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Ecological niche differentiation and climate change response of *Origanum elongatum* and *Origanum compactum* in northern Morocco

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ABSTRACT

This study investigates the ecological niches and projected climate-driven distributional shifts of two endemic Moroccan species, *Origanum compactum* and *Origanum elongatum*, both of high ecological and socio-economic importance. The purpose was to characterize their current distribution, identify the key climatic variables structuring their ecological niches, and forecast changes under a severe climate scenario (SSP5-8.5, 2061–2080) to assess vulnerability and inform conservation strategies. An ecological niche modeling framework was applied using occurrence data from published sources and GBIF, combined with six bioclimatic predictors. Multiple algorithms (GLM, GBM, ANN, RF, and MAXENT) were evaluated, with high-performing models (AUC > 0.9, TSS > 0.8) integrated into ensemble projections. Niche overlap was quantified through Schoener's D index and further tested with equivalency and similarity analyses. Results revealed marked ecological differentiation between the two species (D = 0.2; p = 0.001), with *O. compactum* associated with moderately warm, precipitation-sensitive environments and *O. elongatum* showing broader tolerance to temperature and aridity gradients. Projections indicated a drastic reduction in highly suitable habitats for both taxa, with *O. compactum* declining by 87% (from 4.980 to 626 km²) and *O. elongatum* by 89% (from 3.688 to 407 km²). Although moderately and low-suitability zones expanded substantially, these marginal habitats may not fully compensate for the loss of optimal environments. The study, while limited to climatic predictors, without incorporating anthropogenic pressures, highlights clear conservation priorities: safeguarding residual core habitats for *O. compactum* and maintaining ecological connectivity for *O. elongatum*. It provides original insights into the contrasting adaptive capacities of Mediterranean endemics under climate change. Importantly, this is the first comparative niche analysis of these two endemic *Origanum* species in northern Morocco that integrates niche-equivalency testing with forward climate projections, offering actionable and spatially explicit guidance for biodiversity conservation and the sustainable management of medicinal plants.

Keywords: *Origanum compactum*, *Origanum elongatum*, ecological niche modeling, climate change, Morocco.

INTRODUCTION

Climate change is widely recognized as one of the major drivers of biodiversity loss worldwide, altering the distribution, survival, and ecological dynamics of plant species (Shivanna, 2022). In Mediterranean ecosystems, which are considered global biodiversity hotspots, these effects are particularly pronounced due to their sensitivity to temperature rise, irregular precipitation, and increasing anthropogenic pressures (IPCC, 2022). Northern Morocco, located at the junction of the Mediterranean Sea and the Atlantic Ocean, harbors a unique combination of microclimates and habitats shaped by complex topography and ecological gradients. Such environmental diversity acts as a refuge for a wide array of endemic and economically important plants, although it also exposes these species to considerable risks under increasing climatic instability (Arabi et al., 2024; Walas and Taib, 2022).

In this context, the genus *Origanum* (Lamiaceae) has drawn considerable attention because of its ecological significance, medicinal value, and socio-economic relevance. Morocco harbors several species of this genus, but *Origanum compactum* and *Origanum elongatum* are particularly noteworthy as endemic taxa with contrasting ecological distributions. *O. compactum* is relatively widespread, occurring across northern and central Morocco where it occupies semi-arid to sub-humid environments, whereas *O. elongatum* has a much narrower range, largely confined to the Rif and Middle Atlas mountains (Benabid, 2000; Valdés et al., 2002). Both species are prized for their essential oils, which are rich in bioactive compounds and continue to play a central role in traditional medicine while also attracting interest for pharmacological and industrial applications. Although their ethnobotanical uses, phytochemical composition, and essential oil variability have been widely studied (Aboukhalid et al., 2017; Bakha et al., 2020; Abdelaali et al., 2021), little attention has been paid to their ecological niches or to how these niches may shift under climate change. Understanding such dynamics is particularly relevant for species of high socio-economic value, since anticipating distributional changes can guide both conservation priorities and the sustainable use of medicinal and aromatic plants that represent significant natural resources for local communities.

In this regard, ecological niche modeling (ENM) has become a cornerstone method in modern ecology for linking species occurrences with environmental conditions and forecasting future distributions under climate change. By combining occurrence data with both current and projected bioclimatic variables, ENMs enable the identification of areas at risk of habitat loss and support informed conservation planning (Elith and Leathwick, 2009). This approach has proven especially insightful in Mediterranean systems. For instance, Mendoza-Fernández et al. (2022) used MaxEnt to model the current and future distribution of a high-mountain endemic of the Sierra Nevada, revealing up to an 80 % decline in habitat suitability under worst-case climate scenarios. This underscores the technique's capacity to pinpoint vulnerable endemic species and guide conservation priorities in biodiversity-rich Mediterranean regions.

The present study therefore aims to (i) characterize the current spatial distribution of *O. compactum* and *O. elongatum* in northern Morocco and identify the key climatic variables shaping their niches, (ii) project future changes in suitable habitats under a severe climate scenario (SSP5-8.5, 2061–2080), and (iii) assess the resilience or vulnerability of each species to climate change and propose targeted conservation recommendations. To fill a major gap in current knowledge, this is the first study to conduct a comparative ecological niche analysis of these two endemic species in northern Morocco, coupling niche-equivalency testing with forward climate projections to provide spatially explicit conservation guidance. We hypothesize that the two taxa, despite their close relatedness, follow divergent ecological strategies, with *O. compactum* exhibiting narrower specialization and greater vulnerability, while *O. elongatum* displays broader ecological plasticity and higher resilience. Testing these expectations offers novel insights into how Mediterranean endemics respond to climate drivers, advancing both theoretical understanding of niche differentiation and practical strategies for conserving medicinal and aromatic plants under global change.

MATERIALS AND METHODS

Study area

The Tangier–Tetouan–Al Hoceima (TTA) region, situated in the far north of Morocco, brings together very contrasting landscapes and climates. Administratively it is divided into eight provinces—Tangier-Assilah, Tetouan, Al Hoceima, Larache, Chefchaouen, Ouazzane, Fahs Anjra, and M'diq-Fnideq (Figure 1). The area is bordered by the Mediterranean Sea to the north and the Atlantic Ocean to the west, while inland it is dominated by the Rif Mountains, whose rugged relief shapes both climate and vegetation.

Because of this geography, the region forms a patchwork of environments. Coastal plains and low valleys are generally humid and mild, whereas the interior is marked by steep mountain slopes, higher elevations, and drier valleys with a more continental influence. This sharp ecological gradient generates a wide range of microclimates and plant habitats, from coastal scrub to montane forests. As a result, the TTA region supports a remarkable

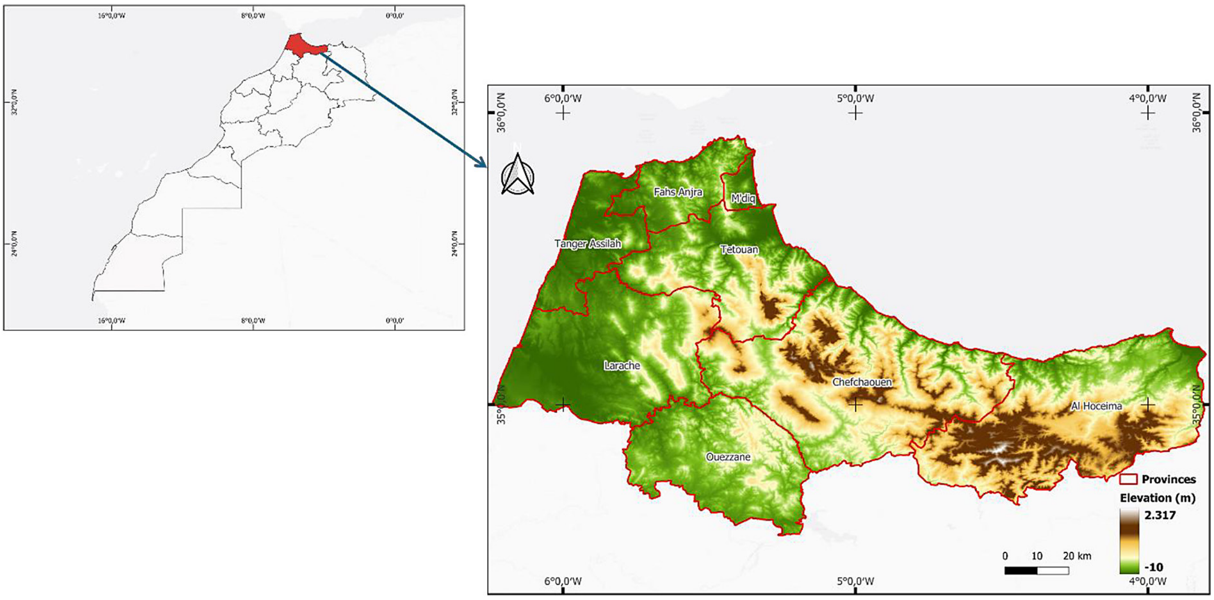

Figure 1. Geographic location of the study area

floristic richness, including numerous endemic species. For this reason, it represents a particularly valuable setting for studying ecological niche differentiation and for examining how Mediterranean endemics may respond to climate pressures.

Target species

This study focuses on two Moroccan endemics of the genus *Origanum* (Lamiaceae): *Origanum compactum* and *Origanum elongatum*. Both species are of considerable ecological and socio-economic value, yet they differ markedly in their ecological ranges and habitat requirements.

Origanum compactum is native to Morocco and southern Spain. Within Morocco, its distribution extends widely across the Rif, the Tangier area, the north-central and northwestern regions, as well as the southwest, the Haouz, and the foothills of the High Atlas (Valdés et al., 2002). The species thrives in dry, rocky habitats, sometimes beneath the partial shade of shrubs or trees, and typically flowers between June and August. It is commonly found in open woodlands, plains, and low limestone mountains, growing on well-drained soils up to 700 m. Ecologically, *O. compactum* is associated with the thermo-Mediterranean and meso-Mediterranean zones, spanning semi-arid to sub-humid bioclimates (Benabid, 2000).

In addition to its ecological presence, *O. compactum* has long been valued in Moroccan folk medicine for treating ailments such as diarrhea, urinary stones, hypertension, diabetes, and inflammatory conditions. Its essential oil dominated by carvacrol, thymol, p-cymene, and γ-terpinene has been widely investigated and is recognized for a broad range of pharmacological activities. Experimental work has confirmed antibacterial, antifungal, antioxidant, and anticancer properties of its extracts and oils (Aboukhalid et al., 2016; Bouyahya, Abrini, et al., 2017; Bouyahya et al., 2019; El Kharraf et al., 2021; Hamamouchi et al., 2021).

Origanum elongatum, by contrast, is a narrow endemic restricted to northeastern Morocco. Its range stretches from the Middle Atlas to the Rif Mountains, with notable populations in the Tazekka and Bouyablane massifs (Ietswaart, 1980). It generally occurs between 400 and 1500 m of altitude (Christaki et al., 2012), where it grows in open woodlands, on rocky mountain slopes, and in shrublands (matorrals), often on siliceous substrates with deep, well-drained soils. The species displays notable bioclimatic plasticity, being present in zones from semi-arid to per-humid, though it is most commonly associated with the thermo-Mediterranean and meso-Mediterranean belts (Benabid, 2000). Flowering occurs from June to October, producing erect stems topped with light white inflorescences whose abundance and sequential blooming give the plant significant ornamental value (Ietswaart, 1980).

From a pharmacological perspective, *O. elongatum* has received increasing attention. Its volatile compounds and extracts exhibit antibacterial, antifungal, antiviral, and antioxidant activities, while additional studies point to vasodilatory, hepatoprotective, and anticorrosive effects. Importantly, available toxicological assessments indicate no significant harmful effects, suggesting a favorable safety profile (Abdelaali et al., 2021).

Species occurrence data and environmental variables

The occurrence records of *O. elongatum* and *O. compactum* were compiled from both published literature (Aboukhalid et al., 2016; Bakha et al., 2020; Bouyahya, Abrini, et al., 2017; Bouyahya et al., 2019; El Harsal et al., 2018; El Kharraf et al., 2021; Ramzi et al., 2017) and the Global Biodiversity Information Facility (GBIF, http://www.gbif.org ; accessed 8 October 2024). To improve reliability, we retained only occurrences located inside the study area, defined by a geographic polygon, with valid coordinates, no geospatial inconsistencies, and confirmed presence status. In addition, we restricted the dataset to records provided by trusted institutions such as the Institut Botànic de Barcelona (CSIC-CMCNB), the Real Jardín Botánico (CSIC), the Department of Plant Biology and Ecology at the University of Seville, the Lund University Biological Museum, and the Plant Biodiversity Documentation Center (CeDocBIV), University of Barcelona.

After removing duplicates, anomalies, and erroneous records, the cleaned dataset included 52 occurrences of *O. elongatum* and 58 of *O. compactum*. Climatic and elevation data were then retrieved from the WorldClim 2.1 database at 1 km² resolution (Fick and Hijmans, 2017). These comprised 19 bioclimatic variables for both the current baseline (1970–2000) and future projections (2061–2080). Future scenarios were derived from the MIROC6 climate model under the high-emission pathway SSP5-8.5 (Shiogama et al., 2019). To reduce multicollinearity among predictors, we applied a Pearson correlation analysis and excluded variables with |r| ≥ 0.7 (Figure 2). Six variables were ultimately retained for modeling: mean annual temperature (Bio1), isothermality (Bio3), maximum temperature of the warmest month (Bio5), annual temperature range (Bio7), precipitation of the driest month (Bio14), and precipitation of the coldest quarter (Bio19).

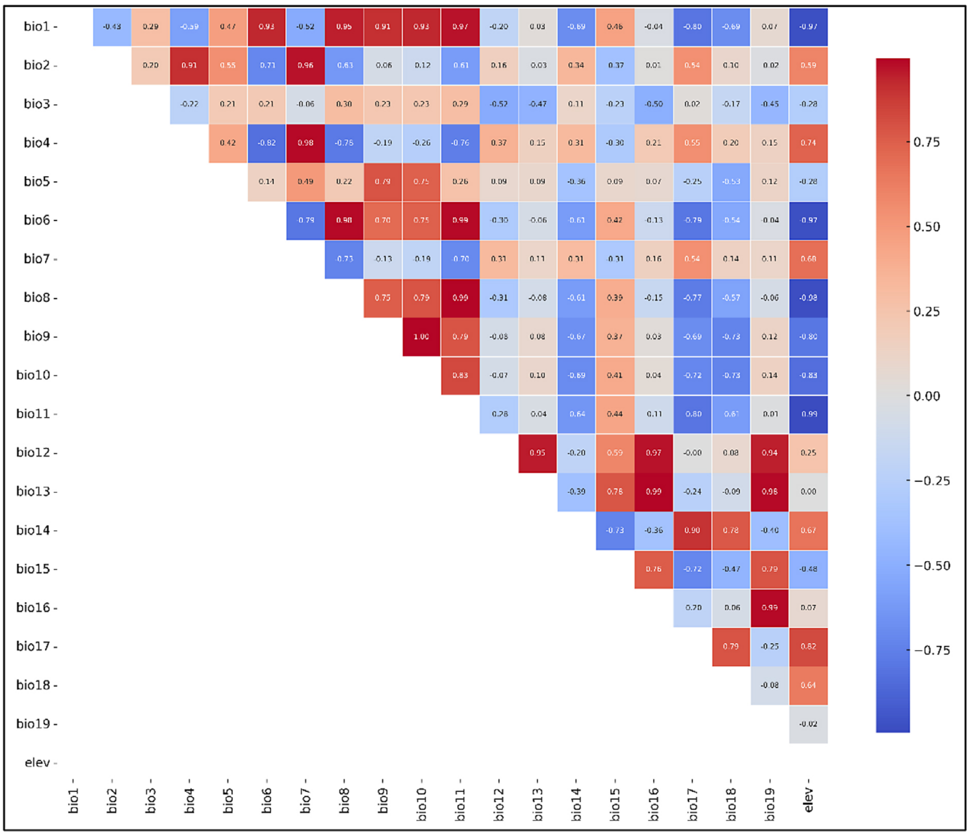

Figure 2. Correlation matrix of bioclimatic variables and altitude

Niche overlap, equivalency, and similarity analyses

For the ecological niche analysis, we applied the *ecospat* package in R (v.4.1-2) to describe the niches of the two focal species and to examine the contribution of environmental variables to their differentiation (Di Cola et al., 2017). To begin with, environmental data associated with species occurrence points were extracted using the *extract()* function of the *raster* package (v. 3.6-32). A principal component analysis (PCA) was then carried out on these variables independently for each species as well as for the combined dataset in order to identify which factors played the largest role in shaping ecological separation, with visualization performed through the *factoextra* package (v.1.0.7).

Niche overlap was quantified using Schoener's D index (Schoener, 1970). This metric takes values between 0 and 1, where 0 indicates a complete absence of overlap and 1 denotes identical niches. The index is calculated as:

$$D = 1 - \frac{1}{2}\sum_{i=1}^{n}\left|p_{i,1} - p_{i,2}\right| \quad (1)$$

where: $p_{i,1}$ and $p_{i,2}$ denote the environmental occupancy frequencies of species 1 and 2 in cell i of the environmental space. This metric provides a quantitative measure of niche similarity.

To further explore niche relationships, we performed equivalency and similarity tests. The equivalency test (*ecospat.niche.equivalency.test()*), based on 500 random permutations of occurrences, evaluates whether the niches of the two species are statistically identical. Equivalency is supported when the observed D value falls within the confidence range generated by the null distribution (Warren et al., 2008). The similarity test (*ecospat.niche.similarity.test()*) examines whether one species' niche is more similar to the other than expected by chance. It keeps the occurrences of one species fixed while generating simulated distributions for the other. A significant result is obtained when the observed D value is greater than the simulated values at the upper limit of the confidence interval (Sillero et al., 2022).

Model construction and distribution simulation

To model the distributions of *O. elongatum* and *O. compactum*, we generated 52 and 58 pseudo-absence points, respectively, matching the number of known occurrences. These occurrence and pseudo-absence data were then integrated with the environmental predictors to construct the models, using the R package *biomod2* (v.4.2-6-2).

We applied five modeling approaches: generalized linear models (GLM), generalized boosted models (GBM), artificial neural networks (ANN), random forests (RF), and maximum entropy models (MAXENT). For each run, 75% of the records were randomly selected for training and 25% for testing, repeated five times. Model performance was assessed with the Receiver Operating Characteristic curve (AUC) and the True Skill Statistic (TSS) metrics (Allouche et al., 2006).

Only models with strong predictive performance, defined as having TSS values above 0.8 and AUC values greater than 0.9, were retained for the construction of an ensemble model (EMmean) (Li et al., 2022). Predictions from these selected models were averaged, and the resulting ensemble was then used to map areas of potential habitat suitability under both current and future climate scenarios.

Predicted habitats were classified into four categories: highly suitable (0.75–1), moderately suitable (0.5–0.75), low suitability (0.25–0.5), and unsuitable (0–0.25) (Wan et al., 2024). To estimate the extent of suitable habitat under present and future conditions, analyses were carried out in R (v.4.2-3) using a 0.5 probability threshold, focusing on highly and moderately suitable habitats. Maps were produced in ArcGIS 10.3, and statistical plots in R (v.4.4-1) (R Core Team, 2024). Figure 3 provides an overview of the workflow for niche overlap analysis and distribution modeling of the two *Origanum* species.

RESULTS

Observed distribution of *O. elongatum* and *O. compactum*

In northern Morocco, the two species show contrasting distributions (Figure 4). *O. compactum* is mainly concentrated in the western provinces of Larache, Tétouan, Ouazzane, and central Chefchaouen, while *O. elongatum* occurs mostly in the east, particularly in the mountainous areas of Chefchaouen and Al Hoceima. An overlap zone in Chefchaouen indicates areas of coexistence, suggesting ecological transition or partial tolerance to similar environmental conditions.

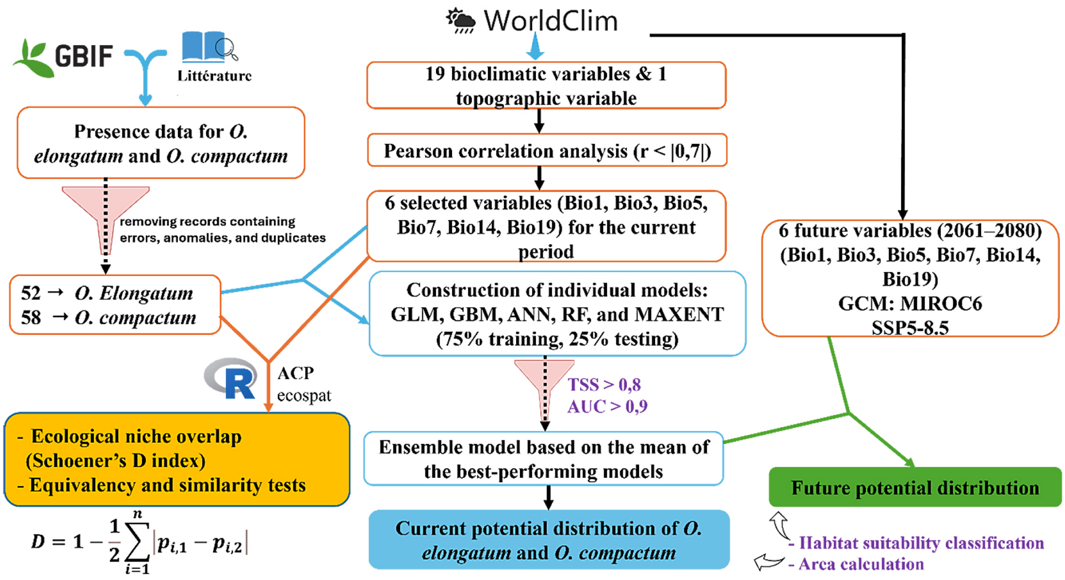

Figure 3. Workflow summarizing the methodology for ecological niche overlap analysis and the prediction of current and future potential distributions of *O. elongatum* and *O. compactum*

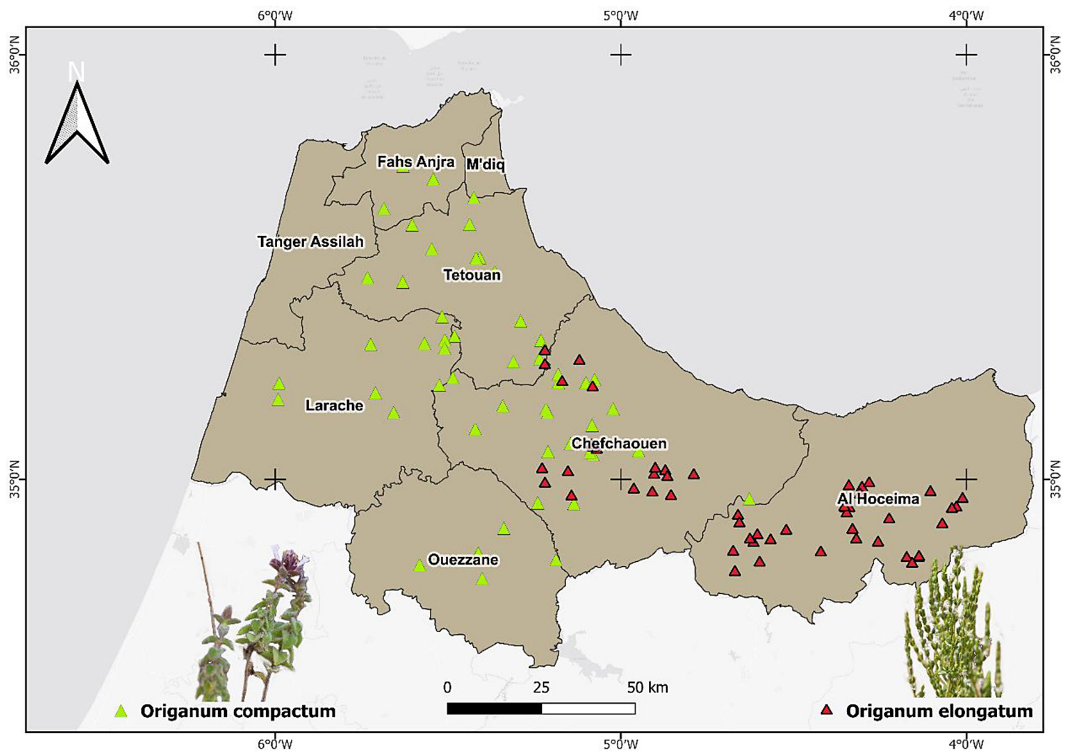

Figure 4. Current geographic distribution of *Origanum compactum* (green triangles) and *Origanum elongatum* (red triangles) in northern Morocco

Results of ecological niche analysis of *O. compactum* and *O. elongatum*

PCA highlighted contrasting ecological patterns between the two species, driven mainly by thermal and hydric gradients.

For *O. compactum*, the first two axes explained 75.2% of the variance (52.5% and 22.7%). PC1 was shaped by maximum temperature of the warmest month (Bio5), mean annual temperature (Bio1), isothermality (Bio3), and precipitation of the driest month (Bio14). PC2 reflected

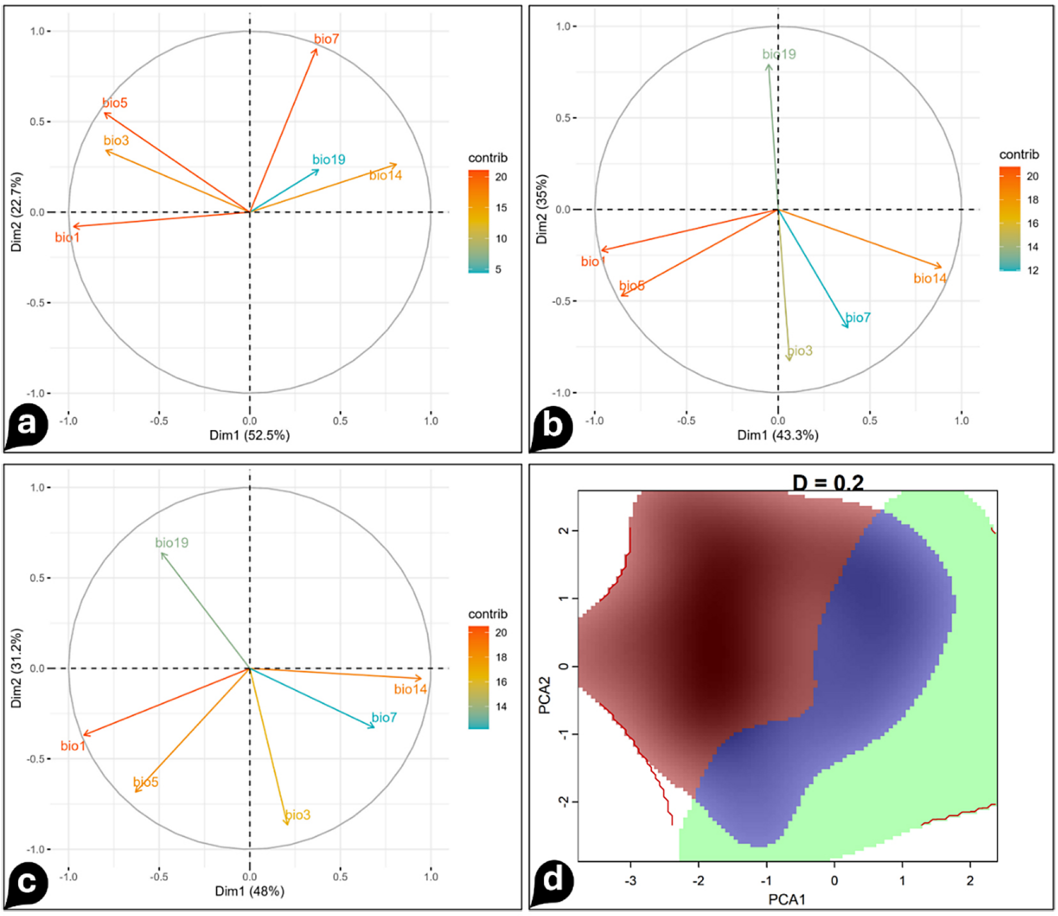

Figure 5. Ecological niche analysis of *O. compactum* and *O. elongatum*. (a–c) Contribution of bioclimatic variables to the first two PCA axes for *O. compactum* (a), *O. elongatum* (b), and both species combined (c).,arrow length indicates variable contribution, (d) Niche overlap in PCA space between *O. compactum* (green) and *O. elongatum* (red), based on six selected variables. Blue area shows overlap (Schoener's D = 0.2)

precipitation of the coldest quarter (Bio19) and annual temperature range (Bio7) (Figure 5a).

For *O. elongatum*, the first two axes explained 78.3% of the variance (43.3% and 35%). PC1 was driven by precipitation of the driest month (Bio14), maximum temperature of the warmest month (Bio5), and mean annual temperature (Bio1), while PC2 was influenced by precipitation of the coldest quarter (Bio19), isothermality (Bio3), and annual temperature range (Bio7) (Figure 5b).

When both species were analyzed together, PC1 (48%) reflected gradients of temperature and aridity, and PC2 (31.2%) reflected winter precipitation and thermal stability, explaining 79.2% of total variance (Figure 5c).

Niche overlap analysis showed clear separation between the climatic niches of the two species (Figure 5d). *O. compactum* (green) and *O. elongatum* (red) occupied largely distinct spaces, with limited overlap (purple). Schoener's D index was 0.2, indicating low overlap and strong ecological differentiation. The niche equivalency test confirmed significant differences (p = 0.001), while the similarity test showed that overlap was not higher than expected by chance (p = 0.001), reinforcing the conclusion of clear ecological specialization (Figure 6).

Ecological niche overlap and climatic preferences

Most bioclimatic variables showed moderate to high Schoener's D values, indicating varying levels of ecological overlap. The highest overlaps were observed for maximum temperature of the warmest month (Bio5, D = 0.80) and isothermality (Bio3, D = 0.63) (Figures 7b–c). In contrast, the lowest overlaps were for annual temperature range (Bio7) and precipitation of the driest month (Bio14), both with D = 0.49 (Figures 7d–e).

Climatic niche spectra revealed clear differences in environmental preferences. Thermally, *O.*

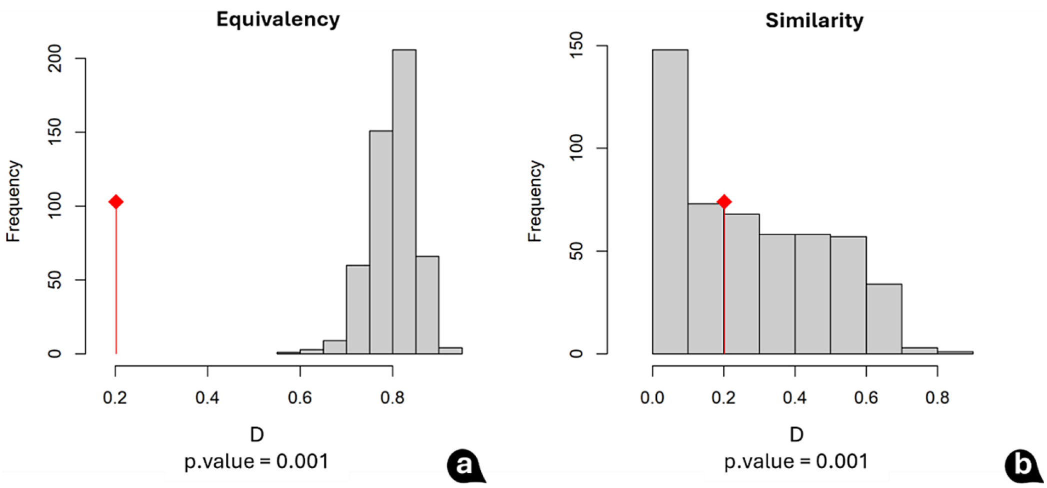

Figure 6. Niche equivalency (a) and similarity (b) tests between *O. compactum* and *O. elongatum*, based on Schoener's D index

compactum occurred in warmer conditions, with mean annual temperatures (Bio1) between 16–18 °C, while *O. elongatum* was more frequent in cooler sites, around 12–13 °C (Figure 7a). This pattern was consistent for Bio5, with *O. compactum* reaching up to 33 °C, whereas *O. elongatum* favored more moderate values (Figure 7c). The strong overlap for Bio5 (D = 0.8) suggests that, despite differing peaks, both species share part of this niche.

Isothermality (Bio3) reflects the ratio of daily to annual thermal variation (O'Donnell and Ignizio, 2012). *O. elongatum* was associated with higher values (~40–41%), indicating adaptation to environments with stable seasonal temperatures (Figure 7b). *O. compactum*, by contrast, occupied a broader range (36–41%), suggesting greater tolerance to daily vs. annual variability.

Annual temperature range (Bio7) proved a key axis of differentiation. *O. elongatum* was concentrated at higher values (28–30 °C), typical of environments with strong seasonal contrasts, while *O. compactum* peaked at moderate ranges

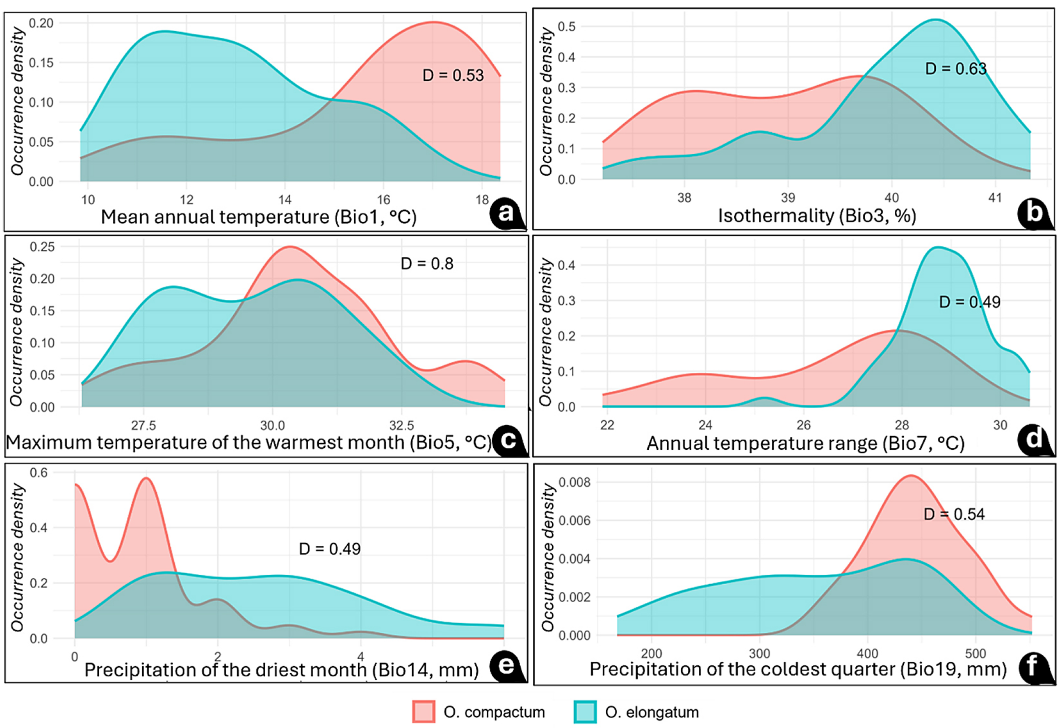

Figure 7. Climatic niche differentiation and overlap of *Origanum compactum* and *O. elongatum* across key bioclimatic variables

(22–27 °C), reflecting preference for more temperate, stable climates. The low overlap (D = 0.49) highlights its role in niche divergence (Figure 7d).

Regarding precipitation, *O. compactum* was more tolerant of arid conditions, with strong presence in areas of very low dry-season rainfall (Bio14) (Figure 7e). *O. elongatum*, in contrast, occupied broader and wetter niches. This pattern reversed for winter precipitation (Bio19): *O. compactum* was associated with higher rainfall (~400–500 mm), whereas *O. elongatum* occurred more often in drier sites (Figure 7f). In summary, density curves across bioclimatic gradients show marked ecological differences. *O. elongatum* exhibited broader tolerance to both thermal and hydric conditions, particularly for Bio1, Bio3, Bio14, and Bio19, reflecting adaptation to variable climates. *O. compactum*, on the other hand, displayed narrower ranges, especially for Bio5, Bio14, and Bio19, suggesting specialization in more restricted environments.

Performance of individual models and the ensemble model

Evaluation of individual models showed variable performance across algorithms and species. For *O. compactum* (Figure 8a), mean AUC values ranged from 0.79 ± 0.12 for ANN to 1.00 for RF, while TSS values ranged from 0.60 ± 0.11 to 1.00. GBM (AUC = 0.99; TSS = 0.906 ± 0.01) and MAXENT (AUC = 0.875 ± 0.10; TSS = 0.70 ± 0.10) also performed well. GLM showed moderate values (AUC = 0.86 ± 0.13; TSS = 0.634 ± 0.17) with higher variability.

For *O. elongatum* (Figure 8b), performances were generally higher. All algorithms yielded AUC > 0.90 and TSS > 0.73, with low dispersion. RF achieved perfect performance (AUC = 1.00; TSS = 1.00), followed by GBM (AUC = 0.99; TSS = 0.883 ± 0.12) and GLM (AUC = 0.95 ± 0.02; TSS = 0.845 ± 0.11). ANN (AUC = 0.91 ± 0.01; TSS = 0.825 ± 0.01) and MAXENT (AUC = 0.922 ± 0.02; TSS = 0.734 ± 0.10) also maintained high performance.

Individual models with excellent results, defined as TSS > 0.8 and AUC > 0.9, were retained for ensemble modeling. Based on these criteria, only GBM and RF were selected. The ensemble model was then constructed by averaging predictions from these two algorithms.

Impact of climate change on the spatial distribution of suitable habitats for *O. compactum* and *O. elongatum*

The current potential distribution of *O. compactum* is concentrated in northwestern Morocco, with highly suitable habitats mainly located in the provinces of Tétouan and Chefchaouen and adjacent areas. Highly suitable habitats currently cover about 4980 km², representing the dominant category of favorable areas. Moderately and low suitable habitats cover 526 km² and 667 km², respectively, while unsuitable areas total around 9871 km² (Figure 9a). Under climate change, a significant shift in the ecological niche of the species is projected. Future distribution maps (Figure 9b) show a sharp contraction of highly suitable habitats, decreasing by more than 87%, from 4980 km² to only 626 km². This decline mainly affects higher mountain zones. Conversely, moderately and low suitable habitats expand markedly, reaching 1938 km² (+268%) and 3392 km² (+408%), respectively, suggesting both altitudinal and latitudinal shifts in favorable climatic conditions. Overall dynamics of suitable habitats

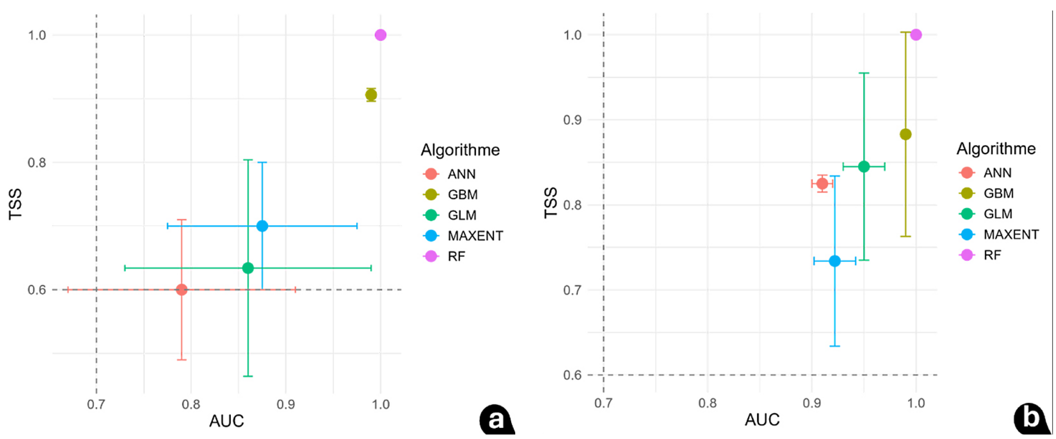

Figure 8. Distribution model performance for *O. compactum* (a) and *O. elongatum* (b) based on AUC and TSS

(Figures 9c–d) also indicate an increase in unsuitable areas, projected to reach 10,117 km². Thus, *O. compactum* may lose much of its optimal habitat while marginally favorable zones expand—potentially less stable over the long term.

The current potential distribution of *O. elongatum* is mainly concentrated in the central and eastern Rif of Morocco, particularly in Al Hoceima Province, with highly suitable habitats covering about 3.688 km². Moderately and low suitable habitats cover 308 km² and 185 km², respectively, while unsuitable areas represent nearly 11,868 km² (Figure 10a). Future climate projections indicate a dramatic shift. Highly suitable habitats are expected to shrink by nearly 89%, from 3.688 km² to only 407 km², signaling a severe loss of optimal niches. In contrast, low-suitability areas expand sharply, reaching 6.340 km² (compared with only 185 km² at present), suggesting a shift toward marginal or lower-altitude habitats. Moderately suitable areas also increase to 1.221 km², nearly four times their current extent (Figure 10b). Overall habitat dynamics (Figure 10c) highlight a major ecological transition, marked by contraction of optimal habitats and partial compensation through gains in lower-quality habitats. Unsuitable areas are reduced to 8.107 km², reflecting the emergence of new colonizable but less ecologically favorable zones (Figure 10d).

DISCUSSION

Ecological niche differentiation and adaptive responses

Climatic niche analysis of *O. compactum* and *O. elongatum* revealed marked differentiation between the two species. The relatively low global Schoener's D values (D = 0.53 for Bio1, and as low as 0.49 for some variables), along with significant results from equivalency and similarity tests ($p = 0.001$), indicate that the two species occupy partially distinct ecological niches with specific environmental preferences.

For *O. compactum*, the niche is closely linked to thermal variables such as maximum temperature of the warmest month (Bio5), mean annual temperature (Bio1), and isothermality (Bio3). This species appears adapted to moderately warm to temperate environments with lower thermal variability. Previous studies reported its occurrence mainly in semi-arid to subhumid bioclimatic zones, both warm and cool variants, within thermomediterranean and mesomediterranean vegetation belts (Aboukhalid et al., 2017; Bouyahya, Guaouguaou, et al., 2017). In contrast, *O. elongatum* shows stronger affinity for arid conditions, particularly low dry-season

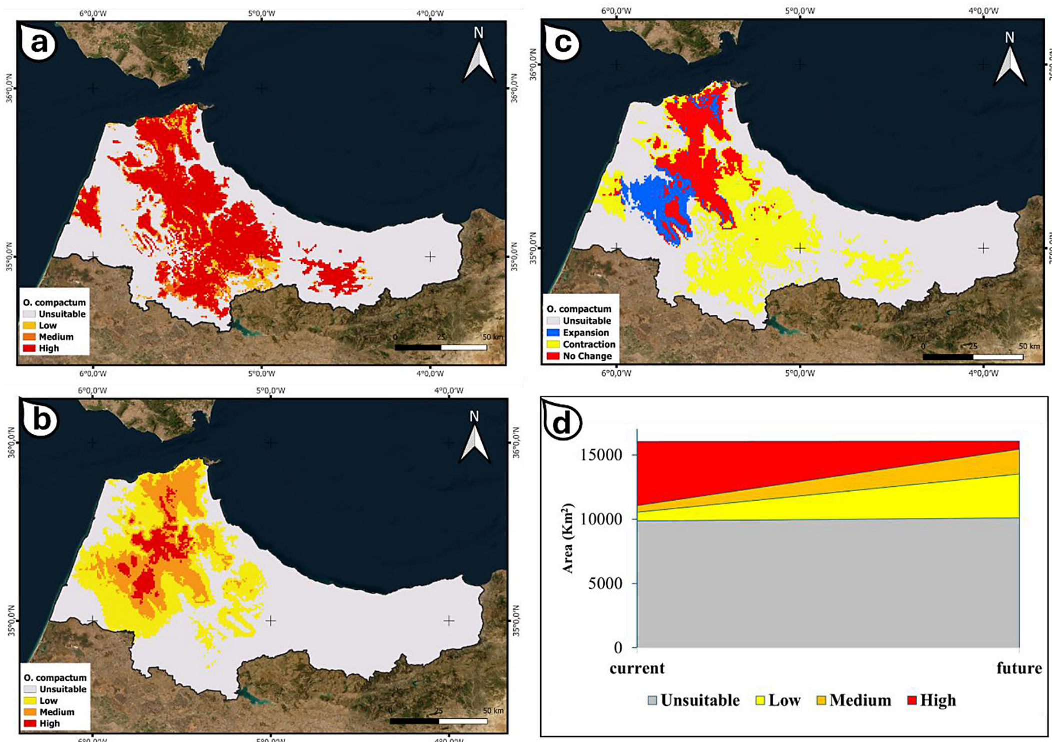

Figure 9. Current (a) and projected (b) potential distributions, and spatial dynamics of suitable habitats (c, d) for *O. compactum*

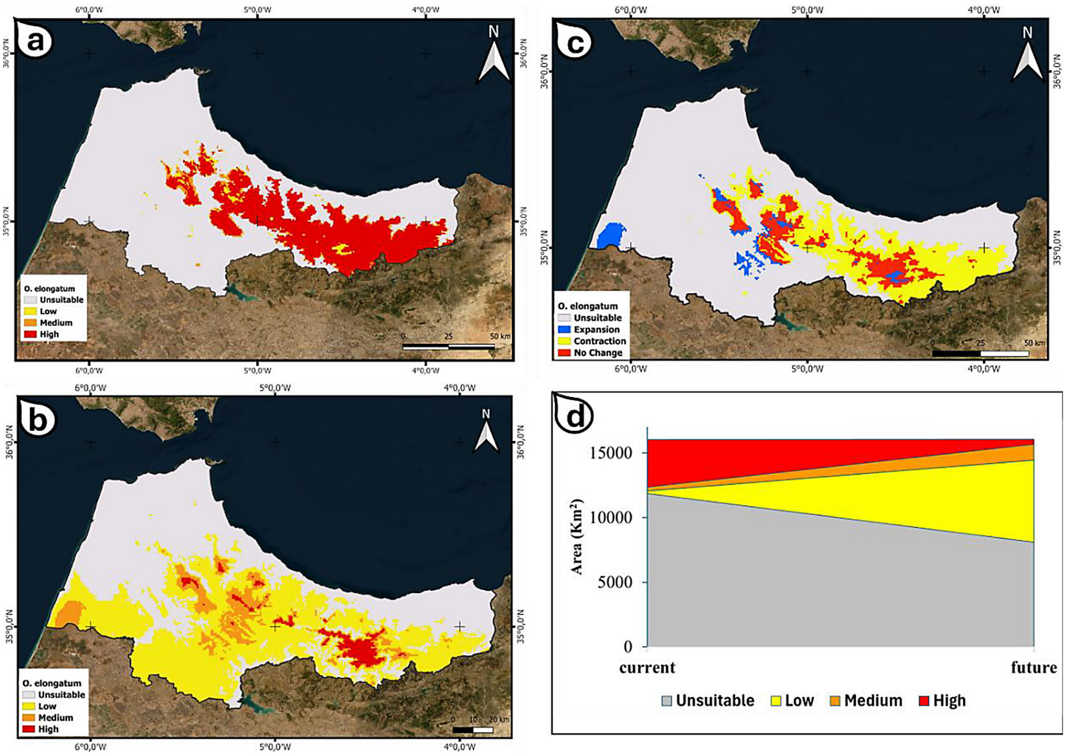

Figure 10. Current (a) and projected (b) potential distributions, and spatial dynamics of suitable habitats (c, d) for *O. elongatum*

precipitation (Bio14) and high annual temperature range (Bio7), reflecting greater tolerance to climatic fluctuations. This tolerance is consistent with field observations of *O. elongatum* thriving in temperate continental climates, where winters are cold and summers hot, although with limited growth in size (Abdelaali et al., 2021).

PCA confirmed that temperature and aridity gradients largely structure species distributions, while niche breadth analysis highlighted contrasting tolerances. *O. elongatum* exhibited broader tolerance ranges, especially for Bio1, Bio3, Bio14, and Bio19, suggesting higher ecological plasticity and the ability to occupy diverse habitats. Conversely, *O. compactum* showed narrower preferences, particularly for precipitation-related variables (Bio14 and Bio19), suggesting greater vulnerability to hydric regime changes (Aboukhalid et al., 2017).

Responses of *Origanum* species to climate change

Climate strongly influences where species can occur, determining both the breadth of their ecological niches and their adaptive potential (Pecl et al., 2017). Across Africa, rising temperatures and declining precipitation are driving the expansion of arid zones (World Meteorological Organization (WMO), 2020). Morocco is no exception, with projections of higher temperatures, more frequent extreme events, and reduced rainfall (Driouech et al., 2010)..

Our projections show substantial shifts in suitable habitats for both *Origanum* species under future scenarios (SSP5-8.5, 2061–2080). Both are projected to face habitat loss and fragmentation, processes known to reduce genetic diversity and increase extinction risk (Pecl et al., 2017).. The situation appears more critical for *O. compactum*, with a projected loss of nearly 87% of its highly suitable habitat. Although low- and moderately suitable areas expand, they do not compensate for the loss of optimal zones, indicating a contraction of core habitat. *O. elongatum* also loses a large share of highly suitable habitats (-89%), but this is offset by major expansions of marginal habitats (+408% for low, +300% for moderate), reflecting greater adaptability due to its broader niche.

Species respond differently to environmental change depending on their niche strategies, resource use, and adaptive capacities (Fei et al., 2017). Our results highlight contrasting vulnerabilities: *O. compactum* appears more at risk due to its specialization in temperate, stable climates, with strong dependence on specific precipitation regimes (Bio14 and Bio19) and moderate maximum summer temperatures (Bio5), all of which are highly sensitive to climate change. *O. elongatum*, in contrast, is structured by more dynamic variables such as annual temperature range (Bio7), isothermality (Bio3), and dry-season precipitation (Bio14), for which it shows broader tolerance, conferring greater resilience to projected changes.

Finally, these projections are based solely on climatic variables and do not account for anthropogenic pressures. In reality, deforestation, urbanization, and habitat fragmentation may further exacerbate declines. Conservation strategies should therefore be species-specific: for *O. compactum*, priority should be given to protecting residual highly suitable areas and exploring restoration in marginal habitats. For *O. elongatum*, maintaining ecological connectivity among newly favorable zones will be key to supporting natural dispersal and persistence.

CONCLUSIONS

In this study, we aimed to better understand the current and future spatial distribution of two Moroccan endemic Lamiaceae species, *Origanum compactum* and *O. elongatum*, as well as the environmental factors shaping their ecological niches. Our results revealed clear differentiation between the two species, both in terms of key climatic drivers and ecological ranges. *O. compactum* is specialized in temperate and humid conditions, whereas *O. elongatum* shows broader tolerance to arid and thermally contrasting environments.

Future climate projections indicate substantial losses of highly suitable habitats for both species, with *O. compactum* being more severely affected. In contrast, *O. elongatum* appears to exhibit greater ecological resilience due to its plasticity, reflected in the marked expansion of moderately and low suitable habitats. These contrasting dynamics highlight the need to account for the specific ecological requirements of each species when designing conservation strategies.

Beyond climate projections, our study emphasizes the importance of integrating adaptive approaches into the management of local plant genetic resources. In the context of increasing anthropogenic pressure and global warming, the preservation of favorable niches, ecological restoration of marginal areas, and in situ protection of natural populations should be prioritized to ensure the long-term sustainability of these species of high cultural, ecological, and economic value.

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