing mean annual temperatures.

3.3. Effects of variation in vegetation functioning and climate change on temporal trends of primary productivity

Within the hotspots experiencing significant EVI increments, significant temporal trends of the EVI occurred in 5718 (65.4 %) out of the 8746 of the CORINE polygons with unchanged land cover – almost all of them experiencing increasing trends (99.3 %). In hotspots where both temperature and EVI experienced significant increments (n = 73), 64 % of the unchanged polygons presented significant temporal variation in the EVI (n = 3415; 99.6 % of them were increments). In 98.6 % of these polygons, temperature also significantly increased over time but none of them had significant changes in accumulated precipitation. The ANOVA results regarding this subset (polygons with a significant temporal change of EVI and within hotspots with significant trends in both the EVI and temperature) revealed differences in the mean EVI values of the 2000 year between vegetation types ($F_{5,3409} = 72.67$, $p < 0.001$). A post hoc Tukey test showed that unvegetated areas had the lowest EVI followed by grassland ($p < 0.05$), whereas forest and mixed areas presented the highest EVI values ($p < 0.05$; Fig. 3a). Based on the effects of forest and shrubland conversion on EVI trends at the hotspot scale, we compared the difference of EVI values of the years 2000 and 2020 between shrubland and forest using a t-test that unveiled significant differences ($t_{1785.3} = -2.20$; $p = 0.028$). Interestingly, the EVI difference over 2000–2020 was greater in shrubland (mean = 0.038) than forest (mean = 0.036). On the other hand, the GLM on the above-mentioned subsample showed only a significant effect of the vegetation type on the r coefficient of EVI ($F_{5,3256} = 3.21$, $p = 0.007$). A Tukey HSD performed on this GLM showed that tree crops presented a significantly greater r coefficient of the EVI compared to the other vegetation types (pairwise comparisons $p < 0.05$; Fig. 3b).

3.4. Degree of environmental protection of reptile hotspots

The coverage of the Natura 2000 network was similar between hotspots experiencing a temporal trend in the EVI and those that are not ($t_{225} = -0.44$, $p = 0.662$), 48 % and 47 %, respectively. Likewise, the distribution of the Natura 2000 network did not differ between the hotspots with and without significant temporal trends in the EVI ($\chi^2 = 2.29$, $p = 0.130$), being the degree of protection by Natura 2000 only moderate in both cases: 31.5 % of the hotspots experiencing EVI change had >80 % of their area under Natura 2000 (Fig. B.7a), whereas the percentage decreased to 23.4 % for hotspots with no EVI temporal trends (Fig. B.7b).

The two most abundant vegetation types within hotspots were forest and shrubland, which accounted for more than a half of the total hotspot area, followed by grassland that covered 17.5 % (Fig. 4). The cover of forest did not differ between all hotspot area (25.87 %) and the area within Natura 2000 limits (23.94 %; $t_{574.18} = 0.96$, $p = 0.337$), whereas the cover of shrubland was slightly greater within all hotspot area (25.25 %) than the area under Natura 2000 (21.23 %, $t_{583.13} = 2.51$, $p = 0.012$, Fig. 4). The cover of grassland and tree crops within all hotspot area (17.54 % and 6.50 %, respectively) was significantly higher than in the area within the Natura 2000 network (10.00 % and 2.68 %, respectively; grassland $t_{612.42} = 6.73$, $p < 0.001$; tree crops $t_{489.45} = 4.35$, $p < 0.001$,
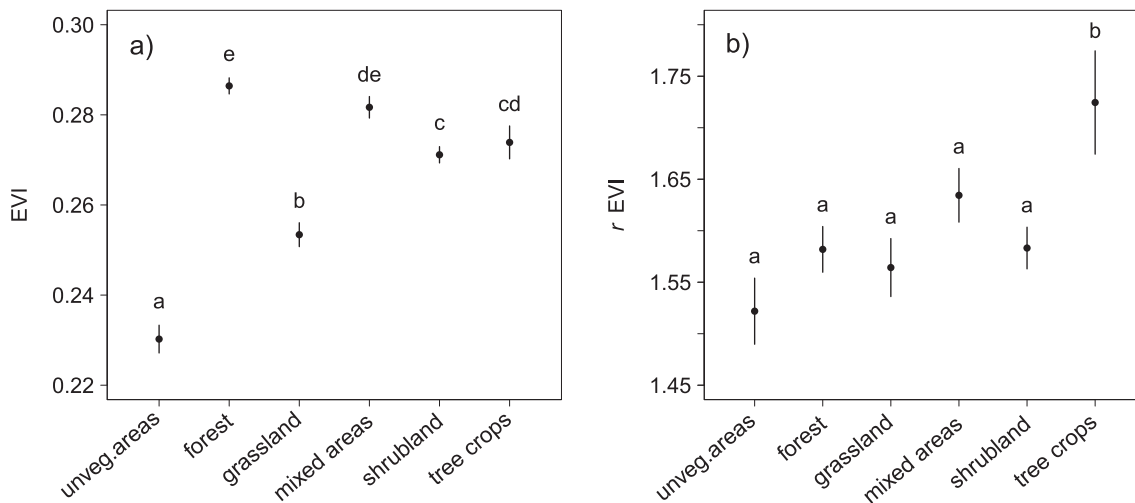
Fig. 3. Mean and standard error of (a) the EVI values of 2000 year and (b) the r coefficient of EVI for the period 2000–2020 of each vegetation type at the landscape (CORINE-polygon) scale. Differences between vegetation types according to Tukey HSD test ($p < 0.05$) are indicated by different letters. Units of r-EVI in graph (b) are rescaled (multiplied by 10ˆ3) for the sake of clarity.

Fig. 4). Similarly, the cover of mixed and unvegetated areas within all hotspot area (11.70 % and 13.14 %, respectively) was higher than in the area under the Natura 2000 network (6.13 % and 6.65 %, respectively; mixed areas $t_{601.98} = 5.61$, $p < 0.001$; unvegetated areas $t_{561.68} = 4.58$, $p < 0.001$, Fig. 4).

The proportion of grassland, tree crops, and unvegetated areas within the Natura 2000 network did not change between hotspots with (grassland = 9.58 %; tree crops = 2.05 %; unvegetated areas = 5.88 %) and without (grassland = 10.27 %; tree crops = 3.12 %; unvegetated areas = 7.10 %) monotonic trends in EVI (grassland $t_{237.39} = -0.48$, $p = 0.634$; tree crops $t_{137.06} = -1.03$, $p = 0.307$; unvegetated areas $t_{192.05} = -0.732$, $p = 0.465$, Fig. 4). However, the proportion of forest and shrubland protected by Natura 2000 network tended to be higher in hotspots where the EVI changed over time (27.81 % and 24.39 %, respectively) than in hotspots without EVI variation (21.43 % and 19.26 %; forest $t_{207.04} = 1.93$, $p = 0.056$; shrub $t_{176.8} = 1.88$, $p = 0.062$, Fig. 4). Mixed areas was the only vegetation type that presented greater cover under Natura 2000 in hotspots

with no EVI change (8.10 %) than in hotspots with significant EVI trends (2.84 %; $t_{246.41} = -4.74$, $p < 0.001$, Fig. 4).

4. Discussion

This study unveils how taxonomically diverse regions of reptiles in the Iberian Peninsula are affected by several drivers of anthropogenic global change. We observed monotonic increments in primary production and temperature over the course of two decades in an important fraction of reptile hotspots (10-Km^2 UTM square resolution), which suggest potential ecosystem instability and thus vulnerability for reptile assemblages. Although primary production and climate did not always follow concomitant changes, the intensity of the increase in primary production and that of temperature were positively related in areas where both factors increased monotonically. However, this effect was only noticeable at the larger spatial scale in this study. Besides, land conversion also influenced the temporal trends of primary productivity in interaction with climate warming.
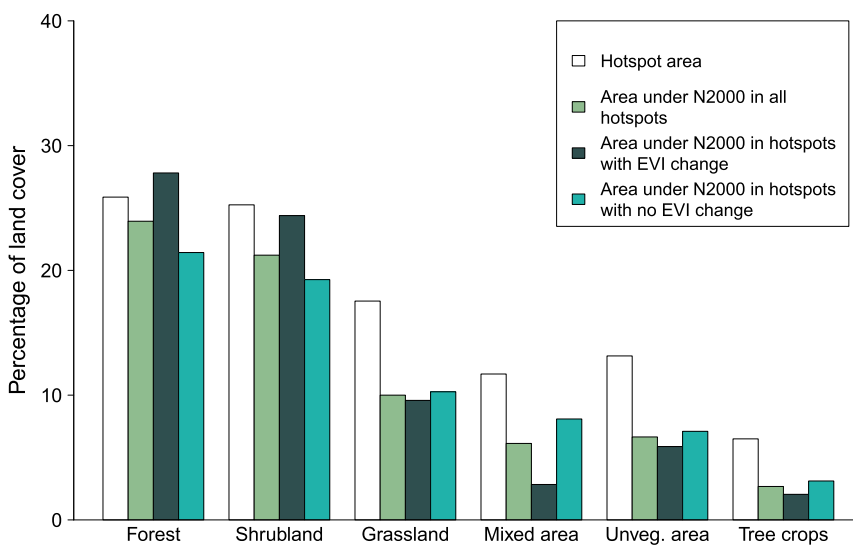

Fig. 4. Mean percentage of land cover of each vegetation type within: (i) all hotspots (white); (ii) the area protected by the Natura 2000 network in all hotspots (light green); (iii) the area protected by the Natura 2000 network within the hotspots experiencing temporal change in EVI (dark green); and (iv) the area protected by the Natura 2000 network within the hotspots not experiencing temporal change in EVI (sea green).

The Iberian Peninsula is a stronghold for the conservation of European reptiles and stands out as a world region of high reptile phylogenetic diversity with a disproportionate number of threatened species (Cox and Temple, 2009; Cox et al., 2022; Sillero et al., 2014). This herpetofauna diversity can be at risk because more than half of the identified reptile hotspots have undergone climate warming in the last two decades. Climate is a major determinant of the local distribution and community composition of ectothermic terrestrial vertebrates due to thermal physiological constraints and limited dispersal capacities (Aragón et al., 2010a, 2010b). Reptile species with Atlantic climatic affinities are the most vulnerable to the direct impacts of climate warming (Carvalho et al., 2010), but Mediterranean reptiles are not exempt from experiencing negative effects as temperature keeps rising (Araújo et al., 2006; Carvalho et al., 2019; Díaz et al., 2022).

Climate warming might also affect reptile populations indirectly through changes in vegetation. Primary production is increasing globally because of different components of global change, including climate warming (Lucht et al., 2002; Mao et al., 2012; Nemani et al., 2003). Increments in primary productivity occurred in about 40 % of the hotspots, but parallel increments in primary productivity and mean annual temperature occurred in only a quarter of reptile hotspots. However, we detected a positive relationship between the strength of the increments in primary productivity and mean annual temperature in hotspots where both factors experienced monotonical increments. In middle-to-high latitudes, the positive effects of increasing temperature on primary productivity are explained by warmer temperatures promoting vegetation growth or expanded growing season (Ciais et al., 2005; Lucht et al., 2002; Madani et al., 2020). How the observed increments of primary productivity would impact reptile communities does not have a one-for-all answer and will depend on species ecological features. Increments in primary productivity can benefit reptile population if they increase prey abundance but it might be pernicious when linked to habitat alteration (Romano et al., 2022). In this sense, Arenas-Castro and Sillero (2021) found that reptiles and amphibians are the groups experiencing greater losses in habitat suitability in the Iberian Peninsula. Therefore, our results should rather inform on where to perform direct ground monitoring of reptile population dynamics at local scales given their degree of exposure to dynamic threats.

Water availability is another major determinant of vegetation activity (Knapp and Smith, 2001; Nemani et al., 2003) and might affect reptile populations through variations in food availability (Rotem et al., 2020). However, we did not detect clear monotonical changes of accumulated precipitation within reptile hotspots although the Mediterranean basin is already suffering increased dryness and extreme droughts (IPCC, 2014). Other studies similarly found that long-term trends of annual precipitations might not correlate with temporal trends of primary productivity (Knapp and Smith, 2001; Lucht et al., 2002). Changes in the timing, frequency, or anomalies in rainfall events can also affect primary productivity (Cabello et al., 2012; Knapp and Smith, 2001; Thomey et al., 2011), so further research using such kind of variables could shed light on the role of precipitation driving temporal changes in primary productivity in water-limited regions such as the Mediterranean basin (Nemani et al., 2003).

Land conversion due to human actions is a major driver of biodiversity loss that alters structural features of the environment and modifies ecosystem properties such as the flux of energy (Haberl et al., 2007; Nemani et al., 2003). Land-use change threatens the persistence of reptile populations because their relatively small distributional and home ranges, narrow ecological niches, and low dispersal abilities make reptiles particularly sensitive to habitat loss (Cox and Temple, 2009; Cox et al., 2022; Gibbons et al., 2000; Todd et al., 2010). In the period 2000–2018, reptile hotspots in the Iberian Peninsula lost mainly forest area in favor of the expansion of transitional shrubland. More than half of all the world's reptile species are linked to forest habitats (Cox et al., 2022), but arid habitats including shrubland formations are characterized by high levels of reptile speciation (Roll et al., 2017). Of the species recorded in the Iberian hotspots, almost three quarters use both forest and shrubland habitats, with only 14 % and 7 % of the species occupying exclusively shrubland or forests, respectively

(https://www.iucnredlist.org/). Therefore, the transition from forest to shrubland in reptile hotspots does not necessarily imply a negative impact on reptile biodiversity and will depend on the conservation interest of local populations or habitat-specific communities.

We found that the intensity of change in primary productivity was linked to the extent of forest loss and shrubland expansion in hotspots where temperature increased. Forests are more productive than other habitats (Fig. 3a; Knapp and Smith, 2001) and forest loss should have likely caused declines in absolute EVI values. However, we observed that the range of change (i.e., the difference of EVI values between the years 2000 and 2020) was larger for shrubland than forest, in accordance with other studies showing a lower inter-annual variation of primary productivity in forest than in grassland and shrubland (e.g., Knapp and Smith, 2001; Nayak et al., 2013). Increasing annual temperatures in such transitional woodland/shrubland formations under scenarios of abrupt forest loss such as clearings or fires can enhance the growth of young trees due to their greater leaf area than shrub species (Knapp and Smith, 2001), causing the observed steeper increments in primary productivity with the expansion of shrubland. This rapid change in vegetation communities with raising temperatures might result in turnover of reptile communities due to habitat alteration.

We expected that variation in primary productivity could be also caused by altered functioning of vegetation communities prompted by climate change within land-uses that had not changed over the study period. 65 % of CORINE polygons not experiencing land conversion showed increments in primary productivity but the positive effect of increasing temperatures on primary productivity observed at the hotspot scale was not detected at the landscape level. At local scales, factors such as human management, soil properties, or even wildlife diversity might better explain variation in primary productivity than changes in mean annual temperature or precipitation (Cabello et al., 2012; Gang et al., 2018; La Pierre et al., 2016; Oehri et al., 2017). In this line, we found a stronger increment of EVI in tree crops at the landscape level. Olive groves and vineyards have been historically cultivated under rainfed farming in southern Europe, but incentives from the Common Agricultural Policy have promoted the adoption of irrigation and use of fertilizers to increase yields (Camarsa et al., 2010). Fertilizers increase primary productivity (Gough et al., 2000) whereas irrigation can release constraints to vegetation activity in water-limited areas such as the Mediterranean basin (Haberl et al., 2007). The intensification of farming practices in tree crops is a plausible cause underlying the steeper increments of primary productivity in this land-use, which might have adverse consequences for certain reptile species (Romano et al., 2022). Studies aiming to detect drivers of species vulnerabilities within biodiversity hotspots should thus be aware of the scale-dependent effects of global change drivers on ecosystem properties (Gao et al., 2012; Qiao et al., 2021).

Protected areas are key in the protection of biodiversity (Chape et al., 2005) and they should incorporate how species or populations are exposed to the dynamic threats of anthropogenic global change to ensure long-term persistence of conservation targets (Abellán and Sánchez-Fernández, 2015; Bellard et al., 2014; Margules and Pressey, 2000). In agreement with previous studies (Araújo et al., 2007; Maiorano et al., 2015), the Natura 2000 network offers only moderate protection to reptile diversity, independently of the existence of temporal trends in primary productivity. However, the Natura 2000 network presented a greater area of forest and shrubland showing temporal trends in primary productivity than outside it. Forest and shrubland are the most abundant vegetation types within reptile hotspots, but only forest ecosystems are well protected under the Natura 2000 network. The greater forest and shrubland area with increasing primary productivity under the boundaries of the Natura 2000 network suggests that reptile communities of these habitats could be more vulnerable to vegetation changes than communities outside Natura 2000 areas. Management plans of the Natura 2000 network should monitor these reptile communities for early detection of positive or negative population- and community-level effects of increased primary productivity and reassess their conservation effectiveness under changing environmental conditions.

Mixed areas and grassland – which has declined over the last two decades in the reptile hotspots – are also poorly represented within the boundaries of the Natura 2000 network. Araújo et al. (2007) already documented a deficient protection of croplands within protected areas of the Iberian Peninsula and most of the high nature value farmland falls outside the Natura 2000 network (Anderson and Mammides, 2020). Therefore, the lower coverage of grassland within the Natura 2000 network, its high susceptibility to components of global change (Anderson and Mammides, 2020; EEA, 2020; Knapp and Smith, 2001), and the negative effects of agricultural intensification on reptile populations (Romano et al., 2022), make reptile communities of grassland habitats especially vulnerable and deserve further conservation focus.

A final consideration is that every biogeographic study may present data bias due to greater sampling efforts on specific areas such as natural reserves. Yet, natural reserves are often designed because of their higher biodiversity values, although their conservation status may differ among countries and/or among administrative regions within countries due to the management strategies applied. Besides, data bias for vertebrate species in European countries is smaller in comparison with other continents and/or taxonomic groups. We used the best data available (i.e., the official digital atlases) for a spatial resolution that trade-off bias attenuation and applicability of information for managers. Despite data limitations, our results provide useful information of basic and applied ecology and identify potential sites where reptile biodiversity is vulnerable to further explore the effects of ecosystem change on reptile populations. Nonetheless, national inventories should keep addressing survey biases that can end up unveiling new hotspots of reptile biodiversity as bias on species richness is reduced over the years. In this line, the observed spatial autocorrelation in species richness can help guide the allocation of efforts for monitoring poorly known areas regarding species distributions, and even to update the boundaries of the Natura 2000 network. Finally, we acknowledge that vulnerability of reptile populations might not be linked only to monotonic temporal trends in environmental conditions such as primary productivity or climate but also to other factors such as the presence of invasive species, which also deserve attention from researchers and administrations to understand how reptile communities are threatened by processes of anthropogenic global change.

5. Conclusions

Identifying regions that urgently need monitoring is of overwhelming importance to efficiently allocate time, energy, and budget for a vertebrate group which has historically lacked sound ecological data and comprehensive risk assessments (Cox et al., 2022; Meiri and Chapple, 2016). Most hotspots of Portugal are of further conservation interest because of the presence of endangered or vulnerable species. In Spain, hotspots located in Cordillera Costera of Catalonia, the bay of Cádiz, south of Doñana National Park, Parque Natural de las Sierras de Cazorla, Segura and Las Villas, and Sierra de Alcazar, Segura y Cañones del Mundo do not only have endangered species, but primary production and/or temperature have also monotonically increased. Focusing monitoring on these sites would allow tracking how populations and communities of several species with different protection status respond to changing ecosystem conditions and deepening on the underlying drivers. The observed increments in primary productivity in reptile hotspots could be caused by differences in primary productivity among vegetation types according to functional and structural features of the vegetation or by differences on the effects of increasing temperatures on primary productivity in combination with local feedbacks between vegetation types and temperature. Our results thus warn that reptile communities can be impacted by several factors of global change that alter ecosystem functioning. The Natura 2000 network should integrate adaptive management strategies that monitor how indicators of population change vary in sites experiencing ecosystem instability to enable rapid mitigation responses.

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CRediT authorship contribution statement

Rocío Tarjuelo: Data Curation, Formal Analysis, Writing- Original draft preparation; Pedro Aragón: Conceptualization, Funding Acquisition, Supervision, Writing- Reviewing and Editing.

Data availability

Data used are from freely available sources.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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