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Greek protected areas fail to fully capture shifting endemism hotspots under future climate and land-use change: The case of Peloponnese

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ABSTRACT

In the Anthropocene, conservation planning must adapt to rapid environmental changes driving the global biodiversity crisis. The impacts of climate and land-use change are particularly severe in biodiversity hotspots like the Mediterranean Basin, where unique taxa and ecosystems are increasingly at risk. To address these challenges, we conducted a forward-looking conservation gap analysis in Peloponnese, Greece, a regional endemism centre and key component of the Mediterranean biodiversity hotspot, providing a case study to support the development of cost-effective conservation strategies. We applied a taxonomically and phylogenetically informed approach to identify endemism hotspots across different time-periods. Persistent hotspots were mapped under future climate and land-use scenarios, and their overlap with protected and roadless areas was assessed. Our analysis revealed that endemism hotspots will likely shift geographically and diminish in extent over the coming decades. While key mountainous regions are expected to retain their hotspot status, our results point to a widespread decline in endemism and overall biodiversity loss. Concerningly, the most critical persistent hotspots overlap with extinction risk hotspots. Moreover, up to 46 % of the persistent endemism hotspots are not covered by designated protected areas, and <8 % of those lie within roadless areas. Our results highlight the need for a coordinated multi-dimensional strategy that should include the expansion of the current network of protected areas, the establishment of plant micro-reserves, and the translocation and reinforcement of populations of endemics. The identified conservation gaps represent regions of enduring resilience to environmental change, making them critical targets for long-term conservation planning.

1. Introduction

Biodiversity hotspots make a disproportionate contribution to global plant diversity, despite covering less than 20 % of the Earth's land surface (Mittermeier et al., 2011). These areas harbour the majority of the world's plant species, including exceptionally high concentrations of endemic, rare, and threatened taxa. However, biodiversity hotspots are increasingly vulnerable to the impacts of human-induced climate and land-use change (Bellard et al., 2012, 2014; Enquist et al., 2019; Habel et al., 2019). As a result, plant species extinctions have reached unprecedented levels in human history (Le Roux et al., 2019), despite the inherent resilience of plants to extinction and their typically long

extinction lag times (Cronk, 2016).

Extensive research has identified climate change as a major contributor to biodiversity loss (Habibullah et al., 2022). This driver is altering habitat suitability, causing species to shift in area and elevation, often resulting in significant range contractions and heightened extinction risk, particularly for species with limited dispersal abilities or those confined to specific ecological niches (Pimm et al., 2014; Rubenstein et al., 2023; Zu et al., 2021). At the same time, habitat loss, degradation, and fragmentation stemming from human-induced land-use change are primary causes of global biodiversity loss (Di Marco et al., 2019; Schulte to Bühne et al., 2021). In addition to the direct impacts of climate and land-use change, which are likely to intensify in the future, the feedback

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mechanisms and interactions between these two stressors can amplify their negative effects on plant diversity (Mantyka-Pringle et al., 2015; Oliver and Morecroft, 2014; Visconti et al., 2016). Endemic plants, often characterized by narrow geographic ranges, are particularly vulnerable to these dual pressures. The conversion and fragmentation of habitats can impede species movement and disrupt the continuity of plant populations, limiting their capacity to respond to climate change and resulting in isolated, smaller populations that are more susceptible to extinction (Keith et al., 2008; Schulte to Bühne et al., 2021). Additionally, climate change can exacerbate habitat degradation, thereby increasing the extinction risk for local populations (de Chazal and Rounsevell, 2009; Habibullah et al., 2022).

In response to the ongoing global biodiversity crisis, the Kunming-Montreal Global Biodiversity Framework, adopted during the 15th meeting of the Conference of the Parties, sets important targets for 2030 (CBD, 2022). This post-2020 Global Biodiversity Framework includes the commitment to protect a minimum of 30 % of the Earth's lands and effectively restore at least 30 % of the degraded terrestrial areas by 2030 (Targets 2 and 3), doubling the targets set by the Strategic Plan for Biodiversity 2011–2020 (CBD, 2010). Moreover, the Framework aims to halt human-induced extinction of threatened species and reduce overall extinction rates tenfold as part of its long-term goals for 2050. While the post-2020 biodiversity agenda intends to systematically increase financial resources for biodiversity conservation (CBD, 2022), there remains a crucial need to effectively allocate the available funds through optimized conservation prioritization planning (Arponen, 2012; Pouzols et al., 2014). In this respect, the identification of endemism hotspots has proven invaluable for establishing global priorities for conservation (Brooks et al., 2006; Myers et al., 2000). This is particularly important because endemic taxa, especially rare and habitat specialists, make an exceptional contribution to biodiversity but are highly vulnerable to environmental changes, placing them at greater risk of extinction (Clavel et al., 2011). Nevertheless, considering the scale-dependency of endemism patterns (Daru et al., 2020a), it becomes essential to map endemism hotspots at fine spatial scales (“hotspots-within-hotspots”; Cañadas et al., 2014).

Human-induced environmental changes are posing serious challenges in Greece, one of the most biodiverse countries in Europe and a vital part of the Mediterranean Basin, the world's second largest biodiversity hotspot (Cheikh Albassatneh et al., 2021; Médail and Quézel, 1997). Its vascular flora comprises over 7000 native taxa (species and subspecies) and nearly 1500 endemic taxa (Dimopoulos et al., 2013, 2016; available at <https://portal.cybertaxonomy.org/flora-greece/>). Concerningly, despite its current biodiversity levels, the overwhelming majority of Greek endemic plant taxa are classified as threatened (approximately 85 %) and over 46 % are facing imminent extinction (Kougioumoutzis et al., 2021b).

To safeguard its biodiversity, Greece has designated 27.3 % of its terrestrial area as part of the Natura 2000 network, which constitutes the world's largest coordinated network of protected areas (European Commission, 2022; European Environment Agency, 2018). Yet, various studies have raised concerns about the effectiveness of this network in adequately representing plant biodiversity, suggesting that a reassessment of these sites may be necessary (e.g., Dimitrakopoulos et al., 2004; Kougioumoutzis et al., 2020a, 2020b; Spiliopoulou et al., 2021; Trigas et al., 2012). As part of its ongoing conservation efforts, in early 2022, Greece introduced the first roadless policy in the EU, prohibiting road construction in six mountainous Natura 2000 sites to preserve biodiversity and ecosystem services (Kati et al., 2022). Roadless areas, often used to delineate wilderness areas, lack road infrastructure, rendering them well-connected and relatively remote (Kati et al., 2020, 2023). Due to their limited accessibility, they are typically characterized by a low level of anthropogenic impact and disturbance (Kati et al., 2023). Thus, the preservation of these sites is considered a cost-effective strategy to mitigate biodiversity decline (Hoffmann et al., 2020; Ibsch et al., 2016; Laurance and Arrea, 2017). However, the current conservation

measures implemented in Greece may not be sufficient to address future shifts in climate and land-use. Amidst accelerating environmental change in the Anthropocene era, conservation strategies face unprecedented challenges due to the uncertainty of future conditions (Rhodes et al., 2022). To enhance the effectiveness of these efforts, it is imperative to develop forward-looking strategies that consider various plausible scenarios of environmental change. Implementing spatial prioritization approaches that remain robust across various environmental scenarios and time periods is critical for devising long-lasting and resilient conservation strategies (Schuetz et al., 2015).

The phytogeographical region of Peloponnese (Fig. 1) harbours the highest absolute number of Greek endemic plants and constitutes a key regional endemism centre, making a significant contribution to the biodiversity of Greece and the Mediterranean (Kougioumoutzis et al., 2021a). This area alone hosts 32 % of all Greek endemic vascular plants, encompassing 464 species and subspecies (Dimopoulos et al., 2016; Kougioumoutzis et al., 2021a). Moreover, it contains 66.6 % of the threatened Greek endemic biodiversity hotspots (Kougioumoutzis et al., 2021b), making it a critical focus for conservation efforts. In light of the region's unique biodiversity and the increasing pressures from climate and land-use change, we have conducted a forward-looking plant biodiversity gap analysis. This analysis accounted for the potential synergistic effects of these environmental stressors in Peloponnese. Our goal is to map areas of high conservation value that have been overlooked by existing schemes and provide a case-study to support the development of a strategy that is both cost-effective and resilient to future environmental change. Specifically, we aim to:

- (i) map persistent endemism hotspots, i.e., areas projected to maintain their status as endemism hotspots across different time-periods extending until 2100, under various climate and land-use change scenarios;
- (ii) assess if and to what extent these endemism hotspots are covered by the Natura 2000 network of terrestrial protected areas and by roadless areas.

2. Materials and methods

We conducted a fine-scale (1 km resolution) taxonomically and phylogenetically informed approach to identify endemism hotspots in Peloponnese (Fig. 1) across different time-periods until the end of this century, under various climate and land-use change scenarios. In addition, we mapped conservation gaps by carrying out a spatial overlay analysis between endemism hotspots and protected and roadless areas. We implemented our analysis using R 4.2.2 (R Core Team, 2024) and QGIS 3.28 (see methodology summary in Fig. 2).

2.1. Species distribution models

We utilized the output of the species distribution models (SDMs) for Greek endemic vascular plant taxa found in Peloponnese (Table A.1) from Braz Pires et al. (2024). These models, built using climatic and land-use/land-cover predictor variables with a resolution of 30 arcsec (~1 km), covered the following periods: 2015 (representing the present year and serving as the baseline), 2020s (2010–2039), 2050s (2040–2069), and 2080s (2070–2099). For the future time-periods, the climatic projections were based on three General Circulation Models (GCMs) from Phase 5 of the Coupled Model Intercomparison Project (CMIP5): CESM1-CAM5, MPI-ESM-LR, and an ensemble of 15 GCMs. Each GCM incorporated two IPCC Representative Concentration Pathway (RCP) scenarios: the milder RCP4.5 and the more extreme RCP8.5. The land-use/land-cover projections were based on three CMIP6 Shared Socioeconomic Pathways (SSP) scenarios paired with RCPs: SSP1-RCP2.6 (sustainable), SSP3-RCP7.0 (medium-high), and SSP5-RCP8.5 (severe). The SDMs were built for every possible combination of climate and land-use scenarios, encompassing 18 scenarios for

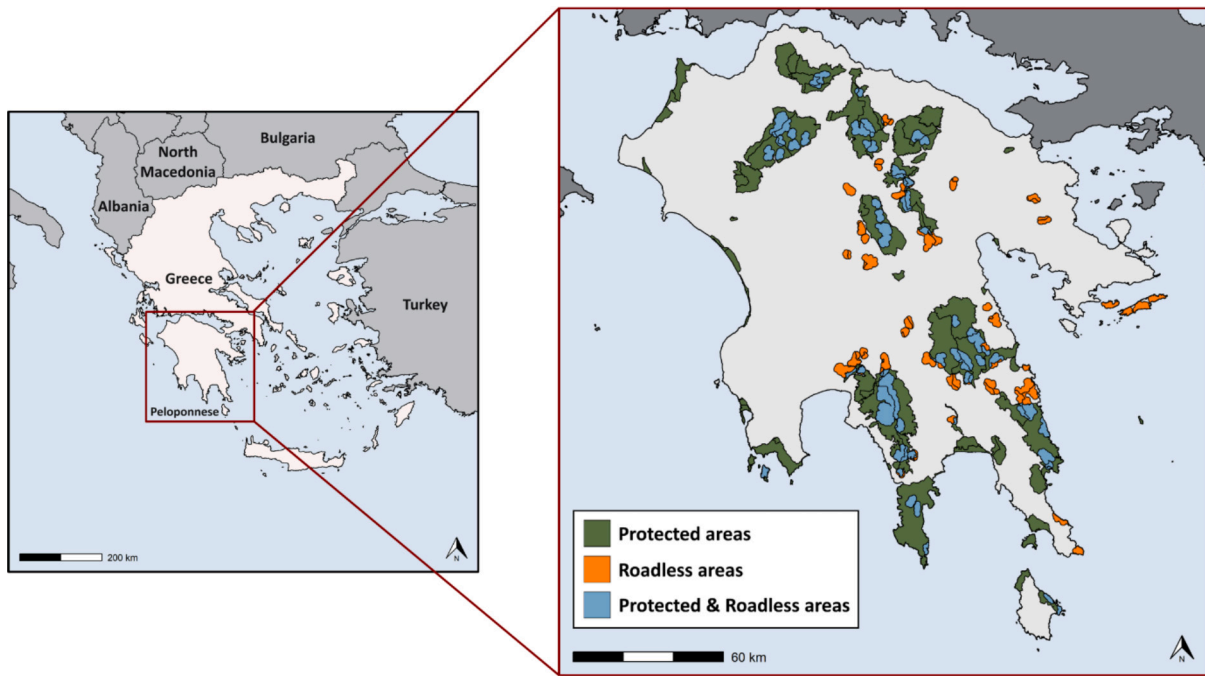


Fig. 1. Study area: phytogeographical region of Peloponnese, comprising the Peloponnese peninsula, the Saronic Islands, Elafonisos, Kythera, and Antikythera. Left panel: Map of Greece and surrounding countries, highlighting the study area with a red polygon. Right panel: Map of Peloponnese, depicting the Natura 2000 network of terrestrial protected areas (including Special Areas of Conservation and Special Protection Areas), roadless areas (Kassara et al., 2022), and their overlapping areas. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

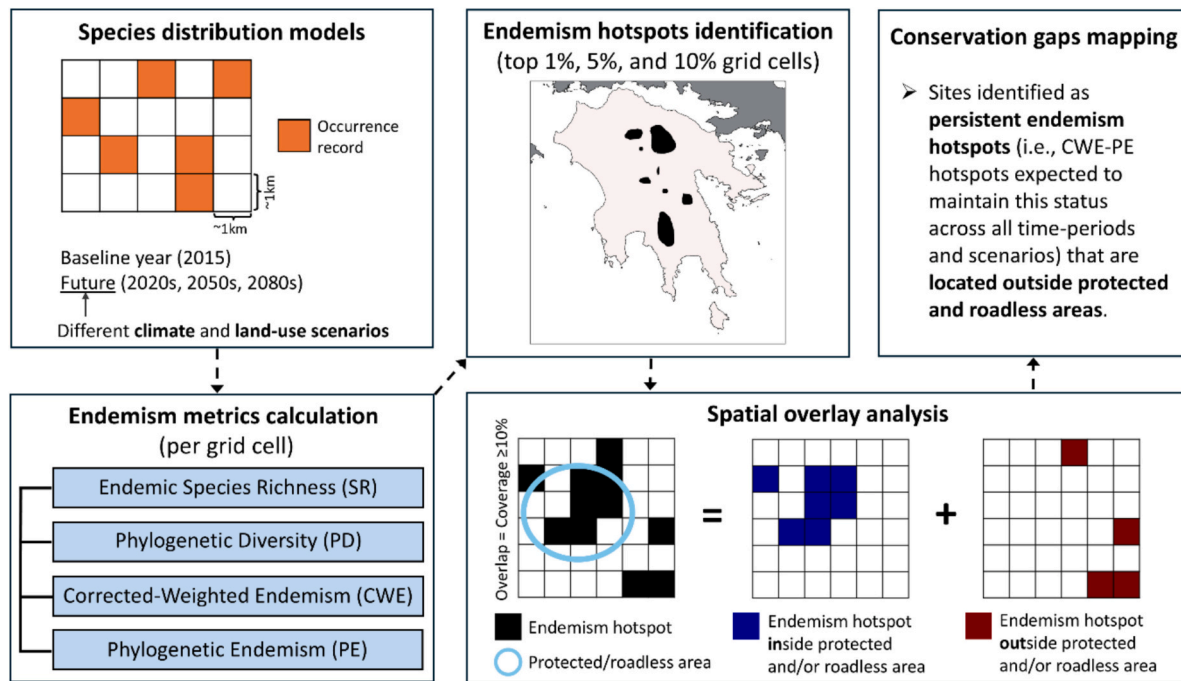


Fig. 2. Diagram illustrating the methodological workflow implemented in the present study.

each future period (see Appendix C for a detailed description of the modelling framework).

2.2. Identification and analysis of endemism hotspots

We computed spatially explicit taxonomic and phylogenetic biodiversity metrics (hereinafter referred to as endemism metrics, as they were calculated exclusively for Greek endemic taxa occurring in

Peloponnese) across all time-periods and scenarios, based on the projected taxa occurrences generated by the SDMs under different climate and land-use scenarios (see Table 1). Specifically, we calculated Endemic Species Richness (SR), Corrected-Weighted Endemism (CWE; Crisp et al., 2001), Phylogenetic Diversity (PD; Faith, 1992) and Phylogenetic Endemism (PE; Rosauer et al., 2009), adapting the R functions originally developed by Guerin et al. (2015) and utilizing the ‘phyloregion’ 1.0.6 (Daru et al., 2020b) and ‘PhyloMeasures’ 2.1

Table 1
Definitions and references for the endemism metrics used in this study.

Metric	Definition	Reference
Endemic Species Richness (SR)	Number of endemic species in a given spatial unit	(Magurran, 2004)
Corrected-Weighted Endemism (CWE)	Sum of the inverse range sizes of species in a given spatial unit, divided by species richness.	(Crisp et al., 2001)
Phylogenetic Diversity (PD)	Total branch length of a phylogenetic tree connecting the taxa in a given spatial unit	(Faith, 1992)
Phylogenetic Endemism (PE)	Phylogenetic diversity weighted by the geographic restriction of each branch.	(Rosauer et al., 2009)

(Tsirogiannis and Sandel, 2016) R packages. To calculate the two phylogenetic metrics, we pruned the phylogenetic tree from Kougioumoutzis et al. (2021a), retaining only the plant taxa present in our dataset (Table A.1). To assess whether the observed values were significantly greater than expected by chance, we followed Guerin et al. (2015) and applied a null model comparing endemism values per grid cell against distributions generated from 1000 randomizations (see Appendix C).

We calculated the mean difference between the future values of SR, PD, CWE, and PE and the baseline year (2015). This difference was computed for each grid cell within our study area by subtracting current endemism metric values from those projected in each future scenario. This analysis was replicated for three future time-periods (2020s, 2050s, and 2080s), and the resulting differences were subsequently averaged to represent the mean change in endemism among all studied taxa.

We classified endemism hotspots into three distinct levels for each metric, time period, and scenario using the methodology outlined by Kougioumoutzis et al. (2021a). This entailed locating areas representing the top 1 %, 5 %, and 10 % highest values of each metric, labelled as HT1, HT5, and HT10 hotspots, respectively. Traditionally, spatial prioritization frameworks have relied on unweighted metrics such as SR and, more recently, PD (Fleishman et al., 2006; Isaac et al., 2007). However, CWE and PE offer a more robust and comprehensive approach for identifying areas of exceptionally high diversity and conservation value, as these weighted metrics assign greater importance to small-ranged (CWE) and evolutionarily distinct (PE) taxa (Daru et al., 2019; Laity et al., 2015). As such, we intersected the two weighted metrics to identify areas of high taxonomic and phylogenetic uniqueness (CWE-PE hotspots) in Peloponnese, following Kougioumoutzis et al. (2021a). The robustness of these identified hotspots, particularly the CWE-PE HT1 persistent ones, was supported by randomization tests, which showed that a large proportion of cells were statistically significant for both CWE and PE values (see Appendix C).

To compare hotspots identified by different metrics, we estimated and analysed the area and altitude of all mapped hotspots. Moreover, we identified the centroids of all HT1 CWE-PE hotspots and used the 'geosphere' 1.5.18 R package to assess potential changes in their spatial and elevational distribution over time.

Finally, we mapped persistent endemism hotspots, defined as current CWE-PE hotspots that are projected to maintain this status in the future. We applied this forward-looking approach with the aim of future-proofing conservation efforts by anticipating potential changes in taxa distributions over time. We achieved this by applying a strict approach, where, for each CWE-PE hotspot level (HT1, HT5, and HT10), we retained only the grid cells identified as hotspots across all time-periods and scenarios.

2.3. Overlap of endemism hotspots with protected and roadless areas

Protected area shapefiles for the Natura 2000 network in Greece were retrieved from the World Database on Protected Areas and processed using the 'wpdar' 1.3.3 R package (Hanson, 2022). In our

analysis, we included Special Areas of Conservation (SACs) that are also designated as Special Protection Areas (SAC/SPA) in Peloponnese, but excluded SACs focused solely on marine protection. Furthermore, we utilized the dataset of roadless areas in Greece provided by Kassara et al. (2022), which includes all areas larger than 1 km² that are further than 1 km from a road. We conducted a spatial overlay analysis, where we intersected the identified endemism hotspots with the terrestrial protected areas (Fig. 2). Similarly, we overlapped the identified hotspots with the Peloponnesian roadless areas. We considered a hotspot grid cell to be located within protected or roadless areas if at least 10 % of the cell's area was covered by them, following Xu et al. (2017). In addition, we calculated the degree of overlap in both cases, i.e., the proportion of grid cells overlapping with protected or roadless areas and analysed potential changes from 2015 to 2100. Moreover, we mapped conservation gaps, defined as persistent endemism hotspots located outside protected and roadless areas (with coverage <10 %). Finally, we calculated the Euclidean distance between each conservation gap and the borders of the closest protected area using the coordinates of the central point of each grid cell representing a conservation gap, employing the 'sf' 1.0.16 and 'raster' 3.6.26 R packages (Hijmans et al., 2023; Pebesma, 2018). This was done to assess the potential expansion required for protected areas to accommodate species distribution shifts driven by climate and land-use changes.

3. Results

3.1. Shifts and persistence of endemism hotspots under climate and land-use change

According to our projections, current and future endemism hotspots are concentrated in the major mountain massifs of Peloponnese (see Figs. 3 and A.1–A.6). Specifically, the Chelmos, Kyllini, and Taygetos mountain ranges exhibit the highest levels of endemism across all calculated metrics, time-periods, and scenarios, followed by Mts Parnon, Mainalo, and Erymanthos. Moreover, we found that no islands within the phytogeographical region of Peloponnese show exceptionally high endemism levels, as all the endemism hotspots identified by our models are located within the Peloponnesian peninsula.

Although we observed fluctuations in the extent and elevation of endemism hotspots across different time-periods and climate and land-use change scenarios, these shifts did not follow a clear or consistent trend. Despite this variability, our analysis shows that current and future CWE-PE hotspots consistently occupy the smallest area (i.e., fewer hotspot grid cells), whereas SR hotspots have the largest extent across all hotspot levels: HT1, HT5, and HT10 (Tables A.6–A.10 and Figs. A.11–A.15). Conversely, CWE-PE endemism hotspots are generally situated at higher median altitudes, while SR hotspots are typically found at lower elevations.

When examining the current and future HT1 CWE-PE centroids, our results indicate that they are expected to shift both geographically and altitudinally as time progresses (Table A.11). The centroids are projected to move northward (toward higher latitudes), with the mean distance from the baseline period increasing from 1.7 km in the 2020s to 4.9 km by the 2080s. In terms of altitude, we observed a slight increase in the 2020s (+45.56 m), followed by decreases of 138.11 m in the 2050s and 305.50 m in the 2080s, indicating a trend toward lower elevations by the second half of the century.

Based on our models' predictions, the mean values of all endemism metrics calculated for the entire study area will be lower in the second half of the century compared to the current values, regardless of the climate and land-use change scenarios considered (see Tables A.2–A.3 and Figs. A.7–A.10). Our projections revealed diverse patterns of change across different endemism metrics in Peloponnese, with weighted metrics (CWE and PE) showing greater variability compared to non-weighted metrics (SR and PD) in future time periods (Tables A.4–A.5). Although few areas are expected to retain their current CWE values by

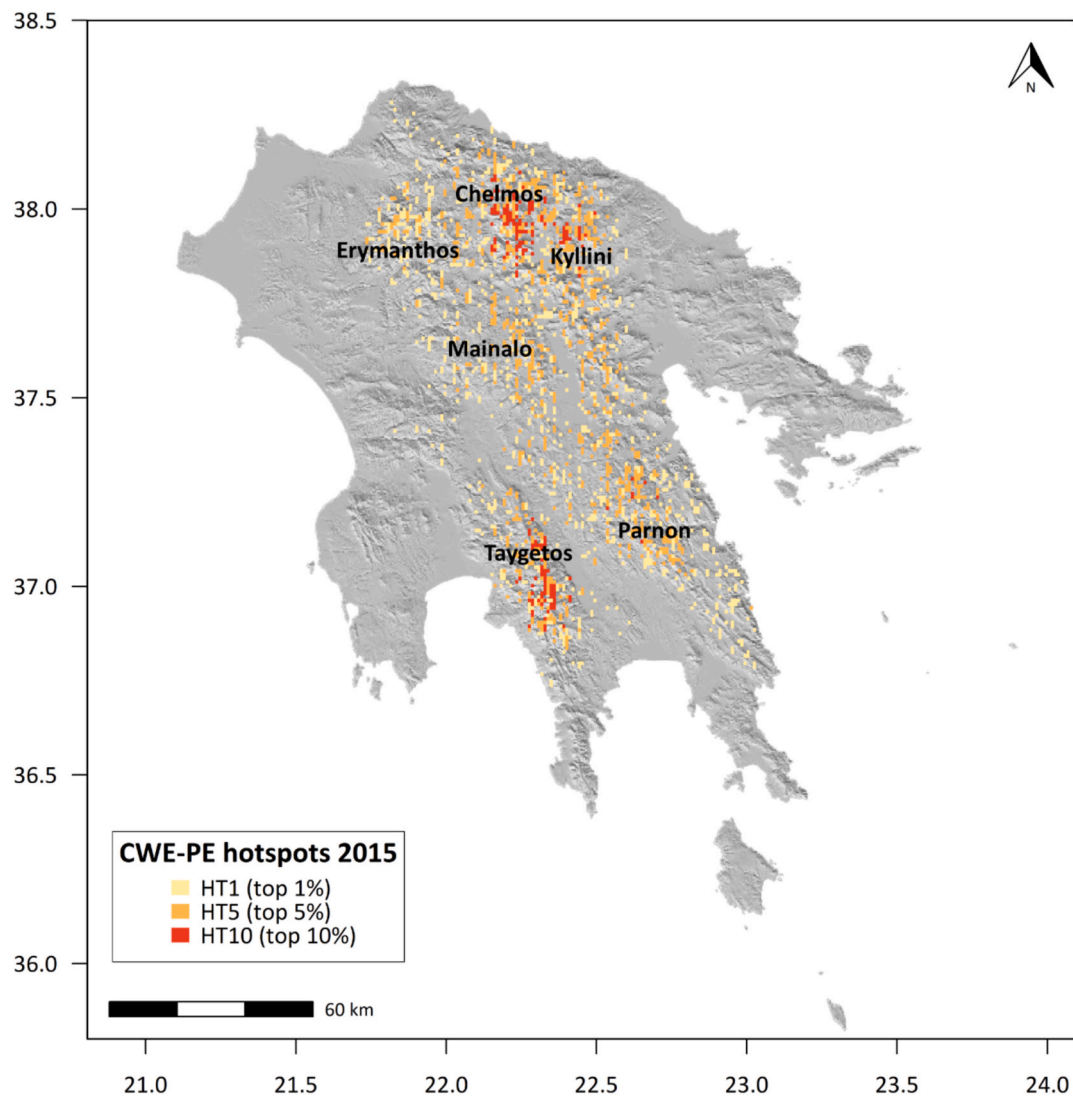


Fig. 3. Location of the Corrected-Weighted–Phylogenetic Endemism (CWE-PE) hotspots mapped for the baseline year (2015) in Peloponnese. The map displays three levels of CWE-PE endemism hotspots (HT1, HT5, and HT10), as well as the main mountain massifs of Peloponnese.

the 2080s, the extent of Peloponnese expected to exhibit higher CWE values (28.7 % to 49.9 % of the total extent, depending on the future scenario; Table A.5) is comparable to the extent projected to experience a decrease in CWE (28.6 % to 51 %). PE showed a slightly different trend, with a larger proportion of the study area being projected to experience increases (36 % to 50.8 %) compared to the proportion expected to show lower values (27.8 % to 43.6 %). In contrast, SR and PD are projected to decline over larger areas. Only 11.2 % to 15 % of the region is expected to show higher SR values, while up to 40.3 % is projected to experience declines. Similarly, for PD, increases are anticipated in 15.6 % to 27.1 % of the area, while decreases are expected in 20.4 % to 40.6 %.

Our results indicate that over 50 % of the current HT1 CWE-PE hotspots are projected to lose their hotspot status under at least one future scenario by the end of the century, with approximately 30 % of HT5 and HT10 hotspots expected to follow a similar trend (Fig. 4 and Table 2). In addition, we found that between 5.5 % and 18.0 % of the hotspots are consistently anticipated to lose their designation as hotspots across all 54 climate–land-use scenarios. In contrast, the emergence of new hotspot areas is expected to be limited, with only 4.3–6.7 % of future CWE-PE hotspots being projected to occur in regions not currently recognized as hotspots (Table 2). However, we identified persistent endemism hotspots that are expected to maintain their high

endemism levels across all time-periods and environmental scenarios from the most sustainable to the most severe. These areas cover approximately 87 km² (HT1), 754 km² (HT5), and 1334 km² (HT10), each consistently maintaining a median altitude exceeding 1000 m above sea level.

3.2. Endemism hotspot coverage by protected and roadless areas

The overlap between the network of terrestrial protected areas in Peloponnese and the current endemism hotspots, identified using different endemism metrics, ranged from 44.3 % (SR) to 85.4 % (CWE-PE; Tables A.6–A.10 and Fig. A.17). The level of overlap was similar for future time-periods, ranging between 42.1 % (SR) and 85.5 % (PE), depending on the hotspot type and the future scenario considered. For roadless areas, the intersection with hotspots averaged below 36 % for all hotspot types, ranging between 23.1 % (SR) and 51.7 % (CWE-PE) for different future scenarios (Tables A.6–A.10 and Fig. A.18). Moreover, we found that only a small fraction (3.1 % to 7.6 %) of the hotspots that are not covered by the Natura 2000's sites are located within roadless areas.

Over 13 % of the HT1 persistent endemism hotspots are located outside the protected and roadless areas of Peloponnese (Fig. 5 and Table A.12). These conservation gaps occupy an extent of approximately

CWE-PE Endemism Hotspots: shifts in extent over time

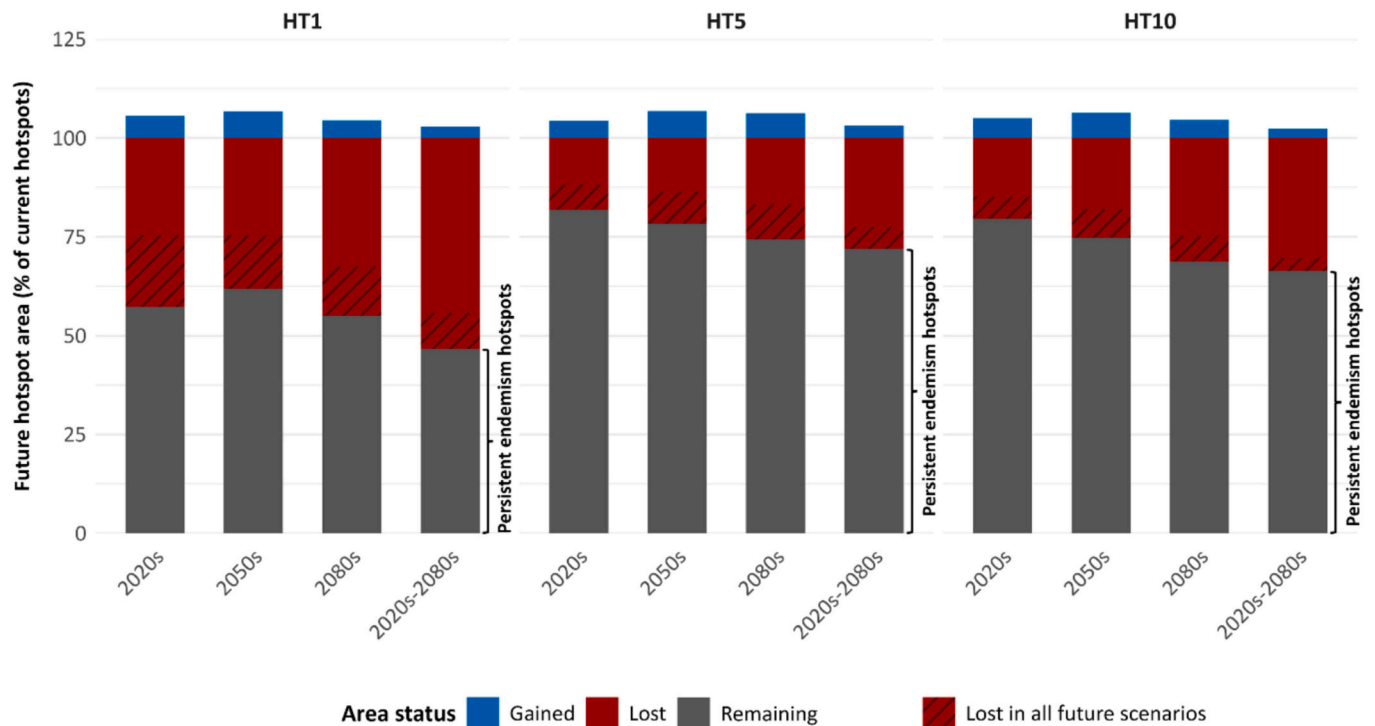


Fig. 4. Stacked bar chart illustrating the projected extent of future Corrected-Weighted–Phylogenetic Endemism (CWE-PE) hotspots, expressed as a percentage of the area occupied by current hotspots. The blue areas represent regions where new hotspots are projected to emerge in the respective time-period, according to all future scenarios. The red areas show the percentage of current CWE-PE hotspots projected to be lost under at least one environmental change scenario, with dark red diagonal stripes within these areas indicating the proportion of current hotspots expected to be lost under all scenarios. The dark grey areas indicate hotspots expected to persist across all scenarios of the respective period. Hotspot levels (HT1, HT5, and HT10) represent the grid cells that simultaneously fall within the top 1 %, 5 %, and 10 % of both CWE and PE values, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

12 km² and are located near the boundaries of the Chelmos-Vouraikos National Park, in Northern Peloponnese (Figs. 6 and A.16). More specifically, the distance of HT1 conservation gaps to the nearest protected areas ranges from 0.5 km to 4.1 km, with a mean distance of <1.7 km (Supplementary table). However, for HT5 and HT10 persistent endemism hotspots, the conservation gaps were notably larger, comprising 31 % and 39 % of their area, respectively, equivalent to nearly 232 km² and 524 km². These sites are primarily distributed along the mountainous regions of the Peloponnese peninsula, with many grid cells being located near the borders of currently protected areas, at average distances of approximately 4.6 km for HT5 and 6.0 km for HT10 from the nearest ones (see also Figs. A.2–A.3 and Supplementary table).

4. Discussion

We conducted a fine-scale, taxonomically and phylogenetically informed identification of endemism hotspots in Peloponnese, considering various climate and land-use change scenarios extending until the end of the century. The results indicate that these endemism hotspots are expected to undergo shifts in their spatial distribution and elevation over time, along with an overall reduction in their extent. To address this, we mapped persistent endemism hotspots, defined as areas classified as CWE-PE endemism hotspots across all time-periods and climate and land-use scenarios. These hotspots represent regions of enduring resilience to environmental change, making them critical for long-term conservation planning. However, a significant portion of these hotspots remains outside formal conservation schemes, uncovering critical conservation gaps that require urgent attention to safeguard the unique biodiversity of Peloponnese.

4.1. Implications of shifting endemism hotspots under climate and land-use change

Our analysis consistently identifies the main mountain massifs of the Peloponnese peninsula as retaining the highest SR, PD, CWE, and PE values across all time-periods and future scenarios. Our findings indicate that multiple areas within Mts Chelmos, Kyllini, Taygetos, Erymanthos, Mainalo, and Parnon, renowned for their current high floristic diversity (Kougioumoutzis et al., 2021a; Trigas et al., 2012), are projected to sustain high levels of endemism in the future. This aligns with previous biogeographical studies that identified several of these mountain ranges as major local biodiversity hotspots within a regional biodiversity hotspot (Médail and Quézel, 1997; Stevanović et al., 2009; Strid, 1986b, 1986a; Tan and Iatrou, 2001) and as long-term refugia that have historically provided climatic stability for plant species (Médail and Diadem, 2009; Strid, 1986b, 1986a; Thompson, 2020). The persistence of these areas as hotspots in our future projections suggests that their role as refugia may continue, supporting the long-term survival of endemic flora. These regions function as low latitude refugia owing to their complex topography. Throughout the transition from the Last Glacial Maximum to the Late Holocene, these areas have buffered against increasing temperatures and aridity and harbour not only several range-restricted Greek endemics, but also numerous cold-adapted species exhibiting distinct patterns of phylogenetic clustering (Kougioumoutzis et al., 2021c; Panitsa et al., 2021). This pattern is consistent with findings from other biodiversity hotspots worldwide, where mountainous regions serve as long-term refugia, namely due to their climatic buffering capacity and topographic complexity (Gómez et al., 2015; Noroozi et al., 2018; Steinbauer et al., 2016; Trew and Maclean, 2021). This is

Table 2

Total extent (in km²) and median altitude (in m above mean sea level) of Corrected-Weighted–Phylogenetic Endemism (CWE-PE) hotspots. The data are presented for hotspots identified in the baseline year (2015) and for three future time-periods (2020s, 2050s, and 2080s). These results are also shown for persistent endemism hotspots, defined as current CWE-PE endemism hotspots expected to maintain this status across all future time periods and scenarios. In addition, the table includes percentages of current hotspots projected to be lost under at least one scenario and those expected to be lost, remain, or emerge as new hotspots across all scenarios. For persistent endemism hotspots, the loss percentages indicate the proportion of current hotspots (2015) that do not persist in all future projections, i. e., those that fail to remain as persistent hotspots. The values are presented for the three levels of hotspots: HT1, HT5, and HT10, corresponding to the top 1 %, 5 %, and 10 % grid cells with the highest endemism values.

	Hotspot level	Total extent (km ²)	Median altitude (m a.s.l.)				
Current CWE-PE endemism hotspots (2015)	HT1	186.91	1402.35				
	HT5	1047.96	1112.1	% Current hotspots lost in at least one scenario	% Current hotspots lost in all scenarios	% Current hotspots remaining	% New future hotspots
	HT10	2009.81	967.15				
2020s CWE-PE endemism hotspots	HT1	117.61	1297.31				
	HT5	902	1114.83	18.24 (191.11 km ²)	6.31 (66.15 km ²)	81.76 (856.85 km ²)	4.31 (45.15 km ²)
	HT10	1699	992.7	20.48 (411.62 km ²)	5.49 (110.26 km ²)	79.52 (1598.18 km ²)	5.02 (100.81 km ²)
2050s CWE-PE endemism hotspots	HT1	128.11	1360.2	38.2 (71.40 km ²)	13.48 (25.20 km ²)	61.8 (115.51 km ²)	6.74 (12.60 km ²)
	HT5	892.55	1108.67	21.64 (226.81 km ²)	7.92 (82.95 km ²)	78.36 (821.15 km ²)	6.81 (71.40 km ²)
	HT10	1628.64	989.68	25.29 (508.23 km ²)	7.11 (142.81 km ²)	74.71 (1501.19 km ²)	6.32 (127.06 km ²)
2080s CWE-PE endemism hotspots	HT1	111.31	1357.68	44.94 (84.00 km ²)	12.36 (23.10 km ²)	55.06 (102.91 km ²)	4.49 (8.40 km ²)
	HT5	845.3	1092.93	25.65 (268.82 km ²)	8.72 (91.36 km ²)	74.35 (779.14 km ²)	6.31 (66.15 km ²)
	HT10	1473.23	1010	31.24 (627.94 km ²)	6.37 (128.11 km ²)	68.76 (1381.88 km ²)	4.55 (91.36 km ²)
Persistent endemism hotspots	HT1	87.15	1273.21	53.37 (99.76 km ²)	8.99 (16.80 km ²)	-	-
	HT5	753.94	1115.27	28.06 (294.02 km ²)	5.41 (56.70 km ²)	-	-
	HT10	1333.58	1018.58	33.65 (676.24 km ²)	3.19 (64.05 km ²)	-	-

particularly relevant given that Mediterranean mountain ecosystems are experiencing shifts in plant species ranges due to climate change, with endemic taxa facing disproportionately high risks of decline (Cañadas et al., 2014; Pauli et al., 2012). On the other hand, no islands in our study area were classified as endemism hotspots, despite prior research identifying Kythira as having high species richness (Kougioumoutzis et al., 2022a; Panitsa et al., 2021). This discrepancy likely stems from Kythira hosting several very rare endemic species, for which the available occurrence data was insufficient to build reliable SDMs (Tzanoudakis et al., 1998, 2006).

Our projections indicate that the mean values for all endemism metrics across the entire study area are expected to decline by the 2080s,

even under the least severe scenarios, suggesting potential (local) extinctions. We forecast more significant shifts in weighted endemism metrics compared to non-weighted metrics, indicating that climate and land-use change exert a greater impact on taxa with small ranges and high evolutionary distinctiveness. Consequently, their populations may undergo larger range contractions or geographic shifts, which could make them more narrowly distributed. In theory, this could increase their weight in the CWE metric, potentially leading to higher CWE values in certain areas as taxa become more range restricted. However, our results show an overall decline in CWE, which indicates that taxa are not only becoming more restricted but are likely facing extinction. Multiple studies have shown that rare and specialist taxa are more

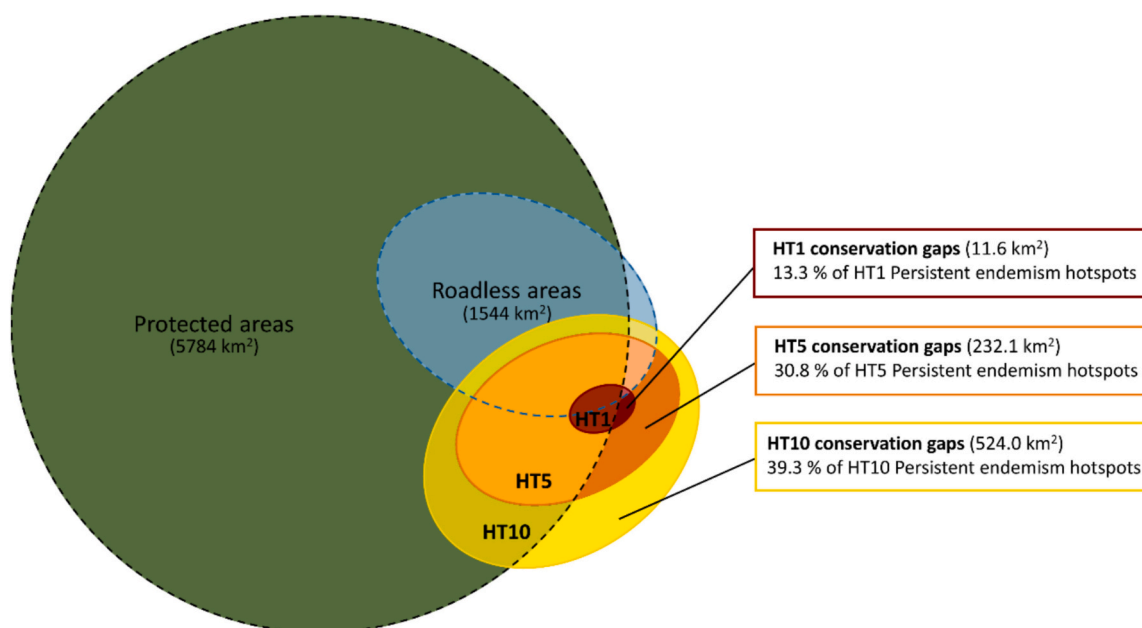


Fig. 5. Venn diagram illustrating the degree of overlap between the persistent endemic hotspots (2015–2100) and the Natura 2000 network of terrestrial protected areas (green circle) and roadless areas (blue circle) in Peloponnese. The red, orange, and yellow circles represent the three levels of persistent endemic hotspots (HT1, HT5, and HT10). The portions of these circles outside both protected and roadless areas indicate the conservation gaps identified in this study, with their extent and proportion being shown in the corresponding coloured boxes. For visualization purposes, the figure is not at scale in terms of area (km^2). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

vulnerable to environmental changes than generalists, thus holding a greater extinction risk (Clavel et al., 2011; Kidane et al., 2019; Loarie et al., 2008). Many endemic and rare taxa are extremely susceptible to changes in their microhabitats due to their specialized adaptations and narrow ecological niches, a pattern observed across multiple Greek mountain ranges (e.g., Fassou et al., 2020; Kougioumoutzis et al., 2020a, 2020b; Kougioumoutzis et al., 2021c; Kougioumoutzis et al., 2022b). A recent study analysing the potential impacts of climate and land-use change on very rare endemic plant species in Chelmos-Vouraikos National Park, Peloponnese, predicts that many of these species may face (near) extinction in the foreseeable future, with some potentially already experiencing long-term extinction debt (Kougioumoutzis et al., 2022b). These projections align with our findings, which may be attributed to the narrow distribution ranges and the high degree of habitat specialization exhibited by Peloponnesian endemic plants, many of which are confined to harsh environments such as cliffs and screes (Panitsa et al., 2021; Trigas et al., 2012).

Despite the expected decrease in endemism, the spatial patterns of change vary among the different metrics, reflecting complex spatial dynamics in response to climate and land-use change. The consistent declines projected for SR and PD across a large portion of Peloponnese highlight widespread biodiversity loss and raise concerns about the potential cascading effects on ecosystem functioning and services. At the same time, smaller areas projected to see increases in these two metrics imply that species that will persist will concentrate in environmentally suitable and topographically complex areas. In contrast, for CWE, the comparable extents of areas projected to experience increases and decreases suggest a redistribution of endemism hotspots rather than a uniform trend. This pattern does not necessarily indicate the emergence of new areas gaining endemic taxa but likely reflects losses of endemic taxa in current hotspots, as indicated by the decline in SR, leading to relative increases in other areas where some taxa remain or become rarer. Since CWE assigns greater weight to rarer taxa, the extinction of these taxa, whether local or widespread, could artificially inflate CWE values in areas where some taxa persist or become rarer. In the case of PE, the larger proportion of areas projected to show increases may be attributed to the loss of phylogenetically close (i.e., less evolutionarily

distinct) taxa, leaving behind more phylogenetically distinct ones. This could occur if more generalist taxa, or those with unique evolutionary histories, are more resilient to changing conditions, resulting in higher PE values despite an overall loss of biodiversity. Conservation efforts should account for areas where increases in CWE and PE are projected, as these regions may become crucial for preserving the remaining endemic and evolutionarily distinct taxa. Moreover, understanding that increases in these metrics may result from species loss elsewhere emphasizes the urgent need to preserve current hotspots to prevent such losses.

The redistribution of taxonomic and phylogenetic endemism across the study area is further supported by the projected geographic and altitudinal shifts observed in the centroids of HT1 CWE-PE hotspots. By the 2080s, these hotspots are expected to shift northward by up to 4.9 km and downslope by over 300 m. Rather than reflecting an absolute increase in endemism in areas at higher latitudes and lower altitudes, this trend likely indicates a redistribution driven by the loss of endemic taxa in current hotspots, leading to relative increases elsewhere. Such shifts are more likely to reflect the contraction of species' niches rather than active migration of endemic plant taxa to new locations.

We mapped conservation priority areas likely to remain resilient to climate and land-use changes, integrating two critical dimensions of biodiversity: taxonomic (CWE) and phylogenetic (PE). Yet, our results predict a troubling decline in the extent of CWE-PE hotspots in Peloponnese. Over half of the current highest priority hotspots (HT1) are projected to lose their status under at least one scenario by the 2080s, translating into the potential loss of nearly 100 km^2 . Likewise, approximately 30 % of HT5 and HT10 hotspots are at risk, translating to losses of 294 km^2 and 676 km^2 , respectively.

Despite this reduction, the remaining areas are expected to continue serving as hotspots under all scenarios. However, the most critical (HT1) persistent endemism hotspots coincide with extinction risk hotspots, previously identified by Kougioumoutzis et al. (2021b). In particular, Mts Chelmos and Taygetos are hotspots for threatened and critically endangered endemics, while Mt. Parnon harbours a large concentration of critically endangered endemics. The anticipated reduction in overall endemism suggests that while these hotspots will persist, their species

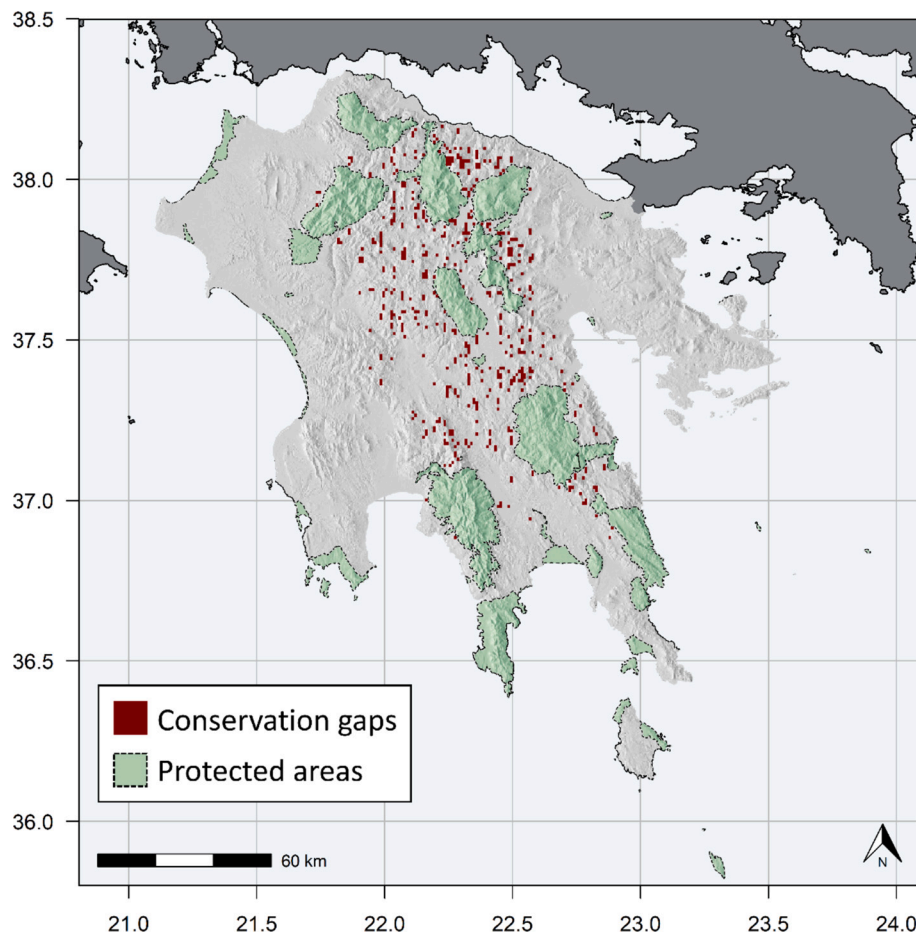


Fig. 6. Location of conservation gaps in Peloponnese. Red grid cells indicate persistent endemism hotspots (HT1, HT5, and HT10) that are located outside protected and roadless areas. The green polygons represent the Natura 2000 network of terrestrial protected areas in Peloponnese. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

composition may shift, and they will likely support fewer endemics. While some extinctions may be unavoidable, concentrating conservation efforts and climate mitigation actions in these resilient areas could effectively preserve the remaining biodiversity and support the adaptation of endemic taxa to changing environmental conditions.

In addition to persistent hotspots, our analysis identified a smaller proportion of new hotspots projected to emerge under future scenarios. Although limited in extent, with only 4.3 % to 6.7 % of future CWE-PE hotspots expected to arise, they may play an important role in future conservation efforts. As discussed above, these newly emerging hotspots likely reflect biodiversity loss in other regions, leading to relative increases in endemism. While our gap analysis focuses on areas resilient across all scenarios, newly emerging hotspots should not be overlooked. As potential centres of biodiversity, they may provide important opportunities for future conservation interventions, particularly considering the expected loss of endemism in areas that are currently highly diverse.

4.2. The future of endemism hotspots: challenges and opportunities for conservation

The overlap between endemism hotspots and the Natura 2000 network of terrestrial protected areas showed a broad range, from 42.1 % to 85.4 % for different hotspot types, time-periods, and scenarios of climate and land-use change (with CWE-PE hotspots ranging from 48.8 % to 85.4 %). Specifically, 80.7 % of the most critical (HT1) persistent endemism hotspots have already been successfully incorporated into a protection scheme (see Fig. 5 and Table A.12). However, the level of

integration is considerably lower for HT5 and HT10 persistent endemism hotspots, with only 62.5 % and 54.1 %, respectively, currently included in the NATURA 2000 network. In a previous study, Kouglioumoutzis et al. (2021a) mapped current CWE-PE hotspots in Greece at approximately 5 km resolution, revealing an overlap with protected areas ranging from 74.9 % to 96.7 %. This level of overlap surpassed our findings for all types of hotspots in Peloponnese, including current CWE-PE hotspots (as detailed in Table A.10) and persistent endemism hotspots. Although their findings cover the entire country, the finer 1 km resolution used here provides a more detailed assessment of hotspot distributions, contributing to the lower overlap observed.

Furthermore, we found that a significant fraction of the persistent endemism hotspots, especially HT5 and HT10, are conservation gaps, i. e., they are outside any form of formal protection and are situated within 1 km of a road, making them more susceptible to human disturbance. The highest priority sites (HT1) cover <math><12\text{ km}^2</math> and are all located near the borders of the Chelmos-Vouraikos National Park, at distances ranging from 0.5 km to 4.1 km (see Fig. A.17 and Supplementary table). This proximity indicates that, even with limited funds, a slight expansion of this protected area could effectively incorporate the most critical conservation gaps into the Natura 2000 network. Moreover, despite the large extent of HT5 and HT10 conservation gaps (232 km² and 524 km², respectively), many of these sites are also located near existing protected areas, with average distances of 4.6 km and 6.0 km, correspondingly (see Figs. 6 and A.17). While the Natura 2000 network was not originally designed to account for climate resilience, ongoing environmental shifts underscore the need to reassess conservation strategies (Bellard et al., 2014; Graham et al., 2019; Lai et al., 2022; Nila et al., 2019; Ranius

et al., 2023). In this context, a partial redesign and expansion of the protected area network in the Peloponnese could significantly enhance the preservation of Mediterranean endemic flora, as previously recommended by Kougioumoutzis et al. (2021a) and Kougioumoutzis et al. (2021b). Such efforts align with broader conservation commitments, including the Kunming-Montreal Global Biodiversity Framework and the EU Biodiversity Strategy for 2030, which set targets for increasing protected area coverage (CBD, 2022; European Commission, 2025).

Our analysis revealed that only a fraction of hotspot areas that presently lack coverage by designated protected areas is located inside roadless areas (<8 % for all endemism hotspots). Although our study and recommendations focus on endemism hotspots outside these areas due to their greater vulnerability to anthropogenic pressures, the vital role of roadless areas should not be overlooked. These sites, being less accessible and thus less impacted by human activities, are essential for preserving biodiversity and maintaining ecological functioning (Hoffmann et al., 2020; Kati et al., 2022, 2023). Although the Greek government has taken a significant step by prohibiting road construction in six mountainous Natura 2000 roadless sites, expanding this policy to additional areas is imperative (Kati et al., 2022). More proactive roadless policies are necessary to prevent habitat fragmentation and other forms of human disturbance. This is especially important in Peloponnese, where approximately 94.5 % of these roadless areas are located within the Natura 2000 network.

Although our projections suggest that the persistent endemism hotspots will retain high endemism levels until the 2080s, many of these sites, such as Mts Chelmos, Parnon, and Taygetos, host a large number of threatened and critically endangered endemic species (Kougioumoutzis et al., 2021b). Therefore, these areas should be prioritised in conservation efforts, aligning with Target 4 of the Kunming-Montreal Global Biodiversity Framework, which emphasizes the need for urgent actions to halt the extinction of threatened taxa, promote species conservation, and maintain and restore genetic diversity (CBD, 2022). However, it is important to consider that, even though we employed a forward-looking approach, our study did not incorporate biotic interactions, such as competition between rare specialists and generalists or invasive taxa. Therefore, further research and frequent monitoring of in situ and ex situ conservation practices in these areas are imperative to ensure the durability and effectiveness of the measures taken.

Given the high dispersion among the mapped persistent endemism hotspots, the design and establishment of a network of plant micro-reserves (PMRs) could be an effective complementary approach to preserve the Greek endemic flora. PMRs are small areas (<20 ha) dedicated to the in situ preservation of populations of rare, threatened, and endemic taxa (Laguna, 2001; Laguna et al., 2016; Médail et al., 2021). PMR networks have already been established in various Mediterranean countries, providing management experience and valuable outcomes (Eliades et al., 2021; Fos et al., 2017; Kadis et al., 2013; Laguna et al., 2016, 2018; Vladimirov, 2014). While our findings provide valuable information on potential general locations for micro-reserves, additional research is required to develop a detailed and efficient implementation approach (but see Kougioumoutzis et al., 2022b). The first PMR network on the Greek mainland was designed and established in Northern Peloponnese in 2023, including populations of six single-mountain rare endemic plants restricted to extremely small areas within the Chelmos-Vouraikos National Park and Mount Kyllini (Kougioumoutzis et al., 2021b; Kougioumoutzis et al., 2022b). This initiative, funded by the Natural Environment and Climate Change Agency, was developed following an assessment of extinction risk and potential climate and land-use change impacts. As part of this effort, pilot programs in Chelmos-Vouraikos National Park are monitoring population trends of some very rare Peloponnesian endemics. Although formal IUCN assessments are now openly available for all endemic and non-endemic plants occurring in Greece, they are largely based on IUCN Criterion B. Further steps should focus on expanding these assessments to identify additional target taxa and conducting a comprehensive evaluation of

suitable habitat characteristics, encompassing aspects such as plant population dynamics and community structure (Kougioumoutzis et al., 2022b). Moreover, quantifying the effects of in situ conservation actions (Cogoni et al., 2022; Grace et al., 2021a; Grace et al., 2021b) is fundamental for understanding their impact and for guiding the use of additional strategies, such as plant translocations, which are crucial tools for preventing plant extinctions and declines (Fenu et al., 2023). Additionally, it is urgent to conserve many threatened plant species of Peloponnese in ex situ collections, such as national botanical gardens and seed banks, to ensure their availability for recovery and restoration programs (CBD, 2010, 2022). Some of these species have already been included in the collections of the National Kapodistrian University of Athens (NKUA) Seed Bank as part of a research project (<https://www.kew.org/science/our-science/projects/flora-of-the-balkans>), marking a critical step, yet underscoring the importance of ongoing and expanded efforts to protect Greece's botanical diversity.

Projections indicate that by 2100, land-use conversions will affect between 13.9 % and 22.7 % of Peloponnese, largely owing to agricultural land abandonment and subsequent afforestation and encroachment in the region (Braz Pires et al., 2024). These changes present both challenges and opportunities for conservation, emphasizing the need for a multi-dimensional approach. Habitat restoration, in situ and ex situ translocation of endemics, and population reinforcement are key strategies to mitigate the impact of environmental change on biodiversity that should be further explored in this context (Serota, 2024; Singh, 2024). While expanding and redesigning the network of protected areas in Peloponnese is pivotal, as discussed earlier in this subsection, effective management, monitoring, and enforcement of regulations within these areas are necessary to ensure these conservation efforts are long-lasting. Yet, we must recognise that protected areas alone may not be able to accommodate all future shifts. Therefore, the land-use of surrounding areas should be reconsidered to promote nature-inclusive landscapes. Integrating these efforts with broader landscape-level conservation strategies will enhance the resilience and connectivity of habitats, which are fundamental for the survival of endemic flora. To further strengthen these initiatives, conservation planning should incorporate dynamic approaches that account for species range shifts as a response to various environmental stressors (Graham et al., 2019; Lai et al., 2022; Mittermeier et al., 2011; Nila et al., 2019; Ranius et al., 2023; Trew and Maclean, 2021). Such approaches, including the integration of dispersal corridors and predictive modelling of future species distributions (Alagador et al., 2016), could ensure that conservation areas remain flexible and resilient to ongoing environmental changes. These strategies should be further explored in future research to complement existing gap analyses and conservation frameworks.

5. Conclusions

Our study revealed that plant endemism hotspots in Peloponnese are projected to undergo significant spatial shifts and contractions over time, across a broad range of environmental scenarios, from the most sustainable to the most severe. Current conservation schemes appear insufficient to address the future challenges posed by climate and land-use change, and without timely adaptation, these shifts could lead to extensive biodiversity loss and jeopardize the resilience of endemic taxa. High levels of endemism are concentrated in the mountainous regions of Peloponnese, but despite their ecological value, our projections point to potential local extinctions, with taxa with small ranges and high evolutionary distinctiveness being particularly at risk. Furthermore, our analysis anticipates an overall decline in endemism and a marked reduction in the size of endemism hotspots.

We identified three levels of taxonomic and phylogenetic endemism hotspots projected to remain resilient under various scenarios of climate and land-use change. Our analysis revealed substantial gaps in the protection of these persistent endemism hotspots, with nearly 20 % to 46 % of these critical areas falling outside the Natura 2000 network of

terrestrial protected areas: a more serious concern than previously documented. Furthermore, <8 % of the unprotected hotspots are located within roadless areas, emphasizing their heightened vulnerability to human pressures. In addition to these persistent hotspots, our analysis identified a smaller proportion of new hotspots projected to emerge under future scenarios. Although their emergence is limited, these new hotspots may become crucial for future conservation efforts, particularly in light of the anticipated endemism decline.

Given that many of the identified conservation gaps are in close proximity to existing protected areas, expanding and partially re-designing these reserves to include persistent endemism hotspots is a critical first step. However, addressing these gaps effectively will require a multi-dimensional approach. This will involve a series of coordinated conservation efforts, including implementing nature-inclusive practices in surrounding landscapes, establishing plant micro-reserves, translocating endemics, and reinforcing populations. Ultimately, the preservation of the unique flora of the Peloponnese is not just a regional concern but a global responsibility, crucial for safeguarding Earth's diverse biological heritage. Our study serves as a case-study that highlights the importance of forward-looking, resilient conservation strategies, particularly in the Anthropocene where rapid environmental changes demand proactive and adaptive planning.

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CRedit authorship contribution statement

Mariana Braz Pires: Writing – original draft, Visualization, Software, Methodology, Formal analysis, Conceptualization. **Konstantinos Kougioumoutzis:** Writing – review & editing, Supervision, Software, Methodology, Conceptualization. **Sietze Norder:** Writing – review & editing, Supervision, Conceptualization. **Panayotis Dimopoulos:** Data curation. **Arne Strid:** Data curation. **Maria Panitsa:** Writing – review & editing, Supervision, Conceptualization.

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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.

Data availability

Data will be made available on request.

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