Received: 11 March 2024 | Accepted: 20 September 2024

DOI: 10.1002/inc3.75

RESEARCH ARTICLE

Forests and Mediterranean squamates: How does crown canopy impact species richness and phylogenetic diversity?

Daniel Escoriza[1] | **Félix Amat**[2]

[1]GRECO, University of Girona, Girona, Spain

[2]Àrea d'Herpetologia, BiBIO, Museu de Granollers – Ciències Naturals, Granollers, Spain

Correspondence
Daniel Escoriza, GRECO, University of Girona, Girona, Spain.
Email: drdanielescoriza@gmail.com

Editor-in-Chief: Binbin Li; **Handling Editor**: Akihiro Nakamura

Funding information
None

Abstract

Intense human disturbances, including changes in the balance between open and forested habitats, have impacted squamate reptile populations in the western Mediterranean. This region has experienced a notable increase in woodland cover, driven by the gradual abandonment of traditional agriculture, native forest regeneration and intensive reforestation. Microclimatic changes associated with dense canopies in native forests or tree plantations could affect squamate assemblages. In this study, we tested the hypothesis that squamates (amphisbaenians, lizards and snakes) would respond negatively to denser crown canopies and taller vegetation. Our study focused on the Iberian and Italian Peninsulas and included 56 squamate species. The analyses indicated that forests (>50% canopy cover) support a limited number of squamate species (24–26 species). The greatest species richness and phylogenetic diversity were found in low woodland formations (2–9.9 m stand height and 20–49% canopy cover) and areas with scattered trees and shrubs (5–19% canopy cover), supporting 40–46 species. To balance reforestation efforts with squamate conservation, areas with low diversity or lack of threatened species should be prioritised.

KEYWORDS

biodiversity, canopy, lizard, plantation, snake

Plain language summary

The western Mediterranean region, which includes the Iberian and Italian Peninsulas, boasts a rich fauna of squamates. However, over the centuries, these ecosystems have undergone dramatic alterations. In recent decades, the decline of traditional agriculture, combined with native forest regeneration and replanting, has led to a notable increase in woodland and forest cover. In this study, we evaluated whether this growing forest extension could negatively impact squamate species richness. Our findings showed a decrease in species richness and phylogenetic diversity in habitats with dense canopy cover (over 50%). The greatest richness of squamate species and phylogenetic diversity were found in habitats with less than 50% canopy cover and vegetation heights between 2 and 10 metres. These results suggest that intensive tree plantations could negatively impact local squamate diversity and even lead to the extinction of some species, mirroring a trend seen in other parts of the globe.

1 | INTRODUCTION

Mediterranean ecosystems harbour diverse herpetofauna, representing ecologically distinct communities with contrasting evolutionary histories that originate from various biogeographic regions (Salvador, 2014; Werner, 2016). Some species are microendemic and highly vulnerable to processes that rapidly alter habitat composition (Monasterio et al., 2010). These vulnerabilities, coupled with centuries of human-driven landscape change and harmful side effects, such as climate change and the increasing presence of alien species (Genovesi, 2005; Winter et al., 2016), make identifying the environmental factors that negatively impact reptile diversity in the Mediterranean region a priority (Cox et al., 2006).

Habitats in this region range in light availability from full sun on rocky outcrops with minimal obstruction to almost complete shade in mature forests (Gallaher et al., 2019). Squamates living at opposite ends of this light diffusion spectrum have developed distinct morphological and physiological characteristics. Species that occupy sparsely vegetated habitats face rapid overheating and increased detection, leading to adaptions for high-speed running and inconspicuous colouration (Chen et al., 2013; Kohlsdorf et al., 2001). In contrast, squamates in forest habitats demonstrate traits such as the ability to climb on vertical surfaces, viviparity and the capacity to function at lower body temperatures while remaining active (Higham et al., 2011; Lynch, 2009; Meek, 2005).

Many Mediterranean squamate species display broad habitat tolerance, using areas ranging from scattered shrubland to open forests, but are rarely found in habitats at either extreme (Castilla & Bauwens, 1992; Reading & Jofré, 2009; Salvador, 2014). This suggests that dense forests may not be optimal for many squamate species that thrive in Mediterranean temperate ecosystems, and where they do occur in these habitats, they are likely confined to open gaps or discontinuities (Delgado-García et al., 2007; Meek, 2014).

Forest cover in southern Europe has gradually expanded in recent decades due to the decline of traditional agriculture (Bracchetti et al., 2012; Mantero et al., 2020; Otero et al., 2015). Part of this land has been used for intensive tree plantation of fast-growing species such as *Eucalyptus* spp., *Pinus radiata*, *Platanus x hispanica*, and *Populus* spp. (981.406 ha in Spain, 2020; https://www.miteco.gob.es). Frequently, these reforestation efforts have not prioritised the preservation of local biodiversity or the protection of threatened species (Vadell et al., 2022). As a result, rapid reforestation poses a significant conservation concern for squamate diversity, potentially leading to population declines and even local extinctions, as seen in other parts of the world (Goodman, 2009; Kellermann et al., 2021).

In this study, we evaluated the hypothesis that densely canopied habitats with greater stand height (i.e., trunk height) are unfavourable for most Mediterranean reptiles. Lower light levels in such forests reduce the efficiency of basking behaviour required for thermoregulation (Suzaki et al., 2003). This hypothesis was tested in the order Squamata (amphisbaenians, lizards and snakes), a monophyletic clade that includes most of the reptile species present in southwestern Europe (Pyron et al., 2013).

Practitioner points

- Dense canopy cover reduces squamate species richness and phylogenetic diversity.
- Open habitats with 5–49% canopy cover support greater squamate species richness.
- Maintaining a balance between forests and open habitats significantly enhances squamate diversity.

2 | MATERIALS AND METHODS

2.1 | Study region

The study region spanned the Iberian Peninsula, southeastern France, the Italian Peninsula and Sicily (Figure 1). This part of Europe is notable for its high diversity of squamate species compared to other temperate regions of the Palearctic (Araújo et al., 2006). However, extensive human activity has substantially reshaped this landscape over time (Falcucci et al., 2007). The main land cover in this region is a heterogeneous mosaic composed of agricultural fields, urbanised areas and fragmented forests (Virgós et al., 2002).

Data collection was carried out each year from March to October between 2014 and 2023, aligning with the seasonal activity periods of the target species (Escoriza et al., 2021, 2023). Most species were encountered opportunistically during random surveys, with habitat selection determined by accessibility rather than a pre-defined sampling strategy. However, an exception was made for microendemic lizard species, which were specifically targeted within their known distribution ranges. Fieldwork teams, consisting of two to four surveyors, characterised 3 to 6 localities per day during 8-h sampling periods. Squamates were detected through visual transects carried out during daylight hours and by lifting large objects such as stones and logs (McDiarmid et al., 2012). In total, 960 sites were assessed across an elevation range of 1 to 2553 metres (Figure 1).

2.2 | Habitat-niche data

Squamate habitat preferences were evaluated by assessing two key variable sets: climate and terrain elevation (abiotic factors) and plant cover density (biotic factors) (Pike et al., 2011; Qian, 2010)

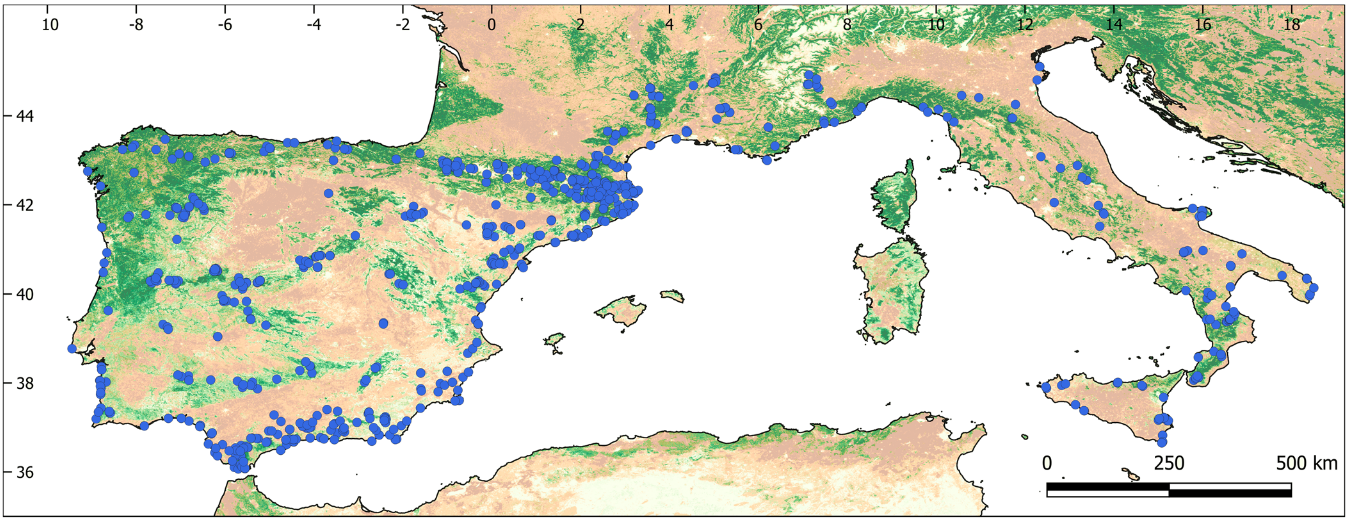

FIGURE 1 Map of the study region, where the proportion of forest area (in green) has been superimposed (based on Tuanmu & Jetz, 2014). The brown regions indicate open, steppe or cultivated, areas and the white ones, unproductive areas and cities. The blue circles show the sampling locations.

(Table 1). Elevation was recorded in situ using a global positioning system with an accuracy of ±15 m (Garmin Etrex 10; Garmin Ltd., Olathe, KS, USA). To quantify climate effects, we used two variables: mean annual temperature (in °C) and mean annual accumulated precipitation (mm per year^{-1}). These variables were obtained from the WorldClim 2 database at 30 arc-seconds resolution (Fick & Hijmans, 2017).

The relative abundance of key plant species (trees, shrubs and perennial herbaceous plants) formed the basis for habitat characterisation. Habitat composition was determined through three 30-m transect surveys. To account for habitat variability, the abundance of plant species was measured along transects with a fixed width of 1 m, sampling from the central point of occurrence in three directions (north, southeast and southwest) (Escoriza et al., 2018). Plant species (trees, shrubs and perennial grasses) were classified following Castroviejo (2014), Thorogood (2018) and Ticli (2018). These data were used to calculate various measures of plant community diversity, including species richness, stem abundance and diversity/evenness indices (Simpson, Shannon-Wiener and Chao1; Kindt & Coe, 2005). These indices were selected because plant diversity is expected to decline with increased human disturbance (Honnay et al., 1999; Kindt & Coe, 2005; Kolb & Diekmann, 2004). Diversity indices were calculated using the BiodiversityR package (Kindt & Coe, 2005) in the R statistical programming environment (version 4.3.2; https://www.r-project.org/).

We employed a randomised sampling approach to measure canopy cover at five points along transects using a spherical crown densitometer (Forestry Suppliers, Inc.). The average height of dominant vegetation (10 stems, randomly selected) was measured as an indicator of forest maturity, as mature forests are typically taller due to the linear relationship between tree age and growth (Molina-Valero et al., 2021). We classified habitats into six distinct groups based on vegetation height and crown canopy cover (Carnahan, 1990): forests (tree crowns covering more than 50% of the area), further divided into medium (mean stand height between 10 and 30 m) and low (mean stand height between 2 and 9.9 m); woodlands (tree crowns covering between 20 and 49% of the area), also divided into medium and low categories; other woody vegetation (open woodland and shrubland with tree crowns covering between 5 and 19% of the area); and non-woody vegetation (shrubland under 2 m tall and grasslands). These classifications encompass various Mediterranean habitat types, including natural and artificially established forests, wooded pastures and shrublands (such as Iberian dehesas, garrigue and other woody vegetation), as well as alpine meadows, steppes and cultivated lands (non-woody vegetation).

2.3 | Phylogenetic analysis

We explored the evolutionary relationships of the 56 squamate species recorded in this study using a Bayesian inference framework implemented in BEAST 2.6.7 (Bouckaert et al., 2014). Our data set comprised one nuclear and three mitochondrial genes, with a maximum sequence length of 2,586 nucleotides (Supporting Information file I). The data were divided into subsets, and the best-fitting model for each was identified using MEGA 11 (Tamura et al., 2021). The GTR model was applied to the ribosomal 12S and 16S genes and cytochrome b, while the T92 model was used for RAG1. A relaxed molecular clock model was implemented to account for variations in evolutionary rates and to estimate species divergence times, using seven calibration points. Three Markov Chain Monte Carlo (MCMC) simulations were run, each with 150×10^6 iterations. Convergence and effective sample size

TABLE 1 Environmental variables used in this study.

Class	Variable	Spatial resolution	units	Explanation
Climate	Average annual precipitation	1 km^2	mm y^{-1}	Available moisture
	Mean annual temperature	1 km^2	Celsius scale	Available energy
Topography	Elevation	5–10 m	m above sea level	Terrain elevation
Vegetation structure	Species richness	1 m	*N* species	Community diversity
	Vegetation abundance	1 m	*N* stems	Vegetation cover
	Simpson index	1 m	–	Species evenness
	Shannon-Wiener index	1 m	–	Species diversity
	Chao1 index	1 m	–	Species diversity

were monitored using TRACER 1.7.1. Samples were collected every 10,000 iterations, and the first 99% of each chain was discarded as burn-in. TreeAnotator 2.6.2 was used to generate the maximum credibility tree (MCT).

The MCT was used to calculate Faith's phylogenetic diversity (Faith, 1992). This index represents the combined branch length of the species in the phylogenetic tree, traversed by all lineages that compose a biotic assemblage (Faith, 1992). Higher values of this metric correlate positively with phylogenetic diversity (Faith et al., 2004). This index was calculated using the picante package (Kembel et al., 2010) in R.

2.4 | Data analysis

The outlying mean index (OMI) was used to investigate the niche occupancy of squamate species (Dolédec et al., 2000). OMI analyses species occurrence patterns to compute the average niche of each species and contrasts it with the average niche of the overall species assemblage (species marginality). This analysis provides measures of inertia (the variability in species occurrence that can be directly attributed to the environmental gradients used in the analysis), niche breadth (tolerance) and unexplained variability in species occurrence (residual tolerance) (Dolédec et al., 2000). OMI analysis offers the advantage of being robust against multicollinearity among response variables (Dolédec et al., 2000).

In this study, we used the within-outlying mean index (WitOMI), an extension of the OMI analysis, to assess the environmental responses of species grouped by their specific niches (Karasiewicz et al., 2017). WitOMI also tests for significant subniche differences compared to average habitats using permutation tests (Karasiewicz et al., 2017). The *p*-values obtained were adjusted for multiple comparisons using Holm's correction (Holm, 1979). These analyses were carried out using the R packages ade-4 (Dray & Dufour, 2007) and subniche (Karasiewicz et al., 2017).

3 | RESULTS

A total of 56 squamate species were recorded during sampling (2 species of amphisbaenians, 37 species of lizards and 17 species of snakes) (Figure 2 and Supporting Information file II). No forest-obligate species were identified, although one snake, *Zamenis longissimus*, was more commonly found in habitats with canopy density over 50% (present at more than 75% of sites). Two other species were predominantly found in habitats with over 20% canopy cover, also appearing at over 75% of sites: *Chamaeleo chamaeleon* (88%) and *Vipera aspis* (88%). Although most species did not show strong preferences for specific habitat types (Figure 3), some were predominantly associated with sparsely wooded environments featuring 5–19% canopy cover. This group mainly comprised cursorial (*Acanthodactylus erythrurus*, *Psammodromus edwarsianus*) and xeric specialists (*Timon nevadensis*) (see Figures 3 and 4).

The first two axes of the OMI explained 89.69% of the total inertia (Table 2). The first axis (inertia = 68.15%) separated the sites based on their abiotic conditions, following a gradient determined by opposing temperature and precipitation vectors (Figure 4). This axis differentiated Mediterranean thermophilic species from subalpine temperate species (Figure 4). The second axis (inertia = 21.54%) separated the sites based on plant community diversity, distinguishing squamate species that occupy habitats with dense and complex vegetative communities (e.g., native forests) from those that inhabit compositionally simpler habitats, such as steppes and subalpine meadows (Figure 4).

The WitOMI results indicated a reduction in niche sizes in habitats with denser canopies (Figure 5). Medium forest represented 30.25% of the total area, low forests 34.00%, medium woodland 44.81%, low woodland 68.83%, other woody vegetation 80.55%, and non-woody vegetation 83.14% (Figure 5). WitOMI analysis revealed significant differences between these forest categories in terms of habitat properties: forests

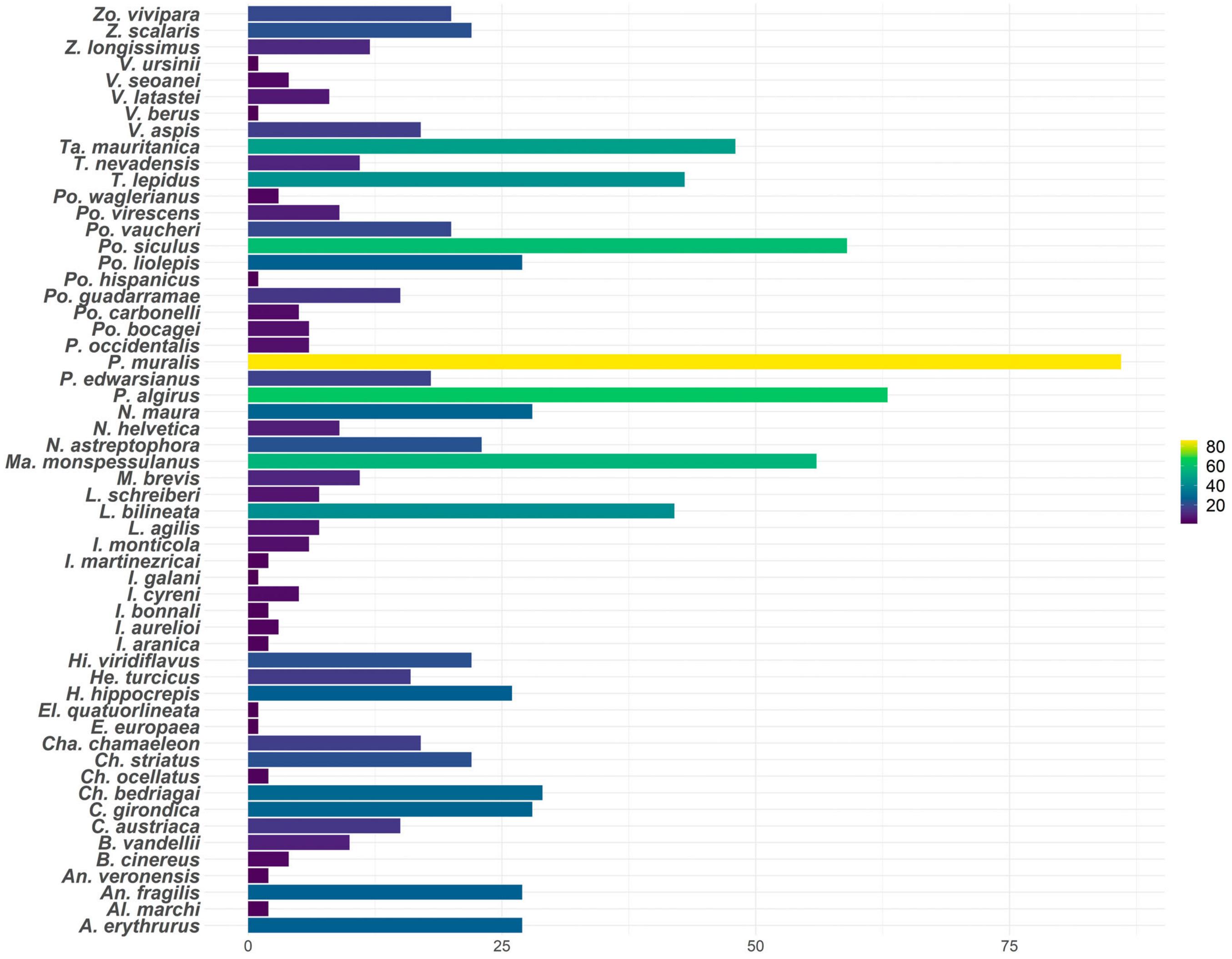

FIGURE 2 Species of squamates (amphisbaenians, lizards and snakes) included in the study. The bar plots represented the number of sites included per species.

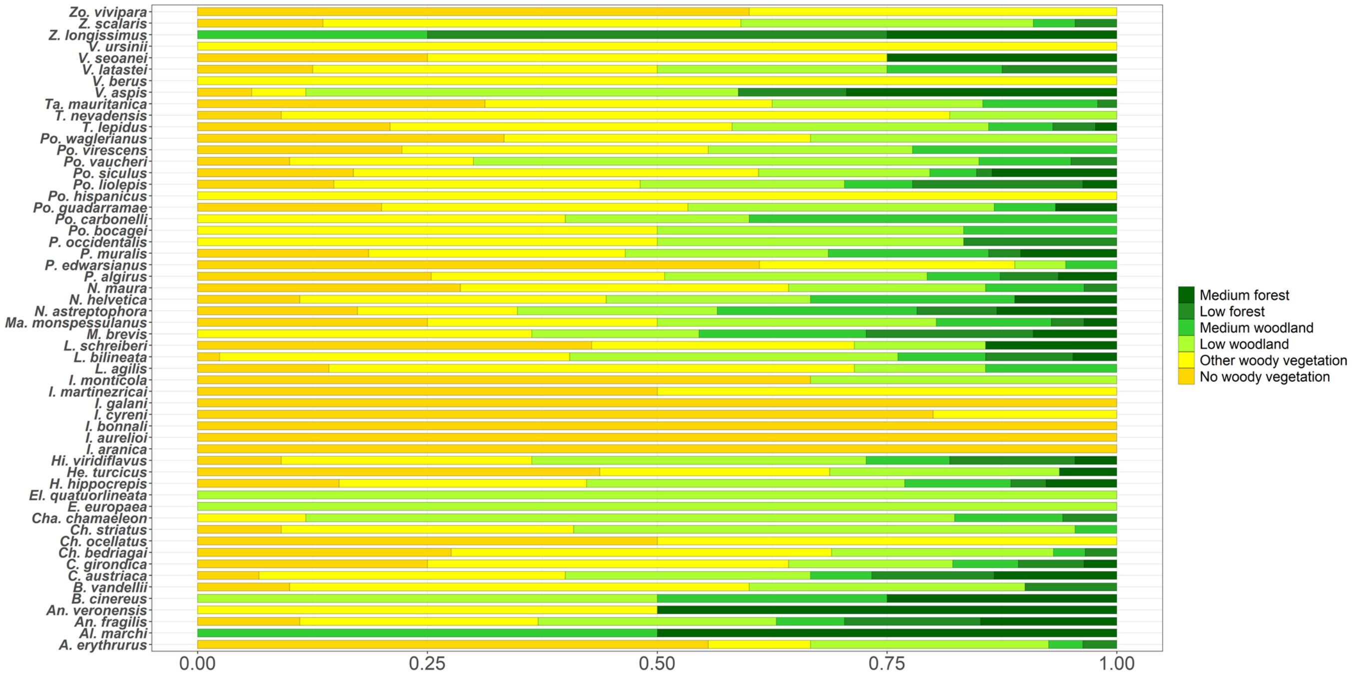

FIGURE 3 Habitat types: forest (>50% canopy cover), woodland (20–49% canopy cover) used by the 56 species of squamates found in this study. The other woody and non-woody vegetation categories include scattered tree habitats with <20% canopy cover.

and woodland supported richer plant communities than other woody or non-woody vegetation (Table 3).

The WitOMI results also showed that habitats with denser canopies support lower squamate species richness and lower phylogenetic diversity (Table 4). For example, medium forests included 24 species, whereas low woodland supported 40 species (Table 4). Furthermore, species occupying forests showed greater marginality (WitOMI = 80.6–85.3) and lower tolerance (6.9–7.4) compared to species occupying non-forest habitats (other woody/non-woody vegetation; WitOMI = 50.0–65.8; tolerance = 9.4–11.4) (Table 4). Residual tolerance was consistently low (7.8–38.6) (Table 4), indicating that predictor variables accounted for a substantial part of the environmental variance between species. The OMI parameters and their statistical significance for each vegetation category are provided in Supporting Information file III.

TABLE 2 Relative contribution of the environmental variables to the first two axes of the OMI analysis (component scores of the first axis, CSA1 and component scores of the second axis, CSA2).

Variable	CSA1	CSA2
Explained variance	68.145%	21.542%
Average annual precipitation	0.683	0.145
Mean annual temperature	–0.638	0.114
Terrain elevation	0.638	0.114
Species richness	–0.270	0.382
Vegetation abundance	–0.232	0.153
Simpson index	–0.249	0.227
Shannon-Wiener index	–0.280	0.312
Chao1 index	–0.203	0.348

4 | DISCUSSION

For thousands of years, human activities have shaped the ecosystems of the Mediterranean region. Traditional agriculture maintained a patchwork of habitats that supported highly diverse biotic communities (Baiamonte et al., 2015). However, industrialisation intensified forest exploitation, introduced nonnative tree species and homogenised open areas through urbanisation and intensive agriculture, leading to biodiversity loss (Brotons et al., 2018; Henle et al., 2008). Additionally, the disuse of open areas due to reduced grazing has allowed forests to reclaim land, negatively impacting species reliant on open habitats (Preiss et al., 1997; Stefanescu et al., 2011; Suárez-Seoane et al., 2002), potentially including reptiles. These trends highlight the long-term, complex effects of human activity on Mediterranean biodiversity.

In this study, we tested the hypothesis that squamate reptiles would show negative responses to denser crown canopies and greater vegetation stand height. Our results confirmed that canopy cover exerts a strong influence on squamate presence. We found that open woodland formations and open habitats with scattered trees (canopy cover between 5 and 49%) support higher species richness and phylogenetic diversity. These ecotones provide

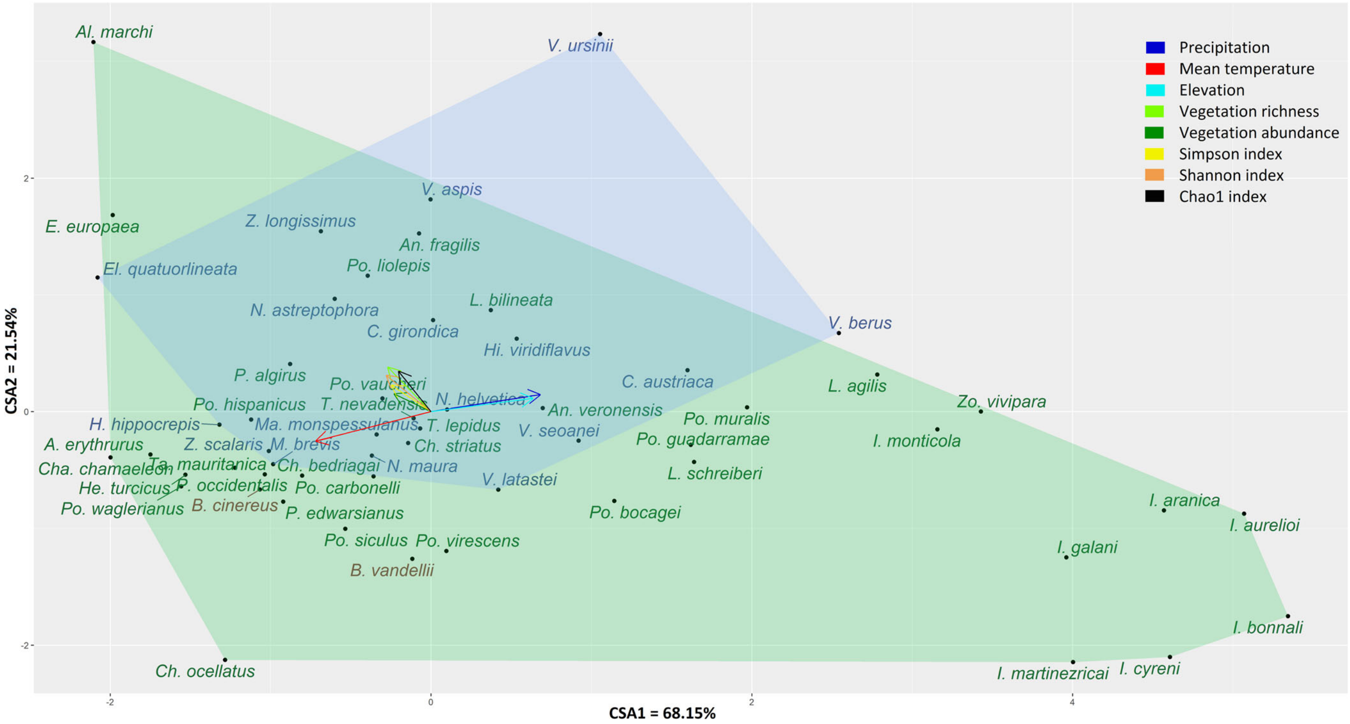

FIGURE 4 Plot showing the results of the OMI analysis, with the position of the species and the response variables represented as vectors. The origin (0,0) represented the average environmental conditions. Green: lizards; blue: snakes. CSA1, proportion of variance explained by the first component; CSA2, proportion of variance explained by the second component.

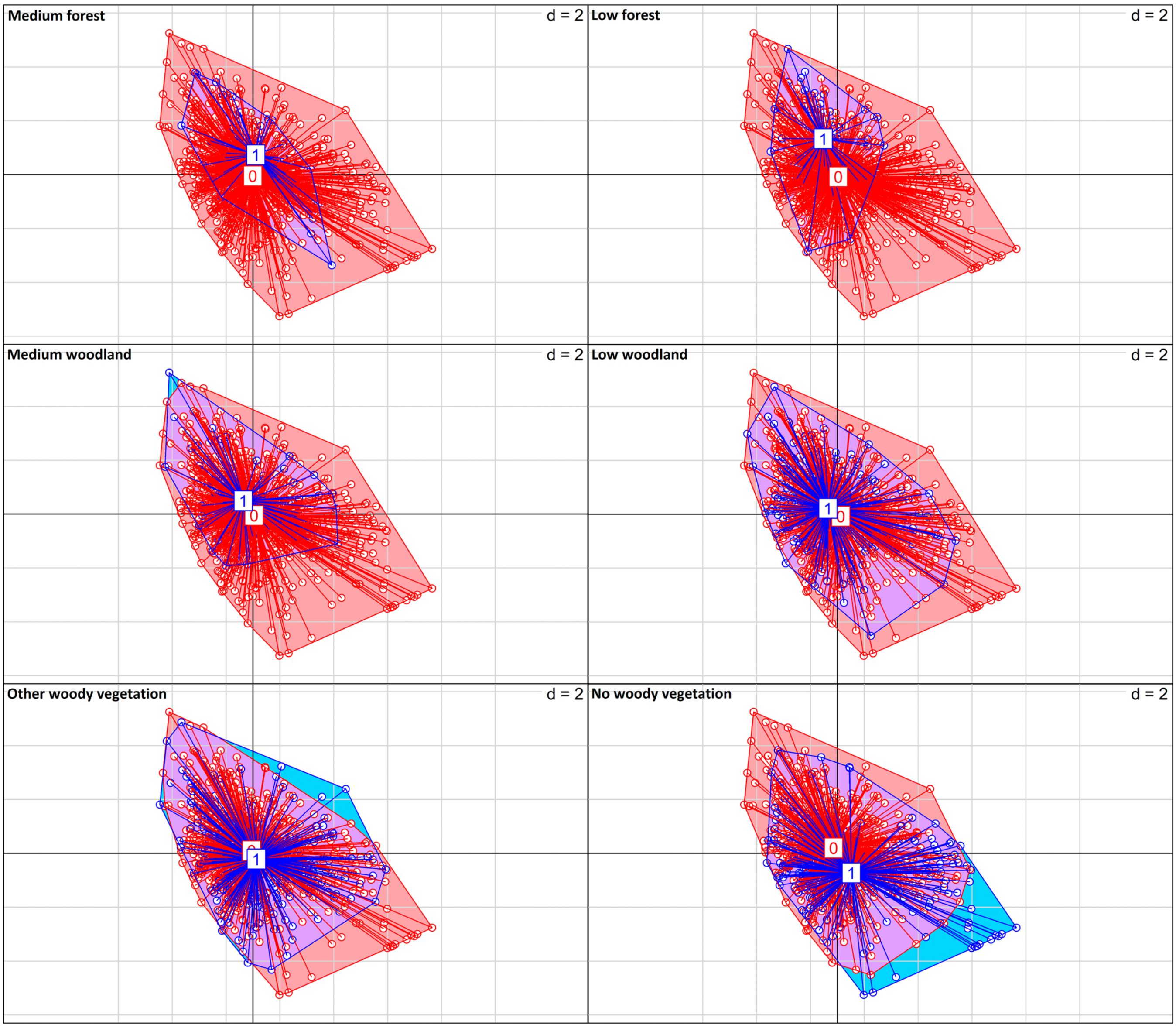

FIGURE 5 Plot showing the results of the WitOMI analysis, with the niche breadth of each habitat category (1, in blue) relative to that occupied by the other habitat categories (0, in red).

suitable environments for both generalists and specialists alike, as cursorial forms benefit from open patches, while mesic species find protection from temperature extremes within vegetation cover (Gregory & Tuttle, 2016; House & Spellerberg, 1983; Salvador, 2014). Furthermore, similar findings from transitional woodland in southern Greece (Ioannidis et al., 2008) suggest that these results may apply across the entire Mediterranean ecoregion.

We also observed that forest habitat quality measures (such as stand height, crown density and plant community diversity) are inversely related to squamate diversity. In contrast, other temperate faunal groups such as salamanders, bats, birds and insects often prefer mature primary forests, which support greater biodiversity and provide crucial habitats for rare species (Basile et al., 2021; Curtis & Taylor, 2004; Ford et al., 2002; Piksa et al., 2022; van Halder et al., 2015).

These findings align with the observation that forest canopy cover can have a significant negative impact on habitat quality for heliothermic reptiles (Thompson et al., 2018; Webb et al., 2005). Reduced sunlight exposure forces adults to exert more effort to regulate body temperature, increasing their exposure to predators and decreasing embryo survival rates (Downes, 2001; Schlaepfer, 2003). Climbing species, such as *Chamaeleo chamaeleon*, can thermoregulate by using the elevated and potentially sun-exposed branches of trees and shrubs (Hódar et al., 2000), while species with lower thermal requirements, like *Zamenis longissimus*, may have an advantage in shaded environments (Rugiero et al., 2002). However, a substantial number of Mediterranean squamates either avoid densely shaded habitats or use them by favouring discontinuities such as rock outcrops, paths or forest edges (Amo et al., 2007).

Human management of habitats can enhance squamate diversity, as demonstrated by traditional agro-pastoral oak woodland pastures, which

TABLE 3 Comparison of characteristics between groups of forest habitats, categorized by canopy cover and stand height, using WitOMI analysis. Only statistically significant variables are shown.

	N sites	Variables	Coefficient	*p*-value	Adjusted *p*-value
Medium forest	57	Precipitation	0.302	0.021	0.104
		Richness	0.362	0.005	**0.032**
		Simpson	0.319	0.014	0.084
		Shannon	0.433	0.001	**0.009**
		Chao1	0.263	0.040	0.160
Low forest	55	Richness	0.828	0.0001	**0.001**
		Simpson	0.548	0.0003	**0.002**
		Shannon	0.725	0.0001	**0.001**
		Chao1	0.725	0.0001	**0.001**
Medium woodland	89	Elevation	−0.218	0.032	0.149
		Richness	0.301	0.003	**0.020**
		Simpson	0.340	0.001	**0.007**
		Shannon	0.376	0.0001	**0.001**
		Chao1	0.218	0.029	0.149
Low woodland	254	Temperature	0.186	0.001	**0.003**
		Elevation	−0.166	0.002	**0.008**
		Richness	0.189	0.001	**0.003**
		Simpson	0.195	0.0004	**0.003**
		Shannon	0.235	0.0001	**0.001**
		Chao1	0.136	0.013	**0.038**
Other woody	297	Richness	−0.150	0.002	**0.016**
		Shannon	−0.134	0.005	**0.036**
		Chao1	−0.101	0.036	0.215
No woody	208	Temperature	−0.143	0.020	**0.049**
		Elevation	0.195	0.002	**0.005**
		Richness	−0.463	0.0001	**0.001**
		Simpson	−0.509	0.0001	**0.001**
		Shannon	−0.566	0.0001	**0.001**
		Chao1	−0.378	0.0001	**0.001**

Note: *p*-values were adjusted for multiple testing using Holm's correction. Statistically significant values are shown in bold.

TABLE 4 WitOMI analysis results, showing niche parameters (species mean + standard error).

	N species	Faith's index	WitOMI	Tolerance	Residual tolerance
Medium forest	24	1326.8	80.6 ± 5.2	7.4 ± 2.6	11.9 ± 3.3
Low forest	26	1628.2	85.3 ± 3.8	6.9 ± 2.6	7.8 ± 1.9
Medium woodland	33	1769.3	71.2 ± 5.5	6.4 ± 1.6	22.4 ± 4.3
Low woodland	40	2064.7	53.1 ± 5.0	12.9 ± 2.1	33.9 ± 3.7
Other woody vegetation	46	2113.7	50.0 ± 4.9	11.4 ± 1.8	38.6 ± 4.3
No woody vegetation	42	1910.9	65.8 ± 4.7	9.4 ± 1.9	24.9 ± 3.5

Note: *N* species is the number of squamate species that occur in each forest category. Faith's index represented the combined lengths of the species respective branches on the phylogenetic tree, traversed by all lineages within an assemblage. WitOMI assesses the distance between the preferred conditions of the species and the average available environment. Tolerance is the niche breadth. Residual tolerance is the percentage of unaccounted variability.

support more species than homogeneous native forests due to a dense understory of low shrubs (Martín and Lopez, 2002). Conversely, areas subjected to intensive agricultural practices and aggressive reforestation efforts show a marked decrease in reptile species, likely due to the combined effects of reduced availability of refuges and food resources, as well as the widespread use of toxic chemical agents (Kazes et al., 2020; Luiselli et al., 2018; Rugiero et al., 2021).

5 | CONCLUSIONS

In Europe, forests play a critical role in nature conservation by sequestering atmospheric carbon dioxide and supporting specialised biotic communities in mature forests (Nabuurs et al., 2015; Plath et al., 2024; Vergara-Tabares et al., 2018). However, maintaining a balance between forests and open natural habitats would significantly benefit biodiversity. Our results indicated that species richness peaks in open woody formations with crown canopy densities below 50%. These findings have important implications for the conservation of Mediterranean squamates. Intensive reforestation campaigns should be avoided in areas particularly rich in reptile species, such as nature reserves, Mediterranean coastal mountain ranges (Balletto et al., 2010; Lescure & de Massary, 2012) or areas with high conservation value for threatened species.

When considering strategic reforestation programmes that address soil conservation and long-term timber use within a sustainable framework, trees should be spaced appropriately to allow sunlight to filter through to the ground, or plantations should be intersected with wide gaps (Bragg et al., 2005). A promising approach could involve novel, landscape-scale reforestation strategies that integrate both woodland and open habitats (Douglas et al., 2020).

AUTHOR CONTRIBUTIONS

Daniel Escoriza: Conceptualization; formal analysis; investigation; resources; supervision; writing the original draft. **Félix Amat**: investigation; writing the original draft.

ACKNOWLEDGMENTS

We acknowledge the support provided during the fieldwork by Guillem Pascual, Laia Mestre, Jihene Benhassine, and Roberto López. Authorizations for fieldwork were provided by the Departament de Medi Ambient (ref. SF/574).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available within the article or its supplementary materials.

ORCID

Daniel Escoriza http://orcid.org/0000-0002-6853-0134

REFERENCES

Amo, L., López, P. & Martín, J. (2007) Natural oak forest vs. ancient pine plantations: lizard microhabitat use may explain the effects of ancient reforestations on distribution and conservation of Iberian lizards. *Biodiversity and Conservation*, 16, 3409–3422.

Araújo, M.B., Thuiller, W. & Pearson, R.G. (2006) Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography*, 33, 1712–1728.

Baiamonte, G., Domina, G., Raimondo, F.M. & Bazan, G. (2015) Agricultural landscapes and biodiversity conservation: a case study in Sicily (Italy). *Biodiversity and Conservation*, 24, 3201–3216.

Balletto, E., Bonelli, S., Borghesio, L., Casale, A., Brandmayr, P. & Vigna Taglianti, A. (2010) Hotspots of biodiversity and conservation priorities: a methodological approach. *Italian Journal of Zoology*, 77, 2–13.

Basile, M., Storch, I. & Mikusiński, G. (2021) Abundance, species richness and diversity of forest bird assemblages–the relative importance of habitat structures and landscape context. *Ecological Indicators*, 133, 108402.

Bouckaert, R., Heled, J., Kühnert, D., Vaughan, T., Wu, C.H., Xie, D. et al. (2014) BEAST 2: a software platform for Bayesian evolutionary analysis. *PLoS Computational Biology*, 10, e1003537.

Bracchetti, L., Carotenuto, L. & Catorci, A. (2012) Land-cover changes in a remote area of central Apennines (Italy) and management directions. *Landscape and Urban Planning*, 104, 157–170.

Bragg, J.G., Taylor, J.E. & Fox, B.J. (2005) Distributions of lizard species across edges delimiting open-forest and sand-mined areas. *Austral Ecology*, 30, 188–200.

Brotons, L., Herrando, S., Sirami, C., Kati, V. & Díaz, M. (2018) Mediterranean forest bird communities and the role of landscape heterogeneity in space and time. *Ecology and Conservation for Birds*, 9, 318–349.

Carnahan, J.A. (1990) *Atlas of Australian resources, vegetation*. Canberra: Australian Government Publishing Service.

Castilla, A.M. & Bauwens, D. (1992) Habitat selection by the lizard *Lacerta lepida* in a Mediterranean oak forest. *Herpetological Journal*, 2, 27–30.

Castroviejo, S. (2014) *Flora Ibérica: Plantas vasculares de la Península Ibérica, e Islas Baleares*. Madrid: Real Jardín Botánico-CSIC.

Chen, I.P., Symonds, M.R.E., Melville, J. & Stuart-Fox, D. (2013) Factors shaping the evolution of colour patterns in Australian agamid lizards (Agamidae): a comparative study: evolution of colour patterns. *Biological Journal of the Linnean Society*, 109, 101–112.

Cox, N., Chanson, J. & Stuart, S. (2006) *The status and distribution of reptiles and amphibians of the Mediterranean Basin*. Gland: IUCN.

Curtis, J.M.R. & Taylor, E.B. (2004) The genetic structure of coastal giant salamanders (*Dicamptodon tenebrosus*) in a managed forest. *Biological Conservation*, 115, 45–54.

Delgado-García, J.D., Arévalo, J.R. & Fernández-Palacios, J.M. (2007) Road edge effect on the abundance of the lizard *Gallotia galloti* (Sauria: Lacertidae) in two Canary Islands forests. *Biodiversity and Conservation*, 16, 2949–2963.

Dolédec, S., Chessel, D. & Gimaret-Carpentier, C. (2000) Niche separation in community analysis: a new method. *Ecology*, 81, 2914–2927.

Douglas, D.J.T., Groom, J.D. & Scridel, D. (2020) Benefits and costs of native reforestation for breeding songbirds in temperate uplands. *Biological Conservation*, 244, 108483.

Downes, S. (2001) Trading heat and food for safety: costs of predator avoidance in a lizard. *Ecology*, 82, 2870–2881.

Dray, S. & Dufour, A.B. (2007) The ade4 package: implementing the duality diagram for ecologists. *Journal of Statistical Software*, 22, 1–20.

Escoriza, D., Pascual, G. & Mestre, L. (2021) Climate and habitat niche diversification in a southwest European squamate assemblage. *Evolutionary Ecology*, 35, 761–777.

Escoriza, D., Pascual, G. & Mestre, L. (2023) Habitat turnover in Iberian and Italian lizards: is it climatically, spatially, or phylogenetically determined? *Ecosphere*, 14, e4718.

Escoriza, D., Pascual, G. & Sánchez-Vialas, A. (2018) Habitat use in south-west European skinks (genus *Chalcides*). *PeerJ*, 6, e4274.

Faith, D.P. (1992) Conservation evaluation and phylogenetic diversity. *Biological Conservation*, 61, 1–10.

Faith, D.P., Reid, C.A.M. & Hunter, J. (2004) Integrating phylogenetic diversity, complementarity, and endemism for conservation assessment. *Conservation Biology*, 18, 255–261.

Falcucci, A., Maiorano, L. & Boitani, L. (2007) Changes in land-use/land-cover patterns in Italy and their implications for biodiversity conservation. *Landscape Ecology*, 22, 617–631.

Fick, S.E. & Hijmans, R.J. (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37, 4302–4315.

Ford, W.M., Chapman, B.R., Menzel, M.A. & Odom, R.H. (2002) Stand age and habitat influences on salamanders in Appalachian cove hardwood forests. *Forest Ecology and Management*, 155, 131–141.

Gallaher, T.J., Adams, D.C., Attigala, L., Burke, S.V., Craine, J.M., Duvall, M.R. et al. (2019) Leaf shape and size track habitat transitions across forest–grassland boundaries in the grass family (Poaceae). *Evolution*, 73, 927–946.

Genovesi, P. (2005) Eradications of invasive alien species in Europe: a review. *Biological Invasions*, 7, 127–133.

Goodman, B.A. (2009) Nowhere to run: the role of habitat openness and refuge use in defining patterns of morphological and performance evolution in tropical lizards. *Journal of Evolutionary Biology*, 22, 1535–1544.

Gregory, P.T. & Tuttle, K.N. (2016) Effects of body size and reproductive state on cover use of five species of temperate-zone natricine snakes. *Herpetologica*, 72, 64–72.

van Halder, I., Barnagaud, J.Y., Jactel, H. & Barbaro, L. (2015) Woodland habitat quality prevails over fragmentation for shaping butterfly diversity in deciduous forest remnants. *Forest Ecology and Management*, 357, 171–180.

Henle, K., Alard, D., Clitherow, J., Cobb, P., Firbank, L., Kull, T. et al. (2008) Identifying and managing the conflicts between agriculture and biodiversity conservation in Europe—a review. *Agriculture, Ecosystems & Environment*, 124, 60–71.

Higham, T.E., Korchari, P. & McBrayer, L.D. (2011) How to climb a tree: lizards accelerate faster, but pause more, when escaping on vertical surfaces. *Biological Journal of the Linnean Society*, 102, 83–90.

Hódar, J.A., Pleguezuelos, J.M. & Poveda, J.C. (2000) Habitat selection of the common chameleon (*Chamaeleo chamaeleon*) (L.) in an area under development in Southern Spain: implications for conservation. *Biological Conservation*, 94, 63–68.

Holm, S. (1979) A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, 6, 65–70.

Honnay, O., Endels, P., Vereecken, H. & Hermy, M. (1999) The role of patch area and habitat diversity in explaining native plant species richness in disturbed suburban forest patches in Northern Belgium. *Diversity and Distributions*, 5, 129–141.

House, S.M. & Spellerberg, I.F. (1983) Ecology and conservation of the sand lizard (*Lacerta agilis* L.) habitat in Southern England. *The Journal of Applied Ecology*, 20, 417–437.

Ioannidis, Y., Chiras, G. & Kardakari, N. (2008) Comparison of reptile communities in three types of thermophilous Mediterranean forest in Southern Greece. *Journal of Natural History*, 42, 421–433.

Karasiewicz, S., Dolédec, S. & Lefebvre, S. (2017) Within outlying mean indexes: refining the OMI analysis for the realized niche decomposition. *PeerJ*, 5, e3364.

Kazes, K., Rotem, G. & Ziv, Y. (2020) Effects of vineyards and olive plantations on reptiles in a Mediterranean agroecosystem. *Herpetologica*, 76, 414–422.

Kellermann, A.G., Scalon-Luchese, M., Vieira, R.C., Brack, I.V. & Verrastro, L. (2021) Local extinction of *Tropidurus catalanensis* caused by plantation forestry in the pampas of Brazil. *Herpetological Conservation and Biology*, 16, 295–302.

Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D. et al. (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26, 1463–1464.

Kindt, R. & Coe, R. (2005) *Tree diversity analysis: a manual and software for common statistical methods for ecological and biodiversity studies*. Nairobi: World Agroforestry Centre (ICRAF).

Kohlsdorf, T., Garland Jr., T. & Navas, C.A. (2001) Limb and tail lengths in relation to substrate usage in *Tropidurus* lizards. *Journal of Morphology*, 248, 151–164.

Kolb, A. & Diekmann, M. (2004) Effects of environment, habitat configuration and forest continuity on the distribution of forest plant species. *Journal of Vegetation Science*, 15, 199–208.

Lescure, J. & de Massary, J.C. (2012) *Atlas des Amphibiens et Reptiles de France*. Mèze: Biotope Éditions.

Luiselli, L., Vignoli, L., Rugiero, L. & Meek, R. (2018) Declining occupancy rates in the hibernacula of aspic vipers (*Vipera aspis*) in Italy and France; evidence for climatic effects? *Herpetological Journal*, 28, 137–142.

Lynch, V.J. (2009) Live-birth in vipers (Viperidae) is a key innovation and adaptation to global cooling during the cenozoic. *Evolution*, 63, 2457–2465.

Mantero, G., Morresi, D., Marzano, R., Motta, R., Mladenoff, D.J. & Garbarino, M. (2020) The influence of land abandonment on forest disturbance regimes: a global review. *Landscape Ecology*, 35, 2723–2744.

Martín, J. & Lopez, P. (2002) The effect of Mediterranean dehesa management on lizard distribution and conservation. *Biological Conservation*, 108, 213–219.

McDiarmid, R.W., Foster, M.S., Guyer, C., Chernoff, N. & Gibbons, J.W. (2012) *Reptile biodiversity: standard methods for inventory and monitoring*. Oakland: University of California Press.

Meek, R. (2005) Null models and the thermal biology of the anguid lizard *Anguis fragilis*; evidence for thermoregulation? *Amphibia-Reptilia*, 26, 445–450.

Meek, R. (2014) Temporal distributions, habitat associations and behaviour of the green lizard (*Lacerta bilineata*) and wall lizard (*Podarcis muralis*) on roads in a fragmented landscape in Western France. *Acta Herpetologica*, 9, 179–186.

Molina-Valero, J.A., Camarero, J.J., Álvarez-González, J.G., Cerioni, M., Hevia, A. Sánchez-Salguero, R. et al. (2021) Mature forests hold maximum live biomass stocks. *Forest Ecology and Management*, 480, 118635.

Monasterio, C., Salvador, A. & Díaz, J.A. (2010) Altitude and rock cover explain the distribution and abundance of a Mediterranean alpine lizard. *Journal of Herpetology*, 44, 158–163.

Nabuurs, G.-J., Delacote, P., Ellison, D., Hanewinkel, M., Lindner, M., Nesbit, M. et al. (2015) *A new role for forests and the forest sector in the EU post-2020 climate targets, From Science to Policy No 2*. Joensuu: European Forest Institute.

Otero, I., Marull, J., Tello, E., Diana, G.L., Pons, M. Coll, F. et al. (2015) Land abandonment, landscape, and biodiversity: questioning the restorative character of the forest transition in the Mediterranean. *Ecology and Society*, 20, art7.

Pike, D.A., Webb, J.K. & Shine, R. (2011) Removing forest canopy cover restores a reptile assemblage. *Ecological Applications*, 21, 274–280.

Piksa, K., Brzuskowski, T. & Zwijacz-Kozica, T. (2022) Distribution, dominance structure, species richness, and diversity of bats in disturbed and undisturbed temperate mountain forests. *Forests*, 13, 56.

Plath, E., Trauth, C., Gerhards, J., Griebel, L. & Fischer, K. (2024) Dieback of managed spruce stands in Western Germany promotes beetle diversity. *Journal of Forestry Research*, 35, 48.

Preiss, E., Martin, J.L. & Debussche, M. (1997) Rural depopulation and recent landscape changes in a Mediterranean region:

consequences to the breeding avifauna. *Landscape Ecology*, 12, 51–61.

Pyron, R., Burbrink, F.T. & Wiens, J.J. (2013) A phylogeny and revised classification of squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology*, 13, 93.

Qian, H. (2010) Environment–richness relationships for mammals, birds, reptiles, and amphibians at global and regional scales. *Ecological Research*, 25, 629–637.

Reading, C. & Jofré, G. (2009) Habitat selection and range size of grass snakes *Natrix natrix* in an agricultural landscape in Southern England. *Amphibia-Reptilia*, 30, 379–388.

Rugiero, L., Capizzi, D. & Luiselli, L. (2002) Interactions between sympatric snakes, *Coluber viridiflavus* and *Elaphe longissima*: are there significant inter-annual differences in coexistence patterns? *Ecologia Mediterranea*, 28, 75–91.

Rugiero, L., Capula, M., Di Vittorio, M., Dendi, D., Meek, R. & Luiselli, L. (2021) Ontogenetic habitat use and density of the Green lizard (*Lacerta bilineata*) in contrasted landscapes in France and Italy. *Conservation*, 1, 1–16.

Salvador, A. (2014) *Fauna Ibérica, Reptiles: 2ª edición*. Madrid: Museo Nacional de Ciencias Naturales-CSIC.

Schlaepfer, M.A. (2003) Successful lizard eggs in a human-disturbed habitat. *Oecologia*, 137, 304–311.

Stefanescu, C., Torre, I., Jubany, J. & Páramo, F. (2011) Recent trends in butterfly populations from north-east Spain and Andorra in the light of habitat and climate change. *Journal of Insect Conservation*, 15, 83–93.

Suárez-Seoane, S., Osborne, P.E. & Baudry, J. (2002) Responses of birds of different biogeographic origins and habitat requirements to agricultural land abandonment in Northern Spain. *Biological Conservation*, 105, 333–344.

Suzaki, T., Kume, A. & Ino, Y. (2003) Evaluation of direct and diffuse radiation densities under forest canopies and validation of the light diffusion effect. *Journal of Forest Research*, 8, 283–290.

Tamura, K., Stecher, G. & Kumar, S. (2021) MEGA11: molecular evolutionary genetics analysis version 11. *Molecular Biology and Evolution*, 38, 3022–3027.

Thompson, M.E., Halstead, B.J. & Donnelly, M.A. (2018) Thermal quality influences habitat use of two anole species. *Journal of Thermal Biology*, 75, 54–61.

Thorogood, C. (2018) *Guide des fleurs sauvages de Méditerranée occidentale*. Paris: Delachaux et Niestlé.

Ticli, B. (2018) *Alberi d'Italia e d'Europa*. Firenze: Giunti.

Tuanmu, M.N. & Jetz, W. (2014) A global 1-km consensus land-cover product for biodiversity and ecosystem modelling. *Global Ecology and Biogeography*, 23, 1031–1045.

Vadell, E., Pemán, J., Verkerk, P.J., Erdozain, M. & De-Miguel, S. (2022) Forest management practices in Spain: understanding past trends to better face future challenges. *Forest Ecology and Management*, 524, 120526.

Vergara-Tabares, D.L., Lammertink, M., Verga, E.G., Schaaf, A.A. & Nori, J. (2018) Gone with the forest: assessing global woodpecker conservation from land use patterns. *Diversity and Distributions*, 24, 640–651.

Virgós, E., Tellería, J.L. & Santos, T. (2002) A comparison on the response to forest fragmentation by medium-sized iberian carnivores in central Spain. *Biodiversity & Conservation*, 11, 1063–1079.

Webb, J.K., Shine, R. & Pringle, R.M. (2005) Canopy removal restores habitat quality for an endangered snake in a fire suppressed landscape. *Copeia*, 2005, 894–900.

Werner, Y.I. (2016) *Reptile Life in the Land of Israel*. Frankfurt am Main: Chimaira.

Winter, M., Fiedler, W., Hochachka, W.M., Koehncke, A., Meiri, S. & De la Riva, I. (2016) Patterns and biases in climate change research on amphibians and reptiles: a systematic review. *Royal Society Open Science*, 3, 160158.

SUPPORTING INFORMATION

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

How to cite this article: Escoriza, D. & Amat, F. (2024) Forests and Mediterranean squamates: how does crown canopy impact species richness and phylogenetic diversity? *Integrative Conservation*, 3, 342–352. https://doi.org/10.1002/inc3.75