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Jean-yves Barnagaud, Philippe Geniez, Marc Cheylan, Pierre-André Crochet. Climate overrides the effects of land use on the functional composition and diversity of Mediterranean reptile assemblages. *Diversity and Distributions*, 2021, 27 (1), pp.50-64. 10.1111/ddi.13176 . hal-03098720

HAL Id: hal-03098720

<https://hal.science/hal-03098720>

Submitted on 5 Jan 2021

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Climate overrides the effects of land use on the functional composition and diversity of Mediterranean reptile assemblages

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Editor: José Brito

Abstract

Aim: To test the hypothesis that spatial variations in climate and land use explain the distribution and diversity of reptiles' ecological traits in a biodiversity hotspot of the Mediterranean basin.

Location: French Mediterranean region.

Taxon: Reptiles (25 species).

Methods: We defined 288 species assemblages from 27,858 opportunistic occurrence records within 10 × 10 km square grid cells. Using a RLQ analysis, we investigated the distribution of nine ecological traits describing reptiles' reproductive, dietary and behavioural strategies along environmental gradients formed by 10 climatic, topographic and land-use descriptors. After homogenizing survey effort through rarefaction, we used generalized additive models to assess variations in species richness and several measures of functional diversity and composition along these gradients.

Results: Although ecological traits were not structured by environmental gradients at a species level, species richness and all measures of functional diversity varied nonlinearly with climate, elevation and secondarily land use. Species richness and body size peaked at intermediate altitudes, indicating a climatic transition zone between Mediterranean and medio-European herpetofaunas. Conversely, functional diversity increased from Mediterranean plains, dominated by urbanization and agriculture, to higher elevations. These changes were associated with shifts towards less productive, more diurnal and more forest-related species.

Main conclusions: Species-scale patterns are insufficient to assess regional variations in ecological traits in space. Our results support the hypothesis that climatic limitations in species' distributions, rather than environmental filtering, explain the taxonomic and ecological diversity of reptiles at a regional scale. Although secondary to climate, land abandonment has a strong structuring effect which may contribute to homogenize the composition of reptile assemblages.

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KEYWORDS

community assembly, functional diversity, land use, Mediterranean basin, opportunistic data, regional scale, reptiles, RLQ analysis

1 | INTRODUCTION

Understanding how niches and traits affect species coexistence has remained one of the most central and debated issues since the advent of community ecology (Diamond, 1975; Garnier et al., 2016; McGill et al., 2006). The composition of species assemblages stems from a complex interaction among regional processes which ultimately result in the local overlap of multiple species' distributions (Ricklefs, 2004, 2008). The multiplicity of scales involved renders the identification of these assembly processes difficult in non-controlled ecosystems, but some general patterns tend to emerge. In particular, the idea that ecological traits provide a more meaningful interpretation of composition and diversity patterns than species richness alone has emerged with the long-lasting debate on how niche differences structure species assemblages (Diamond, 1975; Keddy, 1992; Münkemüller et al., 2020; Ricklefs, 2008).

Ecological traits can be broadly defined as any qualitative or quantitative characteristics that describes a species' relationship with its abiotic and biotic environment, encompassing functional traits (*sensu* Violle et al., 2007) and traits that have no direct relationship with fitness or performance but may impact the way individuals respond to environmental variation (such as habitat or climatic preference). Trait-based approaches solve two central bottlenecks of the study of biodiversity: first, they reconcile species-focused macroevolutionary approaches with spatial patterns of species assemblages and diversity gradients (Barnagaud et al., 2014; Lavorel & Garnier, 2002; Pigot et al., 2020); second, they allow making hypotheses on processes organizing species assemblages over spatial and temporal scales too large for standardized studies or experimentation (Schmeller et al., 2009). Ecological traits can thus be viewed as proxies of the major dimensions of the realized niche (Díaz et al., 2016; Pianka et al., 2017; Westoby et al., 2002) and as such are a suitable tool to investigate the role of environmental variation in explaining spatial gradients in species diversity and composition.

Species assemblages are largely shaped by biogeographical history and niche-related processes operating over regional extents (Caley & Schluter, 1997; Cornell & Lawton, 1992; Ricklefs, 2004). Their role may be concealed by fine-grained environmental heterogeneity, biotic interactions and population stochasticity at local scales (Huston, 1999): regional-level studies are therefore necessary to reveal the consequences of species' responses to large-scale human-induced environmental changes such as land use (Bennett et al., 2004; Socolar et al., 2016). In turn, these assessments are necessary to evaluate the consistency of threats to biodiversity and assist conservation planning (Beaudry et al., 2011; Socolar et al., 2016). It is now well established that human imprint limits taxonomic and functional diversity from local to macroecological scales even though climatic, topographic and historical constraints remain

key determinants of the species and trait composition of regional assemblages (Barnagaud et al., 2017; Ellis, 2015; Šizling et al., 2016). The pervasiveness of this pattern is, however, little investigated for rare or lowly detectable taxa, in spite of their sensitivity to climate change and artificialization (Hortal et al., 2015; McGill et al., 2015).

Reptiles' species distributions are relatively well delineated in the best surveyed regions, such as Western Europe (Mullin & Seigel, 2009; Sillero et al., 2014). However, beyond a long-identified role of climate, energy, elevation and biogeographic transitions (Busack & Jaksic, 1982; Guisan & Hofer, 2003; Rodríguez et al., 2005), they range among the least known vertebrates with respect to assemblage composition and diversity. In particular, the impacts of anthropogenic land use on the diversity of reptile assemblages remain rarely investigated even at local scales, although species-level studies reveal the counter effects of increasing pressure on habitats resulting from agriculture and urbanization and of post-agricultural land abandonment (Aurari & de Lucio, 2001; De Solan et al., 2019; Ribeiro et al., 2009; Todd et al., 2017). Low dispersal, high ecological specialization and top trophic position are often mentioned to explain reptiles' vulnerability to global changes in general and to these habitat disturbance in particular (Böhm et al., 2013; Fitzgerald et al., 2013; but see Doherty et al., 2020). These species-level patterns of response do not seem, however, to be systematically related to ecological traits, suggesting complex underlying processes which do not necessarily involve environmental filtering (De Solan et al., 2019; Todd et al., 2017). Alternatively, antagonistic responses of reptile species with differing niches may blur trait signals that could still emerge at the scale of species assemblages. This hypothesis can be tested by a two-scale analysis involving species-level trait-environment associations and variations of functional diversity indices and community-level averaged traits along environmental gradients.

The overall rarity and low detectability of many reptile species necessitate unreasonable efforts to achieve an exhaustive sampling of assemblages even at very local scales, which could explain the paucity of studies on their diversity, especially at regional scales. The most realistic way to compensate the practical intractability of standardized designs to survey rare organisms, such as reptile assemblages, remains to rely on volunteer-based databases, which offer a sampling of species occurrence over unequalled spatial coverage and at limited cost (Dickinson et al., 2012; Griffiths et al., 2015). These opportunistic records have already been used convincingly to investigate the imprints of land-use gradients and ecological traits on the distributions of reptiles (De Solan et al., 2019; Todd et al., 2016, 2017) and other vertebrate taxa (Callaghan & Gawlik, 2015; Van Strien et al., 2013). However, due to the lack of standardization, opportunistic data from volunteers suffer from well-identified limitations, in particular heterogeneous reliability, unequal sampling effort

and lack of absence data (Burgess et al., 2017; Geldmann et al., 2016; Isaac et al., 2014; Luck et al., 2004). Part of these limitations can be solved through adequate quantification of survey effort, suitable metadata and expert validation (Isaac et al., 2014; Schmeller et al., 2009; Theobald et al., 2015; Tiago, Ceia-Hasse, et al., 2017; Tiago, Pereira et al., 2017), but these obstacles have impaired advances in the description and understanding of regional patterns of reptile diversity and their relation to environmental features.

In the present study, we tested the hypothesis that land-use and climatic gradients structure the taxonomic and functional diversity of reptile assemblages over regional extents. We focused on the reptile assemblage in and around Mediterranean France, a region characterized by a complex topography which triggers strong gradients in climate and human land use, and by the legacies of past glacial refugia and barriers to dispersal. As for other taxonomic groups, reptile diversity in this region is particularly high due to the transition between typical Mediterranean groups and species of continental-oceanic climates, which exhibit radically different ecologies and biogeographic histories (Geniez & Cheylan, 2012). By concentrating on this area, we thus maximized the range of variation in both environmental features and reptile species assemblage composition that can be found in south-western Europe. We first investigated the influence of environmental gradients on the distribution of species and traits. Following De Solan et al. (2019), we predicted that species, but not ecological traits, would be directionally structured along the dominant climatic and land-use gradients that run across the region, as a consequence of the replacement of Mediterranean species by their continental counterparts. Second, we tested whether these species-level patterns translate into patterns of species and functional diversity, expecting a decrease in species richness from Mediterranean plains towards higher latitudes and elevations accompanied by a decline in functional richness (FRic), but not necessarily in functional dispersion (FDis) and evenness.

2 | METHODS

2.1 | Study area

Our study area encompassed a region of the western French Mediterranean area bounded by three major physical and biogeographic boundaries, the Rhône valley to the east, the Pyrenean chain to the south-west and a range of low-altitude mountains to the north (Figure S1.1 in Appendix S1). The region is structured by an elevation gradient ranging from the sea level to 2,097 m in the Pyrenees (mean 402.6 ± 395.8 m, all uncertainties in standard deviation units unless otherwise stated). This topography generates a climatic gradient from typical warm-dry Mediterranean climates in coastal plains to continental–alpine climates with mild summers, cold winters and high seasonality at higher altitudes. Ecosystems are structured by a long-term human occupancy. All the urban centres of the study area are located in Mediterranean plains, while the north and western parts are essentially forested and agricultural (Appendix S1, Figures

S1.3–S1.8). Anthropogenic patterns have changed in the past century, when coastal plains underwent urbanization and agricultural intensification due to the expansion of groves, vineyards and cereal crops. Yet, landscape mosaics still include vast areas of non-used open habitats, mainly occupied by garrigue, maquis and wetlands. Inland plains and higher elevations are less artificialized and are covered with forests that result from land abandonment following a century of decrease in formerly widespread livestock farming (Sirami et al., 2010).

2.2 | Reptile data

We made use of 49,821 reptile records extracted from the Malpolon data base, a long-term repository of amphibians and reptile occurrence data covering the western French Mediterranean since the 1970s (Geniez & Cheylan, 2012). Seventy per cent of the records were opportunistically reported by volunteer naturalists without any standardized protocol; the remaining 30% were gathered from standardized surveys and literature records. All records (one record = one species at a given date and location) were expert-validated prior to inclusion in the database; we retained only those with the highest level of certainty with respect to species and geographic location. We restricted the present analysis to records gathered between 1996 and 2015, anterior data lacking precise geolocation (final sample size = 27,858 records; spatial variations in survey effort in Appendix S1, Figure S1.1). This data set encompassed the 25 reptile species found in the region (list of species in Appendix S2). The Pyrenean and Northern European populations of Viviparous Lizard (*Zootoca vivipara*) were treated as separate species based on marked differences in some life-history traits coupled with long evolutionary divergence and allopatry (Cornetti et al., 2014; Horreo et al., 2019). *Natrix natrix* was split into several species after the analyses of this study were completed (Speybroeck et al., 2020). The records in our region correspond to *N. astreptophora* (southernmost areas) and *N. helvetica*, whose distribution is still imperfectly known. Traits data have been obtained from populations as close to our areas as possible, but we still use *N. natrix* for convenience here.

We overlaid these data with a 10×10 km regular square grid defined as a compromise between an ecologically meaningful landscape-level resolution and adequacy with the distribution of data. We therefore defined a reptile assemblage on a geographical basis, based on all records occurring within a given cell ($n = 288$ cells, cells truncated by proximity to the coast or regional border and cells with fewer than 20 records were excluded, see “Section 2.6”).

2.3 | Trait data

We selected nine ecological traits assumed to explain reptiles' responses to the distribution of habitats and resources: percentage of diurnal activity, reproductive mode (oviparous or viviparous), body size (continuous), annual fecundity (continuous, product of clutch

size × number of clutches per year), age at sexual maturity (months), main habitat (aquatic or terrestrial), preference along the open habitat–forest gradient (from 1, open-habitat specialist, to 3, forest specialist, calculated as an average over three habitat classes weighted by proportions of use), preference on a vegetation complexity gradient from bare ground to forest (from 1, bare ground specialist to 3, strictly arboreal, calculated as an average over four vegetation strata weighted by proportions of use) and dominant diet (qualitative, modalities defined from the maximum proportion of use among eight diets: generalist, mammals, arthropods, amphibians, fishes, reptiles, birds, molluscs). These traits have been previously shown to reflect key aspects of evolutionary strategies or ecological niche in animals (e.g. body size, age at sexual maturity) or reptiles (e.g. daily activity pattern, see Dunham & Miles, 1985; Pianka et al., 2017; Shine, 2005; Todd et al., 2017). We assigned trait values based on expert knowledge complemented with literature searches (trait table and references in Appendix S2). Aggregating habitat and diet use to a single value per species leads to some information loss as compared to the original coding of traits as frequencies of multiple modalities, but keeping this raw information would have been intractable in our analyses. Exploratory analyses with several alternative trait coding methods yielded results similar to those presented here. Other traits (mobility and yearly activity) were discarded due to missing information at a regional level or lack of variability.

2.4 | Environmental gradients

We defined 11 environmental variables for each 10 × 10 km cell (Table 1, maps in Appendix S2), chosen to represent at best climatic and habitat variation within the study area. We extracted median altitude per cell from a raster numerical terrain model with a 25-m native resolution (French National Geographic Institute, IGN: BD Alti, <https://geoservices.ign.fr/>). We retrieved 1970–2000 climatic 3-month averages as raster layers at a 30-s native resolution from WorldClim V2.0 (Fick & Hijmans, 2017). All reptiles in the region have a low level of activity during winter, and their maximum activity is reached in spring and summer (approx. 50% of reptile records between May and August; activity decreases in mid-summer in strictly Mediterranean areas). We therefore quantified climatic variations through four variables: median temperature and precipitations of the warmest quarter of the year (May–August), and seasonality of precipitations and temperatures. Elevation was expectedly associated with variation in temperature (Pearson's $R^2 = .95$), precipitations ($R^2 = .51$) and seasonality ($R^2 = .45$). Annual averages and winter temperatures were highly correlated with seasonal medians, but were discarded to match reptiles' annual phenology.

We described land use with Corine Land Cover 2006 (CLC; Bossard et al., 2000), which maps categorical land use types down to 25 ha polygons. We used the second level of CLC classification of land uses to construct six variables relevant to describe reptiles habitats, and sufficiently well represented in our region (correspondence with CLC classes in Table 1; open waters and marginally represented

classes were excluded): urban areas, intensive agricultural areas (mainly cereal crops, vineyards and groves), extensive agricultural areas (pastures and mosaics of annual and permanent crops), open habitats (maquis an garrigue), forest and wetlands (mostly coastal marshes and bogs). These seven classes represented 100% of total cell area in 217/288 cells (75%), and <90% of total cell area in 10 cells, all located on brackish-water coastal ponds from which reptiles are rare.

2.5 | Species-level analysis

We analysed trait–environment co-structures at the species level within a multivariate ordination framework. We first synthesized the 288 cells × 25 species presence–absence matrix (hereafter table L) through a correspondence analysis (COA), and the 288 cells × 10 environmental variables matrix (hereafter table R) through a principal component analysis (PCA) weighted by the row weights of the COA. We joined these two tables in a coinertia analysis in order to investigate structures in the distribution of species along the main gradients that describe environmental variation in the region (Dray et al., 2003; Thioulouse et al., 2018).

Second, we synthesized the 25 species × 9 traits matrix (hereafter table Q) with a Hill & Smith analysis, weighted by the row weights of the COA. We then investigated common structures in the distribution of traits and environmental variables in a three-table ordination (“RLQ analysis,” Dray et al., 2014). RLQ analysis is grounded on the combination of two coinertia analyses (tables R–L and tables L–Q), matched by table L (the site–species matrix) and an adequate weighting. We quantified the robustness of trait–environment relationships in this RLQ with a two-step randomization of matrix L which first permutes sites (“model 2” in Thioulouse et al., 2018: tests the environmental contribution to species composition), then species (“model 4”: tests the contribution of traits to species composition). We paralleled the RLQ with a fourth-corner analysis, which tests pairwise relationships among traits and environmental variables with a randomization test (49,999 permutations), adjusted with the false discovery rate to control for multiple testing (Dray et al., 2014; Thioulouse et al., 2018). The fourth-corner analysis provides a more direct overview of associations between each trait and each variable than RLQ, but misses general co-structures between environmental gradients and trait syndromes: the complementary use of these two analyses therefore offers an in-depth overview of trait–environment associations.

2.6 | Community-level analysis

Analyses of species and trait diversity are affected by unequal sampling effort, in particular when analysed through non-standardized, opportunistic data (Higa et al., 2015; Isaac et al., 2014). We therefore investigated the relationship between sampling effort and species richness with rarefaction curves from 1 to the number of individual

TABLE 1 Description and quantitative summary of the environmental variables considered in the study, with corresponding Corine Land Cover codes [CLC] and acronyms for reference to figures and scores on the two first axes of the non-weighted principal component analysis

Variable (acronym) [CLC]	Description	Mean \pm SD (range)	Correlation with PC1	Correlation with PC2
Urbanization (u) [11; 12]	% of continuous or discontinuous built areas	5 \pm 7 (0; 49)	-.53	-.39
Intensive agriculture (ia) [21; 22]	% of areas dedicated to intensive agriculture; in the study region concerns mainly non-irrigated crops, vineyards, fruit plantations and olive groves	20 \pm 22 (0; 84)	-.78	.19
Extensive agriculture (ea) [23; 24]	% of area dedicated to extensive agriculture; in the study region concerns mainly pastures and complex cultivation patterns associating annual crops and spontaneous vegetation	18 \pm 13 (1; 65)	-.09	-.76
Open habitats (oh) [32; 33]	% of open or scrub-dominated vegetation; in the study region, mainly garrigue and maquis	22 \pm 17 (0; 80)	.45	.59
Wetlands (w) [31]	% of wetlands (including inland wetlands and large extents of brackish-water marshes in coastal plains)	1 \pm 5 (0; 45)	-.33	.28
Forest (f)	% of forest (all types pooled, mainly oaks with increasing proportion of conifers towards higher elevations)	33 \pm 24 (0; 86)	.77	-.18
Median elevation (el)	Median elevation (m) per cell (native resolution 25 m)	402.6 \pm 395.8 (0; 2,097)	.93	.02
Median temperature of the three warmest months (tp)	Median temperature ($^{\circ}$ C) per cell for July–September, averaged over the 1970–2000 period	19.61 \pm 2.49 (11.2; 22.8)	-.90	.07
Seasonality of temperatures (st)	Median temperature seasonality (annual range, averaged over the 1970–2000 period)	58.49 \pm 2.33 (53.49; 63.73)	-.36	-.60
Median precipitations of the three driest months (pr)	Median precipitations (cumulated mm) per cell for July–September, averaged over the 1970–2000 period	143.19 \pm 30.87 (88; 285.5)	.89	-.27
Precipitation seasonality (sp)	Median precipitation seasonality (annual range, averaged over the 1970–2000 period)	22.4 \pm 5.87 (12; 35)	-.90	.11

Abbreviations: CLC, Corine Land Cover codes; PC, principal component.

records in each cell. All curves started to bend around 20 records, suggesting this sample size as the best compromise between a representative assessment of the richness of reptile assemblages, and sufficient spatial coverage (Appendix S3). We therefore computed 100 rarefied cell \times species matrices at 20 records per cell, which we converted into presence–absence data and used for all subsequent assemblage-level analyses. From rarefaction curves, we extracted rarefied species richness, the estimated number of species per cell for an equal sampling effort of 20 records, as an assemblage-level measure of species diversity.

We investigated variations in trait diversity with three complementary functional diversity indices computed from the rarefied cell \times species matrices and the species \times trait matrix (table Q). FRic is the closest trait-based analogue to species richness and thus provides an estimate of the range of functional strategies within an assemblage. Computationally, FRic is the minimum convex hull

occupied by an assemblage in the functional space defined by species' traits (Villéger et al., 2008). We defined the dimensionality of this functional space from a principal coordinate analysis on a species \times species Gower's distance matrix based on table Q, and corrected negative eigenvalues with Cailliez' correction (Legendre & Legendre, 2012). We retained two principal coordinate axes, the maximum number of axes ensuring that species number $> 2^{\text{number of axes}}$ in each cell, a condition required for the computation of FRic. The quality of the representation of the initial trait matrix in this two-dimensional trait space was moderate (corrected R^2 -like ratio = .45, Legendre & Legendre, 2012), but increasing dimensionality would have led to drastically reduce the number of cells. For ease of interpretation, we standardized FRic with the global FRic computed on a trait volume encompassing all species, so that it varied from 0 (minimum trait range) to 1 (an assemblage encompassing all the traits of the regional assemblage).

FDis, the mean distance of each species to the centroid of this trait space, measures the spread or tightening of species around an hypothetical functionally average species (Laliberté & Legendre, 2010). Complementarily to FRic, this functional diversity index provides a measure of trait heterogeneity across assemblages structurally independent from species richness.

Functional evenness (FEve) is a measure of the regularity of trait distribution across species within an assemblage (Villéger et al., 2008) and thus shows whether all species are equally distant in the trait space (FEve = 1) or if the assemblage is composed of a group of functionally similar species tightened in a small part of the trait space and a few outliers (FEve = 0).

In addition, we computed community-averaged traits as the cell-mean (quantitative traits) or modal (nominal traits) value of each trait. While functional diversity indices measure the assemblage-level trait heterogeneity, these averaged traits reflect variations in the position of assemblage centroids in the trait space. We only analysed averaged quantitative traits due to lack of variation in the modal values of nominal traits across the study area (see maps in Appendix S4). We computed FRic, FDis, FEve and community-averaged traits for each of the 100 rarefied matrices and averaged their values per cell to obtain a single measure of each index at a 20 records sampling efforts, accounting for the uncertainty in community composition associated with rarefaction. Preliminary checks showed that all diversity indices tested were little affected by increasing the rarefaction threshold from 20 to 40, 60 and 100 records (Appendix S3, pairwise R^2 among indices ranged from .28 to .98, 20 out of 24 pairs above .70).

We then used generalized additive models to regress variations of species richness (log-transformed for normalization), the three functional diversity indices and community-averaged trait values against the land-use gradients defined by the axes of a non-weighted PCA on matrix R. Since we had no hypothesis on the linearity of these relations, we fitted each variable as a penalized regression spline constrained to a maximum of 3 basis dimensions to avoid unnecessary complexity (Wood, 2006). A few of these models exhibited slight residual spatial autocorrelation (Moran's $I < 0.1$), which we chose not to control to the benefit of a uniform model structure across all indices.

All analyses were performed in R 3.5.0 (R Core Team, 2016) with packages ade4 (Thioulouse et al., 2018), FD (Laliberté et al., 2014) and mgcv (Wood, 2006).

3 | RESULTS

3.1 | Species-level variation along environmental gradients

The two first axes of the coinertia analysis accounted for 95% of the co-structures between species and environment tables (CO1: 90%, CO2: 5%; third axis: 3%, not retained). Reptile species were spread along a gradient ranging from lowland plains, mostly occupied by agriculture and urbanization and experiencing warm and dry

summers, to high-elevation areas mostly away from the coast, often covered by garrigue, extensive grazing areas or forest and associated with colder temperatures and higher rainfalls (Figure 1, CO1). This first axis of variation corresponds to the main ecological gradient structuring the study region separating reptile assemblages typical of Mediterranean lowland from those living in the main mountain chains at the extreme south-west and north. Reptile species were organized along this axis from typical Mediterranean and thermophile species in negative values (e.g. *Tarentola mauritanica*, *Psammodromus edwardsianus*) to more widespread species with broader thermal and precipitation ranges in positive values (e.g. *Lacerta bilineata*, *Zamenis longissimus*, *Vipera aspis*). A distinct group emerged at higher positive positions on this axis, encompassing the two *Z. vivipara* lineages and other high-altitude, cold-climate species (*Vipera berus*, *Coronella austriaca*, *Lacerta agilis*). In order to reflect the gradual replacement of Mediterranean species by medio-European reptiles, we call this first axis a "Mediterraneity" gradient. The second axis mainly discriminated species assemblages associated with high temperature seasonality, located along a narrow band between coastal plains and mountain foothills (Figure 1, CO2). This area is characterized by climatic contrasts between dry and warm summers, typical of the Mediterranean zone, and cold and wet winters.

3.2 | Trait variations along environmental gradients

The two first axes of the RLQ analysis explained 96.4% of trait-environment variations (99.3% with the third axis, not retained). An investigation of the projection of species (Figure 2a), sites (Figure 2b), traits (Figure 2c) and environmental variables (Figure 2d) into the ordination space revealed a separation of traits along the mediterraneity gradient, in which aquatic species, insectivores and many generalist species occurred in the low-elevation, warm end of the gradient (negative scores), while the colder and upper end was associated with preference for forest, carnivory and viviparity (the latter concerned only one species however). However, although these trait-environment associations were robust to site permutation (permutation "model 2," $p = .001$), they were not robust to species permutation ("model 4," $p = .330$). This implies that the link between traits (table Q) and environment (table R) was not substantiated. The fourth-corner analysis similarly failed to find any association between traits and environmental variables (no significant pairwise correlation based on a permutation test). The RLQ was therefore structured by strong trait and habitat differences between lizards, reptiles and tortoises, rather by the organization of traits along environmental gradients.

3.3 | Community-level variation along environmental gradients

The two first axes of the non-weighted PCA on matrix R accounted for 63% of total variation in environmental variables (72% with axis

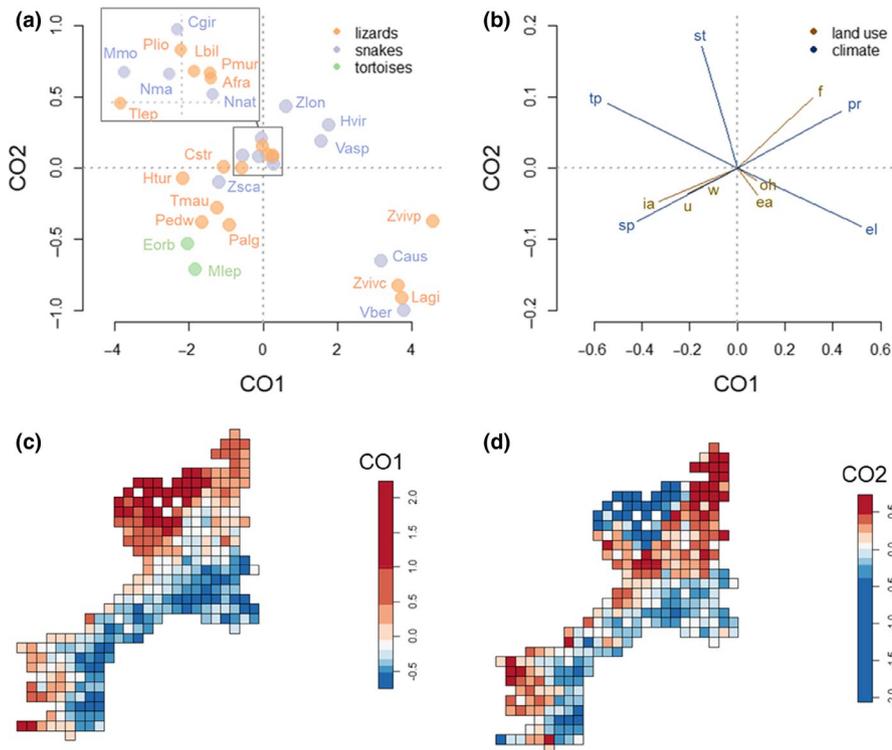


FIGURE 1 Projection of species (a, with focus on the centre) and environmental variables (b) in a coinertia analysis involving 25 reptile species and 11 environmental variables ($n = 288$ reptile assemblages). (c,d) Display the mappings of coinertia axes. See Appendix S1 for species acronyms in (a). In (b): ea, extensive agriculture; el, elevation; f, forest; ia, intensive agriculture; oh, open habitats; pr, sum of precipitations during the driest quarter; sp, precipitation seasonality; st, temperature seasonality; tp, mean temperature of the warmest quarter; u, urban areas; w, wetlands [Colour figure can be viewed at wileyonlinelibrary.com]

3, not retained; see maps in Appendix S1). The first axis ("Land 1," 47%) corresponded to the mediterraneity gradient identified in the coinertia and RLQ analyses, with coastal lowland plains in negative values and high-elevation forests at the positive extreme (Table 1; Appendix S1, Figure S1.13). The second axis ("Land 2," 15%) separated extensive agricultural areas under seasonal climates from arid-climate open habitats (Table 1; Figure S1.14). Land 2 reflected a land-use gradient in which extensive agriculture is relegated to the north-eastern part of the study area, where climate undergoes strong seasonal influences. At the opposite extreme, non-cultivated open habitats are associated with calcareous plateaus and wetlands, mostly along the Mediterranean shore. Synthetically, Land 2 opposed temperate habitats dominated by dense herbaceous cover and deciduous trees to arid and rocky landscapes.

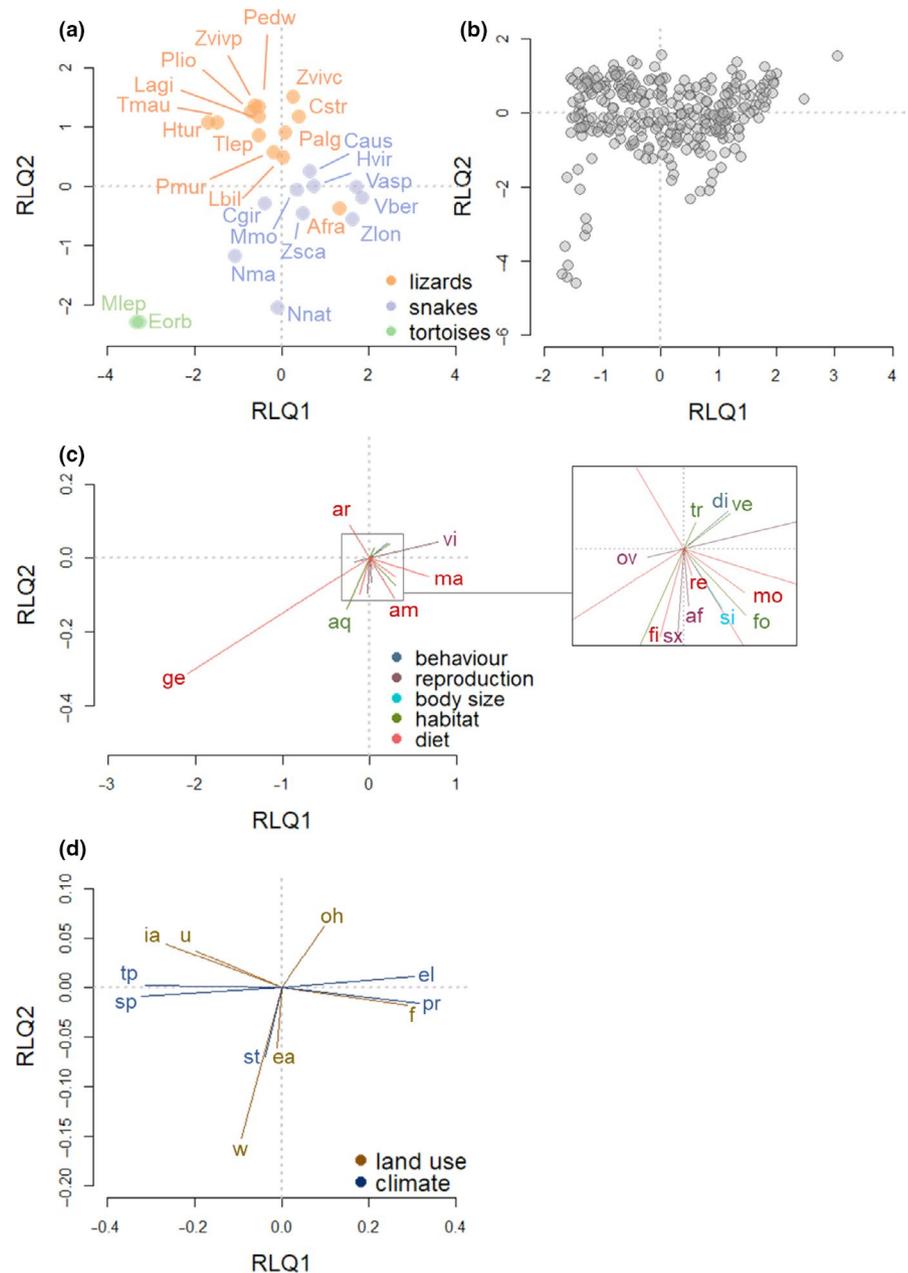
Land 1 and Land 2 explained together 24.8% of log-transformed reptile species richness in a generalized additive model. Species richness was maximum at the centre of the Land 1 axis, decreased slightly towards lowlands plains and more markedly towards high elevations (Figure 3a, estimated degree of freedom of the spline = 1.97, $F = 15.31$, $p < .0001$), reflecting a transition zone between Mediterranean and mountain assemblages consistent with the species-level pattern observed in the coinertia analysis. Species richness increased monotonically from extensive agricultural areas to open habitat mosaics, but stabilized in the garrigues and maquis that correspond to positive values of Land 2 (Figure 3b, edf = 1.95, $F = 36.12$, $p < .0001$).

Contrary to the species-level patterns of the RLQ, most assemblage-level functional diversity indices and community-averaged traits exhibited clear variations along Land 1 and Land 2 (Figures 4 and 5; edf and p -values in Appendix S5). When moving from

Mediterranean plains to higher-elevation areas (negative to positive values along Land 1), assemblages became dominated by more diurnal (Figure 4a) and less productive species (Figure 4f) with later sexual maturities (Figure 4g). Body size increased from the coast to the mid-point of Land 1, then plateaued (Figure 4c). Average habitat preference logically shifted towards forest (Figure 4i) and higher vegetation strata (Figure 4k). Body size, sexual maturity and the two indices associated with habitats plateaued or reversed in high-elevation forests (positive values of Land 1), close to the maximum values of species richness (Figure 3a) and consistent with the change in species composition observed in the coinertia analysis (Figure 1). Unexpectedly, this assemblage-level trait shift was accompanied with a non-monotonous increase in FRic and a monotonous increase in FDis dispersion along Land 1 (Figure 5a,b), the highest trait diversity being found in mountains rather than close to the transition zone identified from species-level analyses. Consistently, FRic was moderately correlated with species richness ($R^2 = .36$) due to trait redundancy among reptile species.

Variations along Land 2 were not anticipated from the species-level results, which did not reveal any substantial pattern along the second axes of the coinertia or RLQ analyses. Interestingly however, body size and fecundity decreased monotonically from cultivated habitats to garrigues and maquis (Land 2, Figure 4d,f, and average habitat preference changed from species associated with forest to species preferring more open habitat (Figure 4j). These shifts were associated with a quadratic variation in FRic (Figure 5b) and a slight yet significant decline in FDis, but did not relate with FRic evenness (Figure 5d), meaning that assemblages in garrigues were overall as trait-diverse as in agricultural areas, but with less original species.

FIGURE 2 Projections of species (a), sites (b), traits (c) and environmental variables (d) in the RLQ analysis. Trait acronyms: af, annual fecundity; am, amphibian diet; aq, aquatic habitats; ar, arthropod diet; di, diurnal; fi, fish diet; fo, forest habitat; ge, generalist diet; ma, mammal diet; mo, mollusc diet; ov, oviparous; re, reptile diet; si, body size; sx, sexual maturity; tr, terrestrial habitats; ve, vegetation strata; vi, viviparous. Variables acronyms: ea, extensive agriculture; el, elevation; f, forest; ia, intensive agriculture; oh, open habitats; pr, sum of precipitations during the driest quarter; sp, precipitation seasonality; st, temperature seasonality; tp, mean temperature of the warmest quarter; u, urban areas; w, wetlands. Acronyms of environmental variables in Table 1, species names in Appendix S1 [Colour figure can be viewed at wileyonlinelibrary.com]



4 | DISCUSSION

The composition and diversity of reptile assemblages varied along a climatic gradient associated with elevation and distance from the Mediterranean coast. The quadratic variation of species richness along this gradient, consistent with a peak in average body size, revealed that a sharp compositional turnover occurred in lowly urbanized, mid-elevational areas with high seasonality. Species positions along the first axis of the coinertia analysis indicated that this turnover was better associated with a climatic transition between Mediterranean and continental climates than with land-use gradients. For instance, strictly Mediterranean species that reach their range limit in the south of the region were on the warm side of the coinertia analysis (e.g. *Mauremys leprosa* or *Hemidactylus turcicus*), while medio-European species reaching their southern limit in the

north of the study area were on the colder side (e.g. central European *Z. vivipara* or *V. berus*). Additionally, the distribution limits of some generalist species, such as *V. aspis*, were inconsistent with those of their suitable habitats, but coherent with well-known biogeographical and climatic patterns (Geniez & Cheylan, 2012).

Because land use, local habitat and climate influence species assemblages synergistically, their respective effects may be hard to decipher (Ferber et al., 2017). In most of our study area, high variability in elevation and in the level of urbanization in lowlands permitted to separate climatic from land-use gradients. Furthermore, most reptile species encompassed in our study were associated with open or semi-open habitats which occur at all latitudes and elevations. Nevertheless, some land-use types, such as low-altitude farmlands or urbanization, were under-represented at the region's northern boundary. As a result, enlarging the study area northwards may

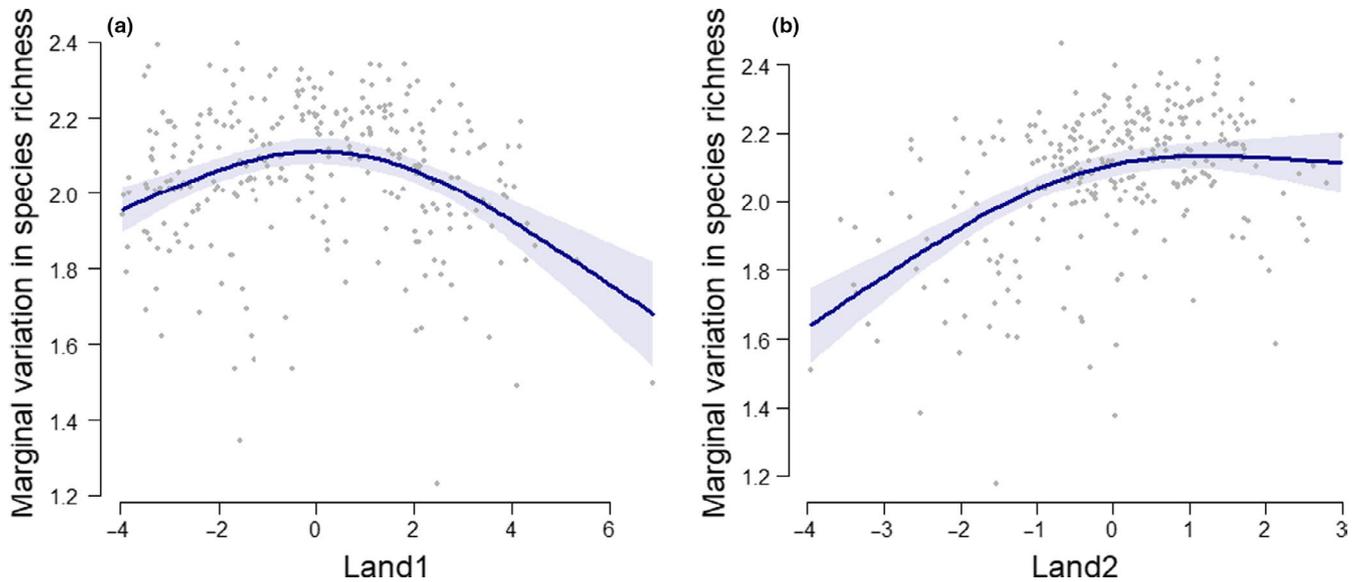


FIGURE 3 Variations of reptile species richness (rarefied to 20 individuals per assemblage, $n = 288$ assemblages) along the two first axes of a PCA synthesizing environmental variation. Blue curves and their 95% confidence bands are marginal effects fitted from penalized splines in a generalized additive model; dots depict partial residuals. Land 1 ranges from warm and anthropogenized Mediterranean plains to high elevations and continental areas (“mediterraneity gradient”); Land 2 ranges from extensive agriculture to garrigues and other open habitats [Colour figure can be viewed at wileyonlinelibrary.com]

increase the imprint of these land-use types on reptile assemblages, but would also intensify climatic contrasts. We therefore doubt that the compositional patterns revealed by the coinertia analysis would fundamentally change with a moderate increase in spatial extent, although reptile data north to our study area were too sparse to test it formally.

At a species level, reptiles' distributions along environmental gradients were not paired with variations in ecological traits, ruling out any role of environmental filtering *sensu stricto* (directional variations in survival or growth rate along an environmental gradient directly explained by traits, Cadotte & Tucker, 2017). This result is in line with a previous study on a subset of the same area and species (De Solan et al., 2019), but diverges from other regions or taxa (Jung & Threlfall, 2016; Öckinger et al., 2010; Reading et al., 2010; Todd et al., 2017), suggesting either a lack of power to detect trait patterns in species-poor regional assemblages, or regionally varying associations between traits and land use or climate. By contrast, assemblage-level trait averages and functional diversity were clearly associated with environmental gradients. Assemblage diversity and composition are a consequence of complex covariations among species' spatial or temporal dynamics within non-saturated assemblages, which are not directly predictable from species-level patterns (Kneitel & Chase, 2004; Micheli et al., 1999). Unlike species' distributions, which may be controlled by idiosyncratic processes, these covariations stem from regional-scale effects of competitive exclusion, dispersal limitations or higher-scale niche processes that are often related to climatic affinities (Cornell & Lawton, 1992; Ramm et al., 2018). The discrepancy between species- and assemblage-level patterns therefore supports the hypothesis that large-scale factors take over local processes to distribute reptiles' traits

along a climatic gradient, consistent with a regional-level explanation of local assemblage composition (Caley & Schluter, 1997; Ricklefs, 1987, 2004). The climatic interpretation of our results was further enforced by the increase in the FDis index towards continental, high-elevation areas, which implies a replacement of functionally homogeneous Mediterranean assemblages (e.g. including strictly aquatic or nocturnal species) by medio-European assemblages with higher ecological disparity. This monotonous pattern was inconsistent with the peak of species richness in mid-elevation assemblages, a likely consequence of the lower trait redundancy within medio-European assemblages as compared with Mediterranean ones (Cox & Moore, 2010).

Past habitat degradation could have selectively removed large and diurnal species from coastal plains, resulting in patterns similar to those expected from climatic determinants (Nowakowski et al., 2018; Rapacciuolo et al., 2017; Santini et al., 2017). Nevertheless, the species occurring on the Mediterranean side of the coinertia analysis were typical thermophile reptiles that cope well with even high levels of artificialization, such as *M. leprosa*, *H. turcicus* and both *Psammodromus*. Accordingly, when moving from Mediterranean plains to higher elevations, assemblages were increasingly dominated by more diurnal, less productive and more forest-dwelling species with older sexual maturity. Nocturnality is a well-known behavioural component of thermal strategies in warm-climate lizards (Pianka et al., 2017): the decrease in summer temperature with elevation far from the Mediterranean shore likely sets the northern boundary of nocturnal species' distributions, as they fail to find suitable thermal conditions.

Lower fecundity in assemblages of the coolest parts of the region was also consistent with known life-history traits correlations in

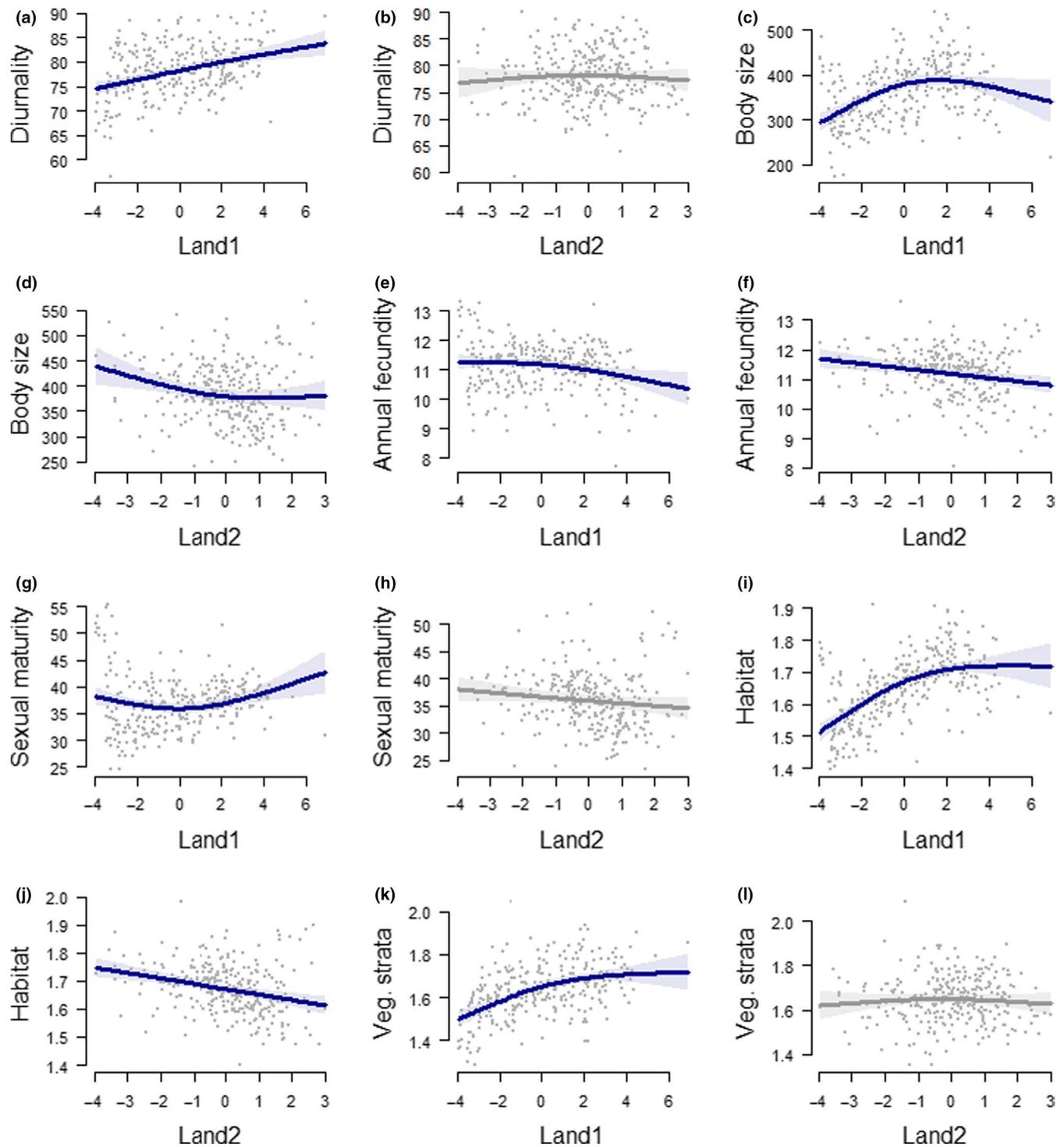


FIGURE 4 Variations of community-averaged traits (mean value over 100 replicates of each assemblage, rarefied to 20 individuals, $n = 288$ assemblages) along the two first axes of a principal component analysis synthesizing environmental variation. Blue curves and their 95% confidence bands are marginal effects fitted from penalized splines in a generalized additive model; dots depict partial residuals. Grey curves indicate non-significant effects at a 95% confidence threshold [Colour figure can be viewed at wileyonlinelibrary.com]

reptiles (snakes: Shine & Seigel, 1996; lizards: Winck & Rocha, 2012). Body size, however, was unexpectedly larger in assemblages of the coolest, high-elevation half of the mediterraneity gradient. Large snakes are regularly found in urban locations under warm climates, suggesting that an anthropogenic filter alone cannot account for this result. Conversely, the large-bodied species found in the north of

the study area were typically associated with continental climates and are unlikely to have formerly occurred in the Mediterranean plains. A bias against the detection of smaller species in the under-sampled higher-elevation parts of the region, and/or a bias against the detection of larger species in warmer areas where they may be less diurnal, could contribute to explain this result. We did not find,

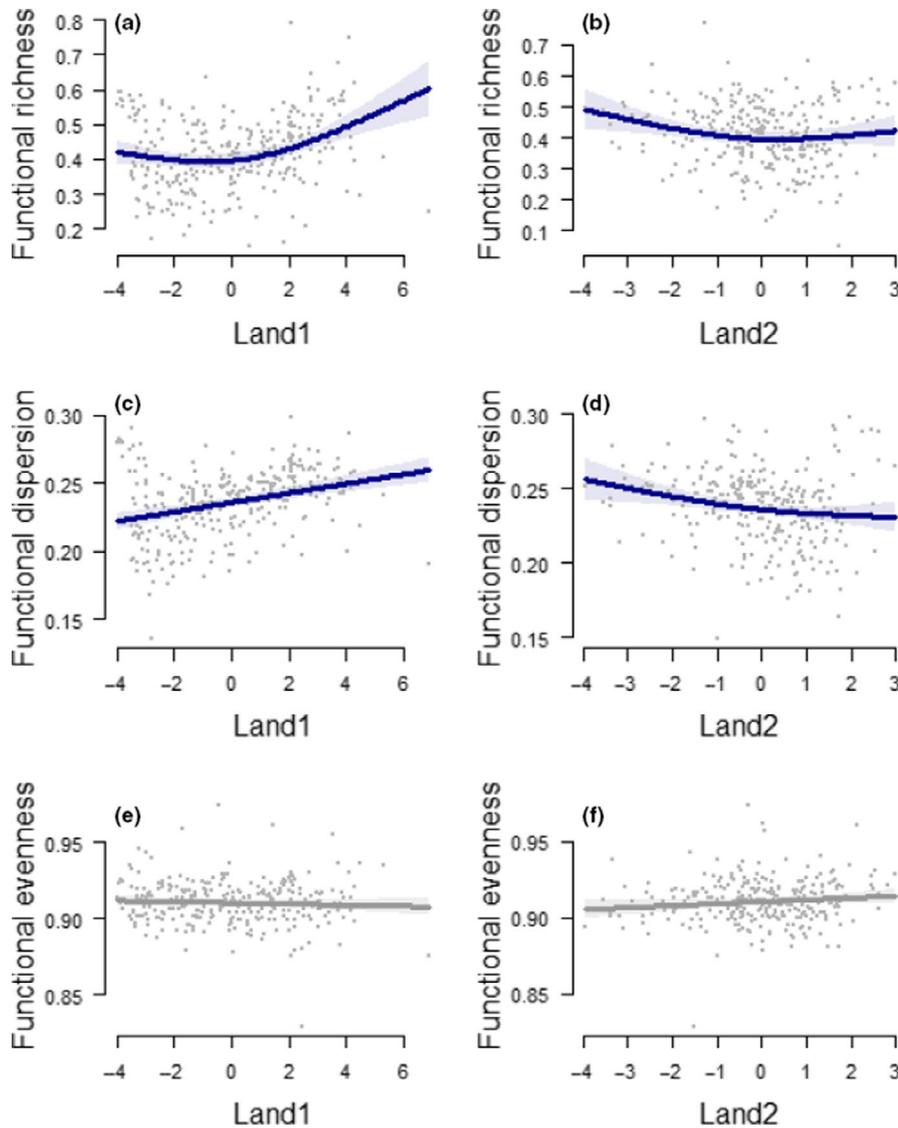


FIGURE 5 Variations of functional diversity indices (mean value over 100 replicates of each assemblage, rarefied to 20 individuals, $n = 288$ assemblages) along the two first axes of a principal component analysis synthesizing environmental variation. Blue curves and their 95% confidence bands are marginal effects fitted from penalized splines in a generalized additive model; dots depict partial residuals. Grey curves indicate non-significant effects at a 95% confidence threshold [Colour figure can be viewed at wileyonlinelibrary.com]

however, any strong evidence of these biases when investigating species' occurrence maps. These patterns suggest that climatic restrictions on species' range limits, secondarily associated with metabolic strategies, still bypass the imprint of anthropogenization, as observed in other vertebrate studies (Barnagaud et al., 2017; De Solan et al., 2019; Rapacciuolo et al., 2017).

Interestingly, FDis decreased from cultivated to abandoned areas, in association with shifts towards smaller-bodied and less productive species, which may come as a result of selective species removal related to shrub encroachment. This result reveals that land use influences substantially regional gradients in the composition of reptile assemblages, even though their main patterns are driven by climate. Land abandonment effects on vertebrates seem to vary with the study context, but usually benefit generalist species most, modifying the structure of species assemblages (Moreira & Russo, 2007; Sirami et al., 2010). A clear shift in averaged habitat preference suggests that in our particular case, land abandonment promoted the intrusion of generalist or woodland species (such as *Z. longissimus*) in assemblages otherwise dominated by open-habitat

reptiles, an effect also observed in other Mediterranean regions (Zakkak et al., 2015). This pattern supports low-intensity agriculture and pasture as a key habitat to preserve the diversity of reptile species and functions, as in other vertebrates (De Solan et al., 2019; Doxa et al., 2010; Loos et al., 2014; Sergio & Pedrini, 2007).

There are little options but using opportunistic data when investigating regional-scale patterns in elusive species such as reptiles, which implies that specific attention must be paid to heterogeneity in sampling effort and detectability (Boersch-Supan et al., 2019; Geldmann et al., 2016). Even though our cautionary approach relying on rarefied assemblage-level indices provides an efficient way to homogenize sampling effort in terms of records number, we cannot fully rule out other possible sources of bias. In particular, the tendency of volunteers to spend more time and accumulate more records in easily accessible or pleasant habitats could increase spatial heterogeneity in sampling (Neyens et al., 2019; Tiago, Ceia-Hasse, et al., 2017; Tiago, Pereira, et al., 2017). A substantial proportion of our data was acquired within consulting office surveys targeting little visited areas or

habitats unattractive to volunteers, limiting the imprint of this possible bias (Tulloch et al., 2013). Still, a formal test of the impact of observer effects would require fully protocolled replicated surveys, leading to a loss in spatial coverage over regional extents (MacKenzie et al., 2005). Methods to hybridize such data with opportunistic records exist (Dorazio, 2014), but their applicability is limited in reptiles due to the extremely low rate of individual encounters necessitating unrealistic sampling effort.

As a result of these data limitations, studies investigating the composition of reptile assemblages over regional extents remain scarce (Böhm et al., 2013; Mullin & Seigel, 2009; Todd et al., 2017). This knowledge gap is of specific concern in European landscapes, where reptiles and other vertebrates are wedged between land conversion associated with urbanization and agriculture on the one hand, and habitat changes arising from land abandonment, on top of larger-scale factors (Gibbons et al., 2000; Reading et al., 2010). In spite of a prevalent role of climate, our results support instead an integration of reptiles in regional planning, in order to limit the adverse consequences of both artificialization and land abandonment on their persistence and diversity in climatically suitable areas (Beaudry et al., 2011; Doherty et al., 2020; Socolar et al., 2016). This regional approach is especially necessary as the low dispersal abilities and high ecological specialization of reptiles likely impairs their recolonization following post-disturbance habitat recovery, unless if assisted by suitable connectivity networks over regional scales. Our results also revealed that assemblage-level patterns are likely to be missed in species-level studies, calling for multiscale comparative approaches to explain the geographic distribution of species and traits at a regional scale. Opportunistic data from volunteers, notwithstanding their limitations, may reveal an invaluable resource to foster these multiscale analyses applied to scarce and shy species such as reptiles.

5 | CONCLUSION

Our results revealed that once dominant climatic influences were accounted for, land abandonment decreases the functional diversity of reptile assemblages over a regional extent. However, individual species are likely too tied to local resources and fine-grained habitat composition to make their responses to land-use changes predictable from their ecological traits. Our results showcase the complementarity of species and assemblage scales of analysis when it comes to investigate the impact of environmental gradients on assemblage composition and diversity: conciliating these two organization levels for better forecasts of reptiles' vulnerability to global changes is a logical next step for which joint distribution models may reveal central (Caradima et al., 2019). In hardly detectable taxa, the complementarity between local protocolled surveys and long-term opportunistic data set spanning wide spatial and temporal extents will be a key to construct biologically realistic models able to assist conservation planning.

ACKNOWLEDGEMENTS

We wish to thank all the professional and volunteer observers who contributed to gathering reptile records used for the present study. The Malpolon database is financially supported by the Direction Régionale de l'Environnement, de l'Aménagement Occitanie et du Logement, as part of the Système d'Information sur la Nature et les Paysages. We are also grateful to J. Brito and two anonymous referees for their insightful comments on a previous version of this manuscript.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ddi.13176>.

DATA AVAILABILITY STATEMENT

Trait data are available in the appendices. All data are deposited on DRYAD: <https://doi.org/10.5061/dryad.pc866t1mg> (Barnagaud et al., 2020).

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BIOSKETCH

Jean-Yves Barnagaud focuses his research on the processes underlying spatial variations in the composition and diversity of vertebrate assemblages at multiple spatial scales, and their temporal dynamics. He uses a combination of ecoinformatics methods coupling standardized data and opportunistic records from citizen sciences. The Malpolon database has gathered hundreds of thousands fully validated records of reptiles and amphibians for over 40 years all over Mediterranean France. It is used for various purposes, including fundamental ecological research, conservation ecology and naturalist surveys.

Author contributions: J.Y.B. and P.A.C. conceived the ideas; M.C., P.G. and P.A.C. constructed the database, validated records and provided herpetological expertise; J.Y.B. performed the analyses and led the writing; all co-authors contributed substantially to the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Barnagaud J-Y, Geniez P, Cheylan M, Crochet P-A. Climate overrides the effects of land use on the functional composition and diversity of Mediterranean reptile assemblages. *Divers Distrib*. 2021;27:50–64. <https://doi.org/10.1111/ddi.13176>