Received: 28 June 2024 | Accepted: 11 September 2024

DOI: 10.1111/icad.12784

ORIGINAL ARTICLE

Insect Conservation and Diversity

Royal Entomological Society

Mitigating the extinction risk of globally threatened and endemic mountainous Orthoptera species: *Parnassiana parnassica* and *Oropodisma parnassica*

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Funding information
Management Agency of Parnassos National Park (NECCA), Grant/Award Number: 5032966; Hellenic Foundation for Research and Innovation, Grant/Award Number: 11266

Editor: Raphael K. Didham and Associate Editor: Og DeSouza

Abstract

1. Orthoptera species are vulnerable to extinction on a global scale. Greece hosts 35% (380 species) of the European Orthoptera fauna with a high degree of endemic (37%) and threatened species (37%).
2. We sampled 46 plots (100 m^2) to investigate the distribution and ecological requirement of two Greek mountain endemic and red-listed species: *Parnassiana parnassica* (Ramme, 1926; Orthoptera: Tettigoniidae; Critically Endangered [CR]) and *Oropodisma parnassica* (Scudder, 1897; Orthoptera: Caelifera; Endangered [EN]). Species had a restricted geographical range, with two isolated populations confined to high altitudes (1527–2320 m) of Mts. Parnassos and Elikonas.
3. Species distribution models showed that slope affected their suitable habitat, together with the topographic position index and the annual temperature range (*P. parnassica*), and the amount of green vegetation and evapotranspiration (*O. parnassica*).
4. Connectivity analysis showed that *P. parnassica*-suitable habitat consisted of few larger and well-connected patches (26 patches: effective mesh size of 1.57 km^2) and that *O. parnassica*-suitable habitat consisted of more but smaller and less connected patches (56 patches: effective mesh size of 0.3 km^2).
5. Generalised linear models showed that the population density of *P. parnassica* was negatively influenced by the height of herbaceous vegetation and that of *O. parnassica* was positively influenced by altitude.
6. The species face three main imminent threats: land take, wildfires and global warming, whereas livestock grazing seems to have a positive impact and skiing a neutral impact on their populations.
7. We assessed both species as EN after International Union for Conservation of Nature (IUCN) criteria and a suite of conservation measures are suggested for their status improvement.

KEYWORDS
bush crickets, connectivity, endemism, grasshoppers, habitat suitability, insects, IUCN, mountain ecosystems, threats

INTRODUCTION

Insects represent the largest percentage of the world's organisms with consensus estimates calculating up to 5.5 million species globally (Stork, 2018). They are key components in the provision, regulation and dynamics of many ecosystem services, such as pollination, pest control and nutrient recycling (Noriega et al., 2018). Over 40% of insect species are in decline due to habitat loss stemming from intensive agriculture and artificial land generation, pesticide use, invasive species and climate change (Goulson, 2019) Data from the International Union for Conservation of Nature (IUCN) on the extinction risk of 12,568 insect species pinpoints that a quarter of them are near-threatened, threatened or extinct (IUCN, 2024), while one third of the insects with documented population trends show declining population trends (Dirzo et al., 2014).The documented decline in insect biomass can trigger negative cascading effects on food webs and ecosystem services (Hallmann et al., 2017; Yang & Gratton, 2014). Insect extinctions will impact the ecosystem in its entirety, as insects are interconnected with many vital roles, a risk that has been strongly highlighted worldwide (Cardoso et al., 2020).

Orthoptera is an important insect group counting about 30,000 species globally (Cigliano et al., 2024) that plays a pivotal role in food webs as a food source for vertebrates (Belovsky & Slade, 1993; Parr et al., 1997) and arthropod predators (Curry, 1993). They have specific microhabitat preferences (Guido & Gianelle, 2001) and are related to vegetation structure (Poniatowski & Fartmann, 2008), rendering them good indicators of ecosystem naturalness (Aleksanov et al., 2023; Báldi & Kisbenedek, 1997), vegetation succession (Marini et al., 2009; Schirmel et al., 2011) and microclimatic gradients at fine scale (Gardiner & Hassall, 2009). They are the fourth most-threatened order globally (after Trichoptera, Coleoptera-dung beetles and Lepidoptera) (Sánchez-Bayo & Wyckhuys, 2019), and more than one third of them are red-listed at a global scale (35%: 520 species) (IUCN, 2024). In Europe, one fourth of its Orthoptera fauna is threatened (270 species) due to human pressures such as livestock grazing, arable farming, increasing wildfire frequencies and touristic development (Hochkirch et al., 2016). In Greece, 37% of the Orthoptera fauna is threatened, and this higher degree of threat is of particular conservation importance at regional and global scale, given the great species richness of the country (380 Orthoptera species: over one third of European species) and its high degree of endemism (37%: 141 endemic species) (Willemse et al., 2018). Research and conservation actions for the 90 endemic and threatened Orthoptera species in Greece should be a top priority, as the improvement of their population status would lead to the improvement of their global assessment.

The globally threatened and endemic Orthoptera species of Greece have a very restricted geographic range and they are encountered in 'ecological islands' (Kenyeres et al., 2009), namely in caves, islands and high mountains. Remote mountainous ecosystems are understudied despite their great ecological value (EEA, 2010), their value as centres of endemism and as refugia for species in the light of climate change (Schickhoff et al., 2021; Spehn et al., 2010). A synergy of elevational gradients and dynamics in climate, hydrology and water chemistry contributes to the formation of a high diversity of microhabitats, hosting numerous species in comparably small areas (McCain & Colwell, 2011), also explaining their high degree of endemism (Rahbek et al., 2019). Mountains offer valuable opportunities to study species distributions and the mechanisms influencing them (Barve & Dhondt, 2017; Graham et al., 2014), but these ecosystems are fragile, holding the greatest proportion of species facing imminent extinction (46% of trigger species) (IPBES, 2018) and particularly so in the Mediterranean, which faces a more pronounced warming (Cramer et al., 2018).

Montane endemic Orthoptera species are often known only from a few localities where they were recorded several decades ago (Willemse et al., 2018), and the ecological gap in knowledge is substantial. Their risk assessment after the IUCN criteria has so far relied mainly on the restricted geographic range (criterion B), in combination with other criteria (IUCN SPC, 2024) that are usually rated through expert opinion and rarely so on a quantitative basis (Kati et al., 2006). Such assessments involve de facto some degree of subjectivity, given that information is largely missing and can only be inferred. There is a pronounced need to collect extensive field data for poorly known species, to employ quantitative tools to assess their current and potential distribution, their habitat quality and fragmentation and to gain a deeper understanding of the ecological requirements of the species at a fine scale, under the scope to guide well-informed conservation actions mitigating species extinction risk (Jackson & Robertson, 2011; Thomaes et al., 2008). Several modern tools are available in this direction. Species distribution models (SDMs) are one of them (Araújo & New, 2007; Marmion et al., 2009), combining species occurrence records with a set of environmental predictor variables to predict potential distributions, allowing extrapolation in space and time (Elith & Leathwick, 2009; Peterson, 2001). Furthermore, understanding and quantifying habitat fragmentation and its effect on species populations is essential for directing management and conservation actions (Miller-Rushing et al., 2019), particularly for species with restricted geographic ranges (May et al., 2019). Small, spatially isolated patches may not be able to sustain viable subpopulations (Haddad et al., 2015), although this remains a subject of debate (Fahrig et al., 2019). For instance, deciding whether a population is 'severely fragmented' or not after the IUCN criteria should rely on a quantitative analysis of the connectivity of suitable habitat patches.

Our study focuses on two high-altitude Orthoptera species of Greece that are endemic and globally threatened, namely *Parnassiana parnassica* (Ramme, 1926; Critically Endangered [CR]) and *Oropodisma parnassica* (Scudder, 1897; Endangered [EN]) (Willemse, Hochkirch, Heller, et al., 2016; Willemse, Hochkirch, Kati, et al., 2016). The genus *Parnassiana* is entirely endemic to Greece, comprising 13 mountain-dwelling species that are all red-listed and hence globally threatened (Hochkirch et al., 2016). They are small to medium-sized (14–18 mm), cryptic, short-winged bush crickets, with adults usually appearing August. They produce a song consisting of scratching sounds lasting 0.5–2.5 s, typically produced in the evening and the night (Willemse et al., 2018) The genus *Oropodisma* comprises 10 mountain-dwelling species, that are all, except one, Greek endemics and are all red-listed

(Hochkirch et al., 2016). They are also small to medium-sized (13–23 mm), compact, apterous grasshoppers, appearing in adult form in August, with no sound production documented (Willemse et al., 2018). *Parnassiana parnassica* and *O. parnassica* are known to be genetically distinct from the other species of the same genera (Grzywacz et al., 2017; La Greca & Messina, 1976). Each species has been reported so far only from two to three localities and has been considered to exhibit a declining population trend due to various pressures such as livestock grazing and tourism (Willemse, Hochkirch, Heller, et al., 2016; Willemse, Hochkirch, Kati, et al., 2016). This is the first ecological study for the target species and any species of the genera *Parnassiana* and *Oropodisma*. We aim to provide an integrated picture of the ecological profile of the two species and apply quantitative tools in the assessment process of the conservation status of the species, as a guideline for other poorly known species with restricted geographic ranges. We set five distinct objectives for both target species: (1) delineate their current distribution pattern; (2) model their potential global distribution based on habitat suitability mapping; (3) quantify the connectivity of suitable habitat patches, reflecting the degree of habitat fragmentation; (4) investigate the environmental factors that shape suitable habitat and affect species population density; (5) update the IUCN Red List status of the species after IUCN criteria and (6) synthesise our findings in concrete measures for the conservation of the species from a conservation management perspective.

MATERIALS AND METHODS

Study area

The study area comprises the global distribution range of the two target species, according to IUCN assessments (Willemse, Hochkirch, Heller, et al., 2016; Willemse, Hochkirch, Kati, et al., 2016). It encompasses two mountains of central Greece: Mt. Parnassos (268 km^2) ranging from 800 to 2457 m, and Mt. Elikonas (150 km^2), being a complex of minor mountains (500–1748 m) (Figure 1).

The climate is continental: the mean annual temperature for the years 2021–2023 was 13.8°C (±3.5°C) (temperature range from −7°C to 32°C), and the mean annual rainfall was 1000 mm (±73 mm) (NOA, 2024). Endemic fir forests (*Abies cephalonica*) dominate at mid-altitudes in the two mountains, interspersed with pine stands (*Pinus nigra*) on Mt. Parnassos, whereas the zone above the tree line includes mountainous grasslands, heaths and rocky slopes. Mt. Parnassos has been declared a national park since 1938, currently being a site of the Natura 2000 network of protected areas in Europe (GR2450005), hosting 35 habitat types and rich fauna and flora (SDF, 2020), but Mt. Elikonas is under no protection status. Livestock grazing and tourism are the two main human activities above the tree line on Mt. Parnassos, where the oldest and largest ski resort in Greece is located. No such activities occur on Mt. Elikonas, but there are plans for constructing wind power stations (RAE, 2024).

Orthoptera sampling

We carried out field surveys for three consecutive years (2021, 2022, and 2023) during August, that is, at the peak adult activity period of the species (Willemse et al., 2018). We surveyed a total of 103 sites within the study area (Figure 1). We attempted to cover different localities deemed adequate microhabitats for the species across the distribution range of the species, that is, mountainous grasslands above the tree line and forest clearings. We employed the time-constrained visit method, actively searching for the target species in each site for 45 min (46 sites with species occurrence). In almost all cases, upon encountering the species, we delineated a quadrat of a standard area of 100 m^2 and counted the number of individuals (40 quadrats). Quadrats were spaced at least 100 m apart, given the low dispersal ability of both flightless target species (Reinhardt et al., 2005).

Microhabitat parameters

We recorded 12 microhabitat parameters at each quadrat with species occurrence (Table 1): altitude (Al), slope (Sl) and the ground cover of soil (So), rocks (R), stones (St) and vegetation (Vg). Vegetation included herbaceous plants (Hcover), characterised by non-woody stems or roots, and robust herbaceous plants and shrubs (Rpcover), distinguished by either a woody stem or a woody base or both following the definitions provided by (Strid, 1986). Plant species identification was mainly conducted in situ, and some specimens were collected and identified in the lab using a stereoscope. We also considered the vegetation structure in the plot by measuring the mean and maximum height of both herbaceous (Ghmean, Ghmax) and robust/shrubby vegetation (Rpmean, Rpmax).

Environmental data

We considered a dataset of 27 variables, including 22 bioclimatic, 4 topographic and 1 vegetation-related variable, at a spatial resolution of 100 × 100 m cells (Table S1). We calculated the bioclimatic variables used in the SDMs with the ClimateEU v4.63 (Marchi et al., 2020), the 'dismo' 1.1.4 (Hijmans et al., 2017) and 'envirem' 2.2 (Title & Bemmels, 2018) R packages, adhering to methodologies described in Hamann et al. (2013), Marchi et al. (2020) and Wang et al. (2012). We calculated topographical metrics using functions from 'raster' 2.6.7, 'terra' 1.7.46 (Hijmans, 2023), and 'spatialEco' 1.2-0 R packages (Evans, 2019). We tested variables for collinearity, using Spearman rank correlation (<|0.7|) and variance inflation factors (VIF <5) (Dormann et al., 2013) with the 'collinear' 1.1.1 R package (Benito, 2023). We used a set of 12 independent variables to feed the SDMs (nine variables per species) (Table S1).

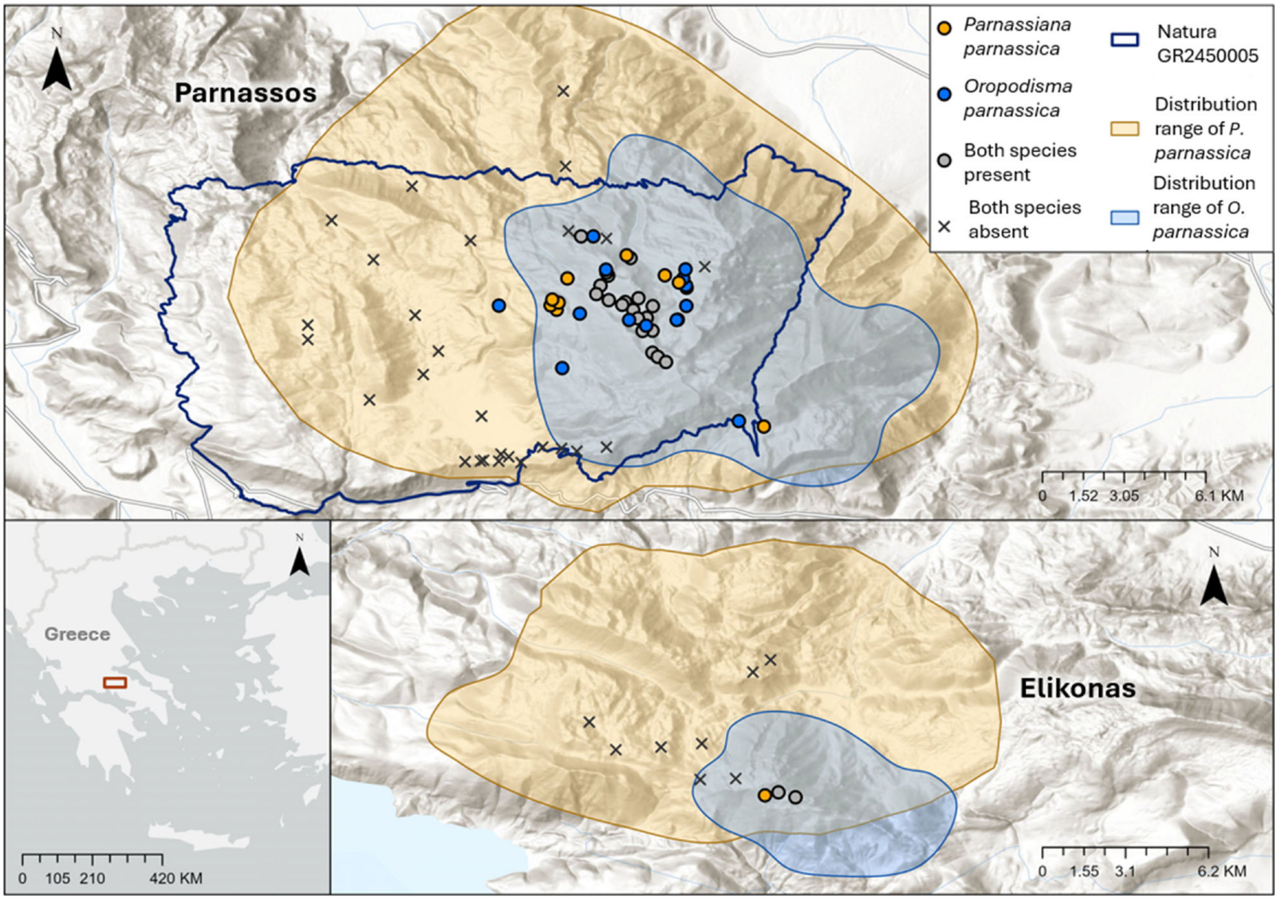

FIGURE 1 Study area across the distribution ranges of the target species at Parnassos and Elikonas Mts., and localities visited in the period 2021–2023: Presence of *P. parnassica* (orange dot), *O. parnassica* (blue dot), species co-occurrence (grey dot) and species recorded absence (cross).

Data analysis

Current distribution area and related metrics

To delineate the current distribution area of each species, we considered a buffer zone of 1 km around the species occurrences and calculated the merged area of the zones. We utilised all presence data to calculate the area of occupancy (AOO) and the extent of occurrence (EOO), using the Geospatial Conservation Assessment Tool (GeoCAT) (Bachman et al., 2011). The AOO is a scaled metric that represents the area of suitable habitat currently occupied by the taxon and is calculated as the sum of occupied cells of 2 × 2 km, often reflecting the population size of the taxon. The EOO is a measure of the spatial spread of the areas currently occupied by the taxon, including areas of non-suitable habitats. It is calculated as the area contained within the shortest continuous imaginary boundary encompassing sites of present occurrence and reflects the spread of risks from threatening factors across the taxon's geographical distribution area (IUCN SPC, 2024).

Species distribution models

We used species distribution modelling to predict the suitable habitat of both target species within their distribution ranges. First, we cleaned the data utilising the 'clean_coordinates' from the 'CoordinateCleaner' 2.0.18 R package (Zizka et al., 2019). We then removed duplicate occurrences using the 'elimCellDups' function from the 'enmSdm' 0.5.3.3 R package (Smith, 2020), followed by spatial thinning of the data with the 'thin' function from the 'spThin' 0.1.0 R package (Aiello-Lammens et al., 2015), as per Aiello-Lammens et al. (2015) and Robertson et al. (2016). The final dataset comprised 33 records for each species at a scale of 100 × 100 m cells.

Second, as the occurrence-to-predictor ratio for both species was below 10:1, we employed an ensemble of small models (ESMs) to precisely model their realised climatic niches, as ESMs were developed to build reliable and robust SDMs for rare species (Breiner et al., 2015). We specifically utilised the Random Forest algorithm via the 'ecospat' 3.1 R package (Broennimann et al., 2021). Pseudo-absences were generated with the 'sample_pseudoabs' function from the 'flexsdm' 1.3.3 R package (Velazco et al., 2022), within a geographical buffer and were environmentally constrained (Barbet-Massin et al., 2012). We then partitioned data into four blocks of presences and pseudo-absences, using the 'BIOMOD_CrossValidation' function from the 'biomod' 4.2.4 R package (Thuiller et al., 2023). Third, we evaluated model performance with several metrics following the recommendations of Collart et al. (2021) and Konowalik and Nosol (2021). Fourth, we selected only the models with a value of True Skill Statistic (TSS)

≥0.4 (Liu et al., 2016) out of 36 ESMs produced for each species, to generate binary maps (presence–absence).

Fifth, we produced the final species maps (habitat suitability and binary maps) by excluding the cells that had high extrapolation values. There are two types of extrapolation: univariate (which extends beyond the observed training conditions) and combinatorial (which occurs within the observed range of training conditions). We created the extrapolation uncertainty maps by employing the 'Shape' metric using the function 'extra_eval' from the 'flexsdm' 1.3.3 R package (Velazco et al., 2022). In line with guidelines from Velazco et al. (2024), we investigated several distance thresholds for both species regarding their extrapolation values (the following values represent in order the p25, median, p75, p100: *O. parnassica*: 28.8, 37.5, 48, 353; *P. parnassica*: 35.1, 44.9, 56.8, 359) for model prediction truncation. This strategy provides a safeguard against potential prediction errors (Elith et al., 2010). Considering the extreme rarity and limited geographic distribution of the target species, we generated habitat suitability maps setting thresholds at 28.8 for *O. parnassica* and 35.1 for *P. parnassica* (Velazco et al., 2024). As a result, we assigned these high extrapolation areas a suitability value of 0, indicating their exclusion from the models' predictive capabilities.

The model was tested with the preliminary dataset of species occurrence collected during the first 2 years (56 occurrences in total). It indicated 10 sites (100 × 100 m cells) of high habitat suitability for both species (top 20%) that were not covered by our sampling. We visited them in the year 2023 and found *P. parnassica* in 9 sites and *O. parnassica* in all 10 sites.

Suitable habitat patch connectivity

We calculated the connectivity of suitable habitat patches by computing the number of patches, the patch cohesion index (Schumaker, 1996), the patch area and the effective mesh size (McGarigal, 2002), using the 'landscapemetrics' 2.0.0 R package (Hesselbarth et al., 2019). Greater values of the patch cohesion index and the effective mesh size indicate less fragmented suitable habitat.

Generalised linear models

We used generalised linear models to identify the microhabitat parameters (explanatory variables) that potentially influence the target species population density (response variable). Thirteen explanatory variables were considered, including 12 continuous variables derived from quadrat sampling and 1 nominal variable representing sampling sites (Table 1).

We created two datasets, each one corresponding to a target species, and we ran the models for each one. To select the environmental variables, first, we tested for multi-collinearity using Spearman rank correlation ($r < |0.55|$) and VIF (<5) (Dormann et al., 2013). Second, we checked for influential values (outliers) and one record was omitted from the dataset of *P. parnassica*. In the *O. parnassica* dataset, no participant coefficient had a Cook's distance value over 1, so all observations were retained in the model (Cook, 2011). Third, we standardised all continuous numerical values, by subtracting their mean

TABLE 1 Environmental parameters, habitat types, and dominant plant species recorded in the quadrats of *Parnassiana parnassica* and *Oropodisma parnassica* occurrences.

		P. parnassica		*O. parnassica*	
	Variable	Mean	Min–max	Mean	Min–max
Topography	Elevation (m)	2002	1527–2320	2052	1527–2320
	Slope (°)	15	2–45	18	2–45
Ground Cover	Soil cover (%)	8.53	0–75	4.21	0–15
	Rock cover (%)	11.73	0–50	12.34	0–55
	Stone cover (%)	27.23	5–85	41.34	5–10
	Total vegetation cover (%)	52.51	5–95	42.11	0–100
Vegetation cover	Herb/grass cover (%)	60.67	5–95	63.28	1–100
	Shrub/robust plant cover (%)	39.33	5–95	36.72	0–99
Vegetation structure	Grass/herb height (cm)	25.58	10–86	22.71	7.25–86
	Shrub/robust plant height (cm)	17.43	5–145	36.72	10–145

		Percentage of plots (%)	
Habitat type	'Endemic oro-Mediterranean heaths with gorse' (4090)	69	60
	'Alpine and Boreal heaths' (4060)	11	24
Dominant plant species	*Astragalus creticus*	56.7	44.8
	Festuca jeanpetrii	36.7	27.6
	Festuca varia	16.7	13.8
	Dactylis glomerata	16.7	13.8

Note: The total vegetation cover is divided into herbaceous plants cover and robust herbaceous plants and shrubs cover.

and dividing by their standard deviations. Finally, we selected the most influential variables to get closer to a ratio of 10 events per variable (Peduzzi et al., 1996), using the Least Absolute Shrinkage Operator (LASSO) regularisation path (Tibshirani, 1996). However, when applying LASSO regression to the *O. parnassica* dataset, all coefficients were driven to zero, suggesting potential over-regularisation. To address this issue, we turned to elastic net regression for that dataset, which combines both L1 (LASSO) and L2 (ridge) penalties (Zou & Hastie, 2005). For this process, we used the function 'cv.glmnet' from the 'glmnet' 4.1-8 R package (Friedman et al., 2010) and reduced the randomness of the function by doing 1000 irritations and choosing the lambda with the minimum average error.

We carried out generalised linear models (GLM) to model the population density of both species. We used Poisson distribution for the five variables selected for *P. parnassica*, and negative binomial distribution, for the four variables selected for *O. parnassica*, accounting for overdispersion. Subsequently, we fitted generalised linear mixed effects models (GLMM) for each dataset, incorporating the site as a random effect using the 'lme' 4 1.1-34 R package (Bates et al., 2015). We assessed the necessity of including sites nested within years as a random effect via likelihood ratio tests (LRT) comparing GLMs and GLMMs for each dataset (Bolker et al., 2009). The difference in log-likelihoods between the two models was calculated, and the test statistic was derived from the chi-squared distribution. For both datasets, a large p-value (>0.05) indicated no significant improvement in model fit when including the random effect.

We continued with GLMs for both datasets, using a multi-model inference approach, to identify confidence sets of best models (Burnham & Anderson, 2002). We compared 32 models for *P. parnassica* and 16 for *O. parnassica*, with all possible combinations of variables using the 'dredge' function from 'MuMIn' 1.47.5 R package (Barton, 2022). We ranked models according to their Akaike Information Criterion value for small-sample size (AICc) to identify those with the best fit. We considered models with ΔAICc <2 as good as the 'best' model (the one with the lowest AICc value) (Richards, 2005) and then we employed model averaging to reduce model selection uncertainty (Burnham & Anderson, 2002). To evaluate the relative importance of each variable for each dataset, we summed the Akaike weights across all models that included the covariate under consideration (Burnham & Anderson, 2002). We measured the goodness-of-fit of the models with Maximum-Likelihood pseudo-R^2 using the 'pR2' function from 'pscl' 1.5.9 R package (Jackman, 2020). We performed all statistical analyses in the R software environment, version 4.3.3 (R Core Team, 2024).

RESULTS

Current distribution pattern

Both species presented a limited distribution range: *P. parnassica* occurred in 33 sites out of the 103 sites visited with an estimated distribution area of 31 km^2 and an average density of 2.5 individuals/m^2. *Oropodisma parnassica* was recorded in 36 sites with an estimated distribution area of 36 km^2 with an average density of 8.7 individuals/m^2 (Figure 1). An important part of the distribution areas of the two species overlapped (27 km^2). AOO and the EOO for *P. parnassica* were 28 and 78 km^2, respectively, and for *O. parnassica* were 44 km^2 and 108 km^2, respectively (Figure S1). The species distribution area overlapped with the ski resort infrastructure of Parnassos and with Parnassos' roadless area (Figure S2).

Potential distribution pattern

The area of suitable habitat for *P. parnassica* was 5 km^2, encompassing 26 patches of an average patch area of 0.99 km^2 (± 4.98 km^2). The respective area of suitable habitat for *O. parnassica* was smaller, totalling 3.28 km^2, and consisted of consisting of a greater number of smaller patches: 56 patches with an average size of 0.16 km^2 (±0.81 km^2). Mt. Parnassos hosted the greatest part of suitable areas for both *P. parnassica* and *O. parnassica* (99% for each), while in Mt. Elikonas the suitable areas were restricted to its summit (0.02 km^2) (Figure 2; Figure S3). Both models exhibited high performance (TSS - True Skill statistic and AUC- Area Under the Curve ranging from 0.98 to 1).

Connectivity of suitable habitats

The connectivity among patches for *P. parnassica* was high, showing a patch cohesion index of 98.66% and an effective mesh size of 1.57 km^2. It was lower for *O. parnassica*, showing a patch cohesion index of 95.1% and an effective mesh size of 0.3 km^2.

Habitat

Microhabitat description

We recorded both species in altitudes ranging from 1527 to 2320 m (Table 1). The typical habitat for both species consisted of mountainous grasslands classified as 'Endemic oro-Mediterranean heaths with gorse' (4090) or as 'Alpine and Boreal heaths' (4060) according to the European Habitats Directive (92/43/EEC). Although rarely, we also found *P. parnassica* in fir forest clearings. The phytosociety related to the species' habitats was the *Daphno-Festucetea*, which includes the xerothermic grasslands with dwarf shrubs of the Greek mainland (Mucina et al., 2016). The dominant plant species recorded were *Astragalus creticus*, *Festuca jeanpetrii*, *F. varia* and *Dactylis glomerata*, out of the 28 plant species (10 families) recorded in the quadrats with species occurrences (Table S1). *Parnassiana parnassica* preferred medium slopes above the tree line, covered by extensive herbaceous vegetation of medium height, patches of stony substrates and less bare soil, and substantial cover of low bushes, mainly of the *A. creticus* (Table 1). *Oropodisma parnassica* favoured steeper slopes with important herbaceous vegetation cover of medium height. This species preferred habitats with a substantial cover of stony and rocky substrate

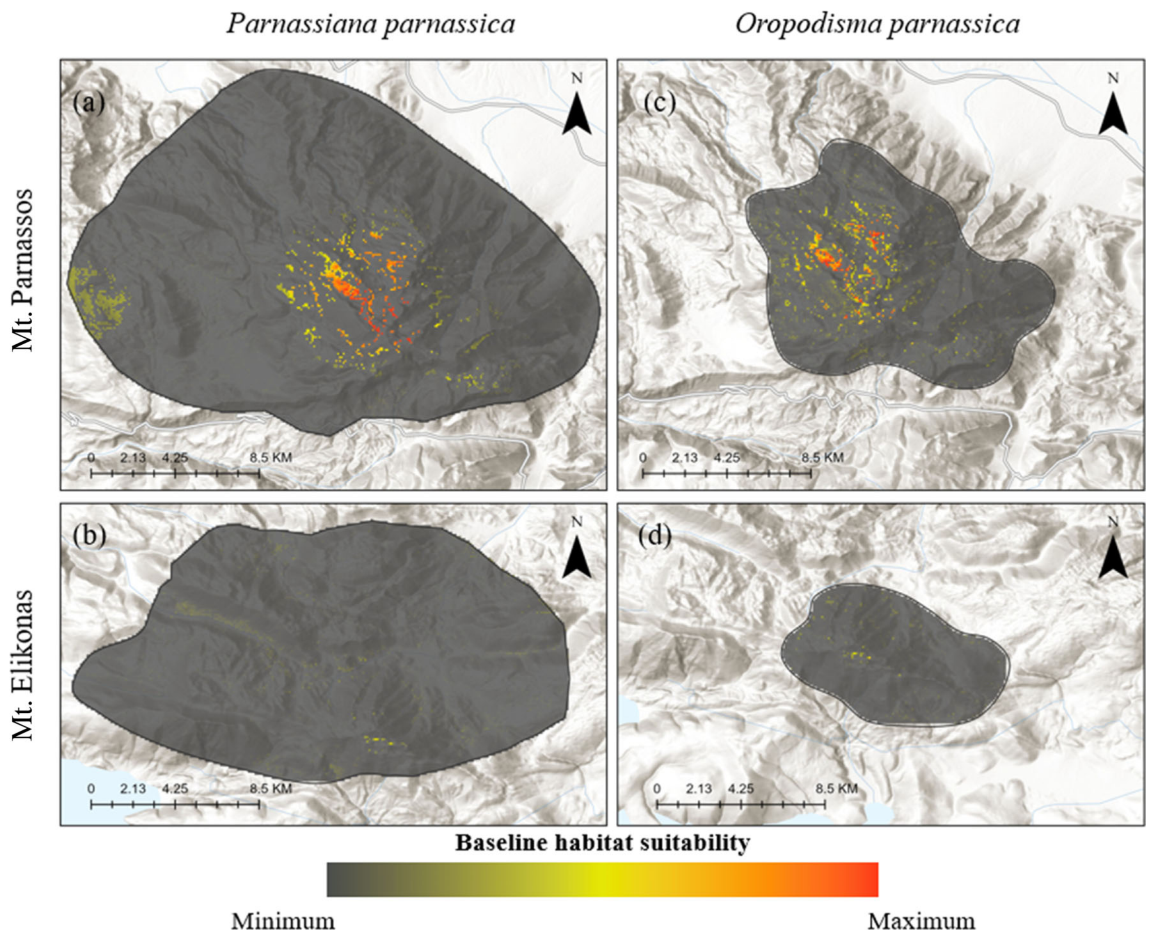

FIGURE 2 Habitat suitability maps for the target species within their potential distribution areas, as defined by the International Union for Conservation of Nature (IUCN). Panels (a) and (b) illustrate the habitat suitability for *P. parnassica*, with an extrapolation threshold of 35.1. Panels (c) and (d) show the habitat suitability for *O. parnassica*, with an extrapolation threshold of 28.8. The maps depict continuous habitat suitability values.

(>50%) and typically hid under loose stones and less under short thorny bushes such as *A. creticus*.

Predictors of habitat suitability

Considering the predictors with an importance value (>1), Topographical Position Index (TPI) (elevation difference between the species cell and vicinal cells) was the main environmental variable well predicted the suitable habitat for *P. parnassica*, followed by slope and TAR (temperature annual range). The respective variables for *O. parnassica* in descending order were the NDVI (Normalised Difference Vegetation Index), followed by slope and the PETWQ (Potential Evapotranspiration of the Wettest quarter) (Figure 3).

Predictors of species population densities

Our confidence sets included four models for *P. parnassica* and three models for *O. parnassica* (ΔAICc <2). Models accounted for approximately a quarter of the variation in the population densities of the species, with pseudo-R^2 ranging from 0.22 to 0.25 for *P. parnassica* and from 0.20 to 0.23 for *O. parnassica* (Table S3). The population density of *P. parnassica* was negatively influenced by the mean height of herbaceous vegetation (Ghmean), whereas the population density of *O. parnassica* was positively influenced by the altitude (Alt) (Table 2). The shrubby vegetation cover, rock, and soil cover did not significantly affect the species population densities.

DISCUSSION

Distribution patterns and connectivity

The global distribution area of each species is very restricted, confined to only two mountains: Parnassos and Elikonas (Figure 1, Figure S1). The distribution pattern consists of two isolated nuclei: one large nucleus on Mt. Parnassos and a small one on Mt. Elikonas. Given the limited dispersal ability of both flightless grasshoppers (Weyer et al., 2012), and the great distance between the two mountains

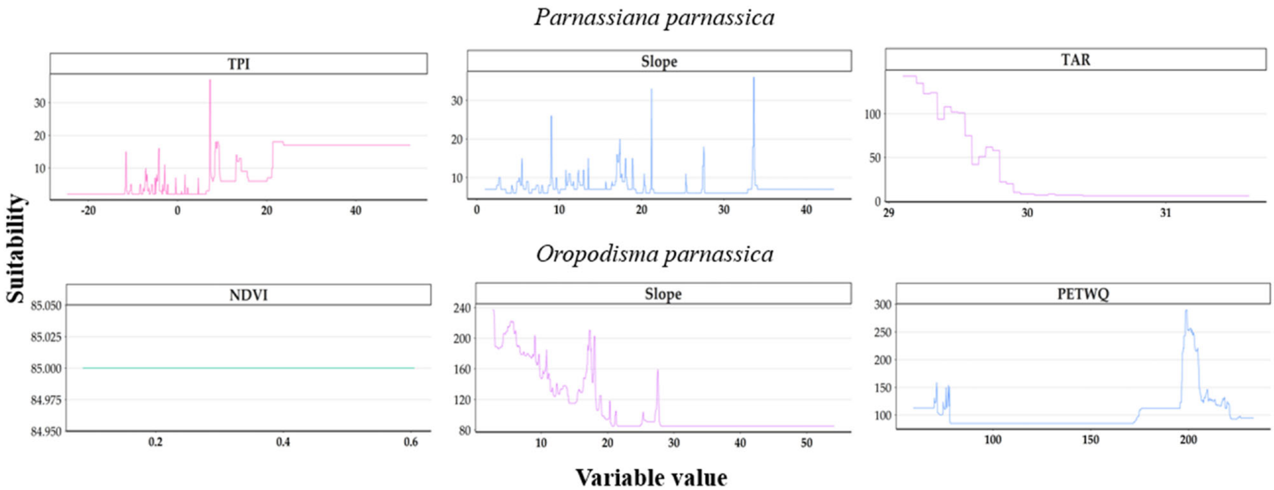

FIGURE 3 Response curves for key predictors of the target species' distribution: TPI: Topographical Position Index (m), TAR: Temperature Annual Range (degrees C, 28.9–31.9), Slope (degrees), NDVI: Normalised Difference Vegetation Index (0.07–0.75), PETWQ: Potential evapotranspiration of the wettest quarter (mm/ month, 58.46–239.74). The suitability scores for the target species are quantified on a scale from 0 to 845 or 889 (depending on the species), indicating the range of habitat suitability. Numbers in parentheses indicate a range of values in the study area.

TABLE 2 Model-averaged coefficients for all variables that were included in the set of best-ranked models (i.e., those with ΔAICc <2), the *p*-value, and cumulative model weights (i.e., summed Akaike weights), indicating the relative importance of each variable (Ghmean: mean height of herbaceous vegetation, Rpcover: shrubby vegetation cover, Alt: altitude, Sl: slope, So: soil cover, R: rock cover).

Species	Variable	Coefficient	Pr(>|z|)	Cumulative weight
Parnassiana parnassica	Ghmean	−0.0450	0.0075*	0.775
	Rpcover	0.0054	0.3189	0.159
	Alt	0.0006	0.3736	0.145
	Sl	0.0101	0.4190	0.133
Oropodisma parnassica	Alt	0.0026	0.0029*	0.750
	So	0.0442	0.2688	0.190
	R	−0.0149	0.2273	0.175

*$p < 0.01$.

(about 30 km), we believe that the populations in the two mountains are isolated.

On Mt. Parnassos, we found *P. parnassica* and *O. parnassica* in a few patches, but their patch cohesion index was high, indicating satisfactory connectivity of suitable habitats within each mountain (Schumaker, 1996). Therefore, the populations of both species cannot be considered as severely fragmented, after the IUCN guideline (IUCN SPC, 2024). Connectivity measures were better in *P. parnassica*, indicating larger and better-connected habitat patches that allow the free movement of the species among patches and the subsequent genetic flow, although the process might be slow due to the limited dispersal ability of the species. Patches should be large enough to function as stepping stones among subpopulations (Saura et al., 2014), a condition that seems to be satisfied for *P. parnassica*, but not for *O. parnassica*. Its patch area was too low and might discourage *O. parnassica* from crossing the habitat patch boundaries and colonising vicinal suitable habitat patches (Schtickzelle et al., 2006). Its habitat presented a more fragmented pattern, with numerous small-sized patches with medium connectivity. On one hand, the effective mesh size was small, but on the other hand the patch cohesion index was high, suggesting some dispersal among habitat patches, but at a slower rate than *P. parnassica*.

The populations of Mt. Elikonas seem to be particularly vulnerable to extinction, due to the very small extent of suitable habitat confined to the summit of the mountain. Habitat destruction stemming from natural disasters or human-induced land use change and habitat degradation can cause fast decline in small populations, affecting particularly rare species with limited dispersal ability (Walker & Gilbert, 2023).

Habitat suitability

Our results showed that both species preferred habitats with medium slopes between 10 and 20 degrees, in line with quadrat data (average slopes of 15° for *P. parnassica* and 18° for *O. parnassica*) (Figure 3, Table 1). Slope affects local temperature and water balance at a fine scale, offering different microclimatic conditions on mountainous terrains (Scherrer et al., 2011). It also influences local vegetation, and the availability of basking spots for Orthoptera (Gardiner, 2022), which are important for montane species thermoregulation (Samietz et al., 2005). Orthoptera utilise the different slopes to modulate their body temperature by positioning in sunlight at steeper slopes with less vegetation or more shaded spots (Anderson et al., 1979; Chappell, 1983; O'Neill & Rolston, 2007). The medium slopes selected by the two target species seem to satisfy their thermoregulation needs.

The most influential factor for the habitat of *P. parnassica* was the TPI. This species preferred localities that were slightly more elevated (by 8 m) than adjacent areas. These elevated regions likely enhance sunlight exposure, as Orthoptera at higher elevations exhibit increased mobility and basking behaviour compared with those at lower elevations (Samietz et al., 2005). The species was also very sensitive to the range between the highest and lowest temperature recorded each year (temperature annual range-TAR). TAR ranged from 28.9 to 31.9 in the study area, but the species preferred a TAR of 29°C with an upper threshold of tolerance of 30°C. An upward shift of the target species is expected in Mt. Parnassos to cope with TAR stability, but further research is recommended on the effect of global warming on local climate and the individual responses of the species.

The most influential factor for the habitat of *O. parnassica* was the Normalised Difference Vegetation Index (NDVI), reflecting the amount of green healthy vegetation in the habitats of the species. NDVI is often used to monitor Orthoptera habitats (Deveson, 2013). In the case of *O. parnassica*, the NDVI had a flat response curve, showing that the species can tolerate very low up to great amounts of green vegetation and suggesting that NDVI may contribute to the model's predictive accuracy, likely through stabilisation or interaction with other variables, rather than exerting a direct effect (Figure 3). The Potential Evapotranspiration of the Wettest Quarter (PETWQ) was another factor shaping the habitat of *O. parnassica*, indicating the potential amount of water loss that is evaporated and transpired by plants during the 3 months receiving the most precipitation. PETWQ presents a peak at 200 mm in the suitable habitats for the species and a weaker peak at 70 mm, related to the xero-thermophilic character of the species. This potential is quite high compared with the study area (59–240 mm). Further research is needed to investigate the response of the species to the changing NDVI trends, and the expected increased rates of potential evapotranspiration related to water stress in Mediterranean mountains due to global warming (Arrogante-Funes et al., 2018; Unnisa et al., 2023).

Microhabitat selection

On a finer scale, we showed that the population densities of *P. parnassica* decreased with the increase in the mean height of herbaceous vegetation (Table 2). Vegetation height is known to affect the abundance and richness of Orthoptera species (Gardiner et al., 2002; Theron et al., 2022). Tall grass vegetation impedes the survival of Orthoptera species by obstructing oviposition and basking activities (Gardiner, 2018; Wingerden et al., 1992). The mild grazing of mixed sheep and goat herds on Mt. Parnassos, and the absence of cattle seem to favour *P. parnassica* populations, by maintaining a medium vegetation high of around 26 cm. Although extreme grazing regimes of non-grazing and overgrazing are known to negatively affect insect communities (Gardiner, 2018), mild grazing favours Orthoptera communities (Kati et al., 2012) and particularly communities in mountainous pastures (Joubert et al., 2016; Rada et al., 2014). The other non-significant factors that positively influenced the microhabitat selection of the species were the cover of robust plants/ shrubs, given that the species preferred patches with a substantial cover of *A. creticus* to hide, altitude (peak at 2.100 m) and slope (15°) (Table 1, Table 2).

We showed a positive correlation between the elevation and population densities of *O. parnassica*, with the maximum density recorded at 2268 m (Table 2). Although the elevation gradient is related to a decrease in species richness and abundance (Crous et al., 2014; König et al., 2024), *O. parnassica* is a montane species that has been adapted to high altitudes. The species coexisted with *P. parnassica* to a great extent (50% of quadrats), but it prevailed at higher altitudes. In mountainous ecosystems, montane species of the same taxonomic group often replace each other along elevational gradients (Barve & Dhondt, 2017; Shepard et al., 2021). The prevalence of *O. parnassica* in higher altitudes might stem from a long-term interspecific competition process to optimise resource utilisation strategies (Chen et al., 2022; Freeman et al., 2022; Senior et al., 2021). This species preferred habitats with a substantial cover of stony substrate and typically hid under loose stones and less under short thorny bushes such as *A. creticus*. As *P. parnassica*, it preferred microhabitats with medium herbaceous vegetation height (23 cm) and might be favoured by the mild grazing of sheep/goat herds on Mt. Parnassos.

Threats and conservation implications

The species face three main imminent threats: land take, wildfires, and global warming, whereas livestock grazing seems to have a positive impact and skiing a neutral impact on their populations. Land take is the conversion of natural land to artificial land leading to direct habitat loss and is considered to be often irreversible and probably the most severe threat to biodiversity (Kati, Kassara, et al., 2023). The primary concern is the expansion of ski infrastructures (buildings, parking, roads) on Mt. Parnassos (Figure S2), and the planting of new wind turbines on Mt. Elikonas (RAE, 2024), which could induce habitat loss for the species. A new road has already been constructed on Mt. Elikonas to this aim, and although the plan has not been yet authorised, such investments pose a direct threat to both species, given the fast development of the wind farm industry in Greece and the substantial land take generated (Kati, Kassara, et al., 2023). Globally threatened species such as *P. parnassica* and *O. parnassica* should be considered by the competent authorities in the environmental authorization process of new investments, and their protection should be integrated into the national legal frameworks. In the case of Greece, endemic and threatened species are legally protected (Biodiversity law: 3937/31-3-2011), but they are rarely considered in the environmental impact assessment studies for new projects. We also propose to include the roadless area of Parnassos, an area of 66.88 km^2 (Kati, Petridou, et al., 2023), as a strictly protected zone of the Natura 2000 network of Parnassos through the Special Environmental Studies that define land uses in different zones of the Natura 2000 network, which are currently ongoing. Road construction and artificial land generation should be banned in this zone, in line with the recent Greek legislation on roadless areas (Kati et al., 2022). Given the extent of the suitable habitats within the roadless part of the mountain (Figure S3), this measure would safeguard the habitat conservation of the species.

Wildfires could also threaten species' populations in the future. Each mountain could lose its entire population due to a single catastrophic event, given the frequency and extent of megafires in Greece in recent years (Papavasileiou & Giannaros, 2022; Troumbis et al., 2023).

Furthermore, our results showed that climate change should be considered a threat to the species because our models pinpointed two climatic variables to significantly influence the habitat suitability of the target species. *Parnassiana parnassica* does not seem to tolerate changes in the temperature annual range in its distribution range, and the future response of *O. parnassica* to increased evapotranspiration in unknown. Projections indicate that global warming will profoundly impact the Mediterranean region, with summer temperatures rising and precipitation decreasing across all seasons, especially in southern areas (Lionello & Scarascia, 2018). Mountain regions particularly those above the tree line are subject to rapid changes (Hotaling et al., 2017; Pörtner et al., 2019). The response of montane species to these changes is not fully predictable, but shifts in the elevational ranges of montane insect species are expected (Menéndez et al., 2014). In our case, the populations of Mt. Elikonas seem to face a high risk of extinction, as the targe species already occupy the highest parts of the mountain. Further research is recommended on the impact of global warming on the population of the two species, and our work offered a first indication of the climatic variables that should be tested under different climatic scenarios.

Although livestock grazing has been reported as a threat for both species (Willemse, Hochkirch, Heller, et al., 2016; Willemse, Hochkirch, Kati, et al., 2016), we recorded only mild traditional sheep/goat grazing during the summer season on Mt. Parnassos and no cattle herds. Our results showed that the current mild sheep/goat grazing scheme maintains the herbaceous vegetation height at medium levels (23–26 cm) favoured by the species and hence has a beneficial role for the species populations. We note that a shift from sheep/goat to cattle herds is currently taking place in Greece (Vrahnakis & Kazoglou, 2022), which might negatively impact Orthoptera populations, as cattle overgrazing and trampling alter soil properties and vegetation composition in Orthoptera habitats (Gardiner, 2018; Kruess & Tscharntke, 2002). We stress the need to integrate the parameter of medium herbaceous vegetation height maintenance and the ecological requirements of threatened Orthoptera species in the grazing management plans currently under development in Greece and we suggest the maintenance of the current grazing scheme of mild sheep/goat grazing on Mt. Parnassos.

Both species seem to inhabit the skiing slopes and not to be affected by their use for skiing during the winter on Mt. Parnassos (Figure S3). We attribute this pattern to the absence of ski run management practices, such as the application of fertilisers, systematic bulldozing and artificial snow generation, which can alter vegetation composition and negatively impact Orthoptera communities in European mountains (Keßler et al., 2012; Wipf et al., 2005). We suggest maintaining the current non-intervention practices of ski run management for the maintenance of the species habitats on Mt. Parnassos.

Finally, we suggest the implementation of a systematic monitoring scheme (Schori et al., 2020) for the two globally threatened species by the competent authorities. Consistent monitoring will provide essential data on population trends, aiding management decisions and assessing the effectiveness of conservation actions (Block et al., 2001; Lyons et al., 2008).

IUCN Red List status

Both species' estimations satisfied the criteria of a very restricted geographic range for critically endangered status (criterion B1: EOO < 100 km^2) and endangered status (criterion B2: AOO < 500 km^2) (IUCN SPC, 2024). Considering the current extent of the threats for the species (land take, wildfires, and global warming), as well as the species distribution patter in two nuclei, two locations can be assigned to each species (Mts. Parnassos and Elikonas) (criterion a), in the sense of two geographically distinct areas in which a single threatening event can rapidly affect all individuals of the taxon present. The populations cannot be considered severely fragmented, given the high connectivity of suitable habitats found. Continuing decline can be inferred for the area and quality of the species habitat and consequently the number of mature individuals, due to former and future land take, in combination with the negative impact of global warming (criterion b). According to the new data from the current study, the IUCN Red List status of *P. parnassica* should be downgraded from critically endangered (CR) to Endangered (EN B1ab (iii, v) + 2ab (iii, v)) and for *O. parnassica* should remain Endangered (EN B1ab (iii, v) + 2ab (iii, v)).

Comparing our findings to the former IUCN species assessments (Willemse, Hochkirch, Heller, et al., 2016; Willemse, Hochkirch, Kati, et al., 2016), the EOO of *P. parnassica* increased by 38 km^2 and that of *O. parnassica* decreased by 100 km^2, indicating the need for field research to update the species distribution information to support evidence-based conservation strategies (Cook et al., 2010).

CONCLUSION

Our work employed an integrated approach to studying the ecology of the two poorly known and globally threatened Orthoptera species, by mapping their current distribution pattern, producing a map of suitable habitats, assessing habitat connectivity, and pinpointing the environmental factors shaping the species' habitats at larger and finer scales. It has a strong applied character, serving as a paradigm for assessing the extinction risk of poorly known species with limited geographical range under IUCN criteria. We call for enhancing basic research on the distribution patterns and ecology of such understudied globally threatened species. We particularly underline the need for extensive field data collection combined with the use of quantitative analytical tools such as species distribution modelling and habitat connectivity metrics, to this aim.

We concluded a change of the extinction risk assessment for *P. parnassica*, downgraded from the critically endangered category to the endangered one and we confirmed the endangered status of *O. parnassica*. Both species might experience habitat loss and degradation in the future stemming from land take, wildfires, and global warming. Our research provided a guideline for the appropriate conservation measures to be implemented by the competent authorities (Natural Environment and Climate Change Agency-NECCA) for the National Park of Parnassos and the non-protected area of Mt. Elikonas. We support the preservation of the current non-intervention practices of ski-slope management, the maintenance of the current mild sheep/goat grazing in the mountainous grasslands, the legal protection of the species habitats from new land-consuming projects and the implementation of a monitoring scheme for the population trends of the species. We finally showed that two climatic variables influenced habitat suitability models, concluding the need for further research on the climatic risk assessment for the target species, projecting their distributions under different climate change scenarios.

AUTHOR CONTRIBUTIONS

Apostolis Stefanidis: Conceptualization; methodology; software; data curation; investigation; funding acquisition; writing – original draft; writing – review and editing; validation; formal analysis; visualization. **Konstantinos Kougioumoutzis:** Methodology; software; formal analysis; visualization; writing – review and editing; writing – original draft. **Konstantina Zografou:** Software; formal analysis; writing – review and editing; writing – original draft. **Georgios Fotiadis:** Methodology; data curation; investigation; writing – review and editing; writing – original draft. **Olga Tzortzakaki:** Investigation; formal analysis; writing – review and editing. **Luc Willemse:** Investigation; validation; writing – review and editing. **Vassiliki Kati:** Conceptualization; funding acquisition; investigation; methodology; project administration; resources; supervision; writing – original draft; writing – review and editing.

ACKNOWLEDGEMENTS

We are grateful to the Natural Environment & Climate Change Agency (NECCA) for providing us with a four-wheel-drive vehicle for carrying out part of the sampling and to Vassia Margaritopoulou from the local Management Unit of Parnassos (NECCA) for her support in the fieldwork. We thank Elvira Sakkoudi and Ilias Blanis for their valuable support and help in our fieldwork and plant specimen identification. Finally, we warmly thank Elli Tzirkalli for her scientific support and advice during the preliminary modelling.

FUNDING INFORMATION

The research was funded by the Management Agency of Parnassos National Park (NECCA) under the EMEPERA scheme for the project 'Improving the knowledge of endemic and threatened insect fauna in Parnassos' (2021–2022: code 5032966). The research work of the first author was supported by the Hellenic Foundation for Research and Innovation (HFRI) under the 4th Call for HFRI PhD Fellowships (Fellowship Number: 11266: 2023–2026). The publication of the article in OA mode was financially supported by HEAL-Link.

CONFLICT OF INTEREST STATEMENT

The authors have no relevant financial or non-financial interests to disclose.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in DRYAD at https://doi.org/10.5061/dryad.xd2547ds6 (Stefanidis et al., 2024), and the R codes used in the current work are openly available in zenodo at https://zenodo.org/doi/10.5281/zenodo.13684517.

ETHICS STATEMENT

All research was conducted under the appropriate annual research permits issued by the Department of Forest Management of the Directorate General of Forests and Forest Environment of the Ministry of Environment and Energy of Greece (Protocol code: 17898/705).

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REFERENCES

Aiello-Lammens, M.E., Boria, R.A., Radosavljevic, A., Vilela, B. & Anderson, R.P. (2015) spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography*, 38, 541–545.

Aleksanov, V.V., Karmazina, I.O., Ruchin, A.B., Esin, M.N., Lukiyanov, S.V., Lobachev, E.A. et al. (2023) Diversity and biology of terrestrial Orthopteroids (Insecta) in the republic of Mordovia (Russia). *Diversity*, 15, 803.

Anderson, R.V., Tracy, C.R. & Abramsky, Z. (1979) Habitat selection in two species of short-horned grasshoppers. *Oecologia*, 38, 359–374.

Araújo, M.B. & New, M. (2007) Ensemble forecasting of species distributions. *Trends in Ecology & Evolution*, 22, 42–47.

Arrogante-Funes, P., Novillo, C.J. & Romero-Calcerrada, R. (2018) Monitoring NDVI inter-annual behavior in mountain areas of mainland Spain (2001–2016). *Sustainability*, 10, 4363.

Bachman, S., Moat, J., Hill, A.W., de Torre, J. & Scott, B. (2011) Supporting red list threat assessments with GeoCAT: geospatial conservation assessment tool. *Zookeys*, 150, 117–126.

Báldi, A. & Kisbenedek, T. (1997) Orthopteran assemblages as indicators of grassland naturalness in Hungary. *Agriculture, Ecosystems and Environment*, 66, 121–129.

Barbet-Massin, M., Jiguet, F., Albert, C.H. & Thuiller, W. (2012) Selecting pseudo-absences for species distribution models: how, where and how many? *Methods in Ecology and Evolution*, 3, 327–338.
Barton, K. (2022) MuMIn: Multi-Model Inference. R package version 1.47.5. Available at: https://CRAN.R-project.org/package=MuMIn
Barve, S. & Dhondt, A.A. (2017) Elevational replacement of two Himalayan titmice: interspecific competition or habitat preference? *Journal of Avian Biology*, 48, 1189–1194.
Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.
Belovsky, G.E. & Slade, J. (1993) The role of vertebrate and invertebrate predators in a grasshopper community. *Oikos*, 68, 193–201.
Benito, B. (2023) *Collinear: R package for seamless multicollinearity management*. doi:10.5281/zenodo.10039489. Available at: https://blasbenito.github.io/collinear/
Block, W.M., Franklin, A.B., Ward, J.P., Jr., Ganey, J.L. & White, G.C. (2001) Design and implementation of monitoring studies to evaluate the success of ecological restoration on wildlife. *Restoration Ecology*, 9, 293–303.
Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. et al. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, 24, 127–135.
Breiner, F.T., Guisan, A., Bergamini, A. & Nobis, M.P. (2015) Overcoming limitations of modelling rare species by using ensembles of small models. *Methods in Ecology and Evolution*, 6, 1210–1218.
Broennimann, O., Di Cola, V. & Guisan, A. (2021) ecospat: spatial ecology miscellaneous methods. R package version 3.2. Available at: https://CRAN.R-project.org/package=ecospat
Burnham, K.P. & Anderson, D.R. (2002) *Model selection and inference: a practical information-theoretic approach*, 2nd edition, New York: Springer.
Cardoso, P., Barton, P.S., Birkhofer, K., Chichorro, F., Deacon, C., Fartmann, T. et al. (2020) Scientists' warning to humanity on insect extinctions. *Biological Conservation*, 242, 108426.
Chappell, M.A. (1983) Metabolism and thermoregulation in desert and montane grasshoppers. *Oecologia*, 56, 126–131.
Chen, C.-C., Liao, C.-C. & Walther, B.A. (2022) Interspecific competition and facilitation coexist in mixed-species bird flocks of montane coniferous forests in Taiwan. *Journal of Avian Biology*, 2022, e02947.
Cigliano, M.M., Braun, H., Eades, D. & Otte, D. (2024) Orthoptera species file. Available at: http://orthoptera.speciesfile.org/ [Accessed 9 May 2024].
Collart, F., Hedenäs, L., Broennimann, O., Guisan, A. & Vanderpoorten, A. (2021) Intraspecific differentiation: implications for niche and distribution modelling. *Journal of Biogeography*, 48, 415–426.
Cook, C.N., Hockings, M. & Carter, R. (2010) Conservation in the dark? The information used to support management decisions. *Frontiers in Ecology and the Environment*, 8, 181–186.
Cook, R.D. (2011) Cook's distance. In: Lovric, M. (Ed.) *International encyclopedia of statistical science*. Berlin, Heidelberg: Springer Berlin Heidelberg, pp. 301–302.
Cramer, W., Guiot, J., Fader, M., Garrabou, J., Gattuso, J.-P., Iglesias, A. et al. (2018) Climate change and interconnected risks to sustainable development in the Mediterranean. *Nature Climate Change*, 8, 972–980.
Crous, C.J., Samways, M.J. & Pryke, J.S. (2014) Grasshopper assemblage response to surface rockiness in afro-montane grasslands. *Insect Conservation and Diversity*, 7, 185–194.
Curry, J.P. (1993) *Grassland invertebrates: ecology, influence on soil fertility and effects on plant growth*. Great Britain, Cambridge: Chapman & Hall.
Deveson, E. (2013) Satellite normalized difference vegetation index data used in managing Australian plague locusts. *Journal of Applied Remote Sensing*, 7, 75096.
Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B. & Collen, B. (2014) Defaunation in the Anthropocene. *Science*, 345, 401–406.
Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G. et al. (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36, 27–46.
EEA. (2010) *Europe's ecological backbone: recognising the true value of our mountains*. Luxembourg: Office for Official Publications of the European Union. Available at: https://www.eea.europa.eu/publications/europes-ecological-backbone
Elith, J., Kearney, M. & Phillips, S. (2010) The art of modelling range-shifting species. *Methods in Ecology and Evolution*, 1, 330–342.
Elith, J. & Leathwick, J.R. (2009) Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, 40, 677–697.
Evans, J.S. (2019) spatialEco—R package version 1.2-0. Available at: https://github.com/jeffreyevans/spatialEco
Fahrig, L., Arroyo-Rodríguez, V., Bennett, J.R., Boucher-Lalonde, V., Cazetta, E., Currie, D.J. et al. (2019) Is habitat fragmentation bad for biodiversity? *Biological Conservation*, 230, 179–186.
Freeman, B.G., Strimas-Mackey, M. & Miller, E.T. (2022) Interspecific competition limits bird species' ranges in tropical mountains. *Science*, 377, 416–420.
Friedman, J.H., Hastie, T. & Tibshirani, R. (2010) Regularization paths for generalized linear models via coordinate descent. *Journal of Statistical Software*, 33, 1–22.
Gardiner, T. (2018) Grazing and Orthoptera: a review. *Journal of Orthoptera Research*, 27, 3–11.
Gardiner, T. (2022) Hillside lagomorph grazing and its influence on Orthoptera. *Journal of Orthoptera Research*, 31, 157–162.
Gardiner, T. & Hassall, M. (2009) Does microclimate affect grasshopper populations after cutting of hay in improved grassland? *Journal of Insect Conservation*, 13, 97–102.
Gardiner, T., Pye, M., Field, R. & Hill, J. (2002) The influence of sward height and vegetation composition in determining the habitat preferences of three *Chorthippus* species (Orthoptera: Acrididae) in Chelmsford, Essex, UK. *Journal of Orthoptera Research*, 11, 207–213.
Goulson, D. (2019) The insect apocalypse, and why it matters. *Current Biology*, 29, R967–R971.
Graham, C.H., Carnaval, A.C., Cadena, C.D., Zamudio, K.R., Roberts, T.E., Parra, J.L. et al. (2014) The origin and maintenance of montane diversity: integrating evolutionary and ecological processes. *Ecography*, 37, 711–719.
Grzywacz, B., Heller, K.-G., Chobanov, D.P. & Warchałowska-Śliwa, E. (2017) Conventional and molecular chromosome study in the European genus *Parnassiana* Zeuner, 1941 (Orthoptera, Tettigoniinae, Platycleidini). *Folia Biologica (Kraków)*, 65, 1–8.
Guido, M. & Gianelle, D. (2001) Distribution patterns of four Orthoptera species in relation to microhabitat heterogeneity in an ecotonal area. *Acta Oecologica*, 22, 175–185.
Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D. et al. (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, 1, e1500052.
Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H. et al. (2017) More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS One*, 12, e0185809.
Hamann, A., Wang, T., Spittlehouse, D.L. & Murdock, T.Q. (2013) A comprehensive, high-resolution database of historical and projected climate surfaces for western North America. *Bulletin of the American Meteorological Society*, 94, 1307–1309.
Hesselbarth, M.H.K., Sciaini, M., With, K.A., Wiegand, K. & Nowosad, J. (2019) Landscapemetrics: an open-source R tool to calculate landscape metrics. *Ecography*, 42, 1648–1657.
Hijmans, R. (2023) terra: spatial data analysis. R package version 1.7-46. Available at: https://CRAN.R-project.org/package=terra

Hijmans, R., Philipps, S., Leathwick, J. & Elith, J. (2017) dismo: species distribution modeling. R package version 1.1-4. CRAN.

Hochkirch, A., Nieto, A. & Criado, M. (2016) *European red list of grasshoppers, crickets and bush-crickets*. Luxembourg: Publications Office of the European Union.

Hotaling, S., Finn, D.S., Joseph Giersch, J., Weisrock, D.W. & Jacobsen, D. (2017) Climate change and alpine stream biology: progress, challenges, and opportunities for the future. *Biological Reviews*, 92, 2024–2045.

IPBES. (2018) The IPBES assessment report on land degradation and restoration. In: Montanarella, L., Scholes, R., and Brainich, A. (eds.) Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Bonn, Germany. 744. Available at: https://doi.org/10.5281/zenodo.3237392

IUCN. (2024) The IUCN Red List of threatened species. Version 2023-1. Available at: https://www.iucnredlist.org [Accessed 27 May 2024].

IUCN SPC. (2024) *Guidelines for using the IUCN Red List categories and criteria. Version 16*. Prepared by the Standards and Petitions Committee. IUCN. pp. 122. Available at: http://www.iucnredlist.org/documents/RedListGuidelines.pdf

Jackman, S. (2020) *pscl: classes and methods for R developed in the Political Science Computational Laboratory. R package version 1.5.9*. Sydney, Australia: University of Sydney. Available at: https://github.com/atahk/pscl/

Jackson, C.R. & Robertson, M.P. (2011) Predicting the potential distribution of an endangered cryptic subterranean mammal from few occurrence records. *Journal for Nature Conservation*, 19, 87–94.

Joubert, L., Pryke, J.S. & Samways, M.J. (2016) Past and present disturbances influence biodiversity value of subtropical grassland ecological networks. *Biodiversity and Conservation*, 25, 725–737.

Kati, V., Kassara, C., Panagos, P., Tampouratzi, L., Gotsis, D., Tzortzakaki, O. et al. (2023) The overlooked threat of land take from wind energy infrastructures: quantification, drivers and policy gaps. *Journal of Environmental Management*, 348, 119340.

Kati, V., Mani, P., von Helversen, O., Willemse, F., Elsner, N. & Dimopoulos, P. (2006) Human land use threatens endemic wetland species: the case of *Chorthippus lacustris* (La Greca and Messina 1975) (Orthoptera: Acrididae) in Epirus, Greece. *Journal of Insect Conservation*, 10, 65–74.

Kati, V., Petridou, M., Tzortzakaki, O., Papantoniou, E., Galani, A., Psaralexi, M. et al. (2023) How much wilderness is left? A roadless approach under the global and the European biodiversity strategy focusing on Greece. *Biological Conservation*, 281, 110015.

Kati, V., Selva, N. & Sjögren-Gulve, P. (2022) Greek roadless policy: a model for Europe. *Science*, 375, 984.

Kati, V., Zografou, K., Tzirkalli, E., Chitos, T. & Willemse, L. (2012) Butterfly and grasshopper diversity patterns in humid Mediterranean grasslands: the roles of disturbance and environmental factors. *Journal of Insect Conservation*, 16, 807–818.

Kenyeres, Z., Rácz, I.A. & Varga, Z. (2009) Endemism hot spots, core areas and disjunctions in European Orthoptera. *Acta Zoologica Cracoviensia-Series B: Invertebrata*, 52, 189–211.

Keßler, T., Cierjacks, A., Ernst, R. & Dziock, F. (2012) Direct and indirect effects of ski run management on alpine Orthoptera. *Biodiversity and Conservation*, 21, 281–296.

König, S., Krauss, J., Classen, A., Hof, C., Prietzel, M., Wagner, C. et al. (2024) Micro- and macroclimate interactively shape diversity, niches and traits of Orthoptera communities along elevational gradients. *Diversity and Distributions*, 00, 1–18.

Konowalik, K. & Nosol, A. (2021) Evaluation metrics and validation of presence-only species distribution models based on distributional maps with varying coverage. *Scientific Reports*, 11, 1–15.

Kruess, A. & Tscharntke, T. (2002) Grazing intensity and the diversity of grasshoppers, butterflies, and trap-nesting bees and wasps. *Conservation Biology*, 16, 1570–1580.

La Greca, M. & Messina, A. (1976) Due nouve specie di Oropodisma (Orthoptera, Acridoidea) di Grecia. *Animal*, 3, 5–16.

Lionello, P. & Scarascia, L. (2018) The relation between climate change in the Mediterranean region and global warming. *Regional Environmental Change*, 18, 1481–1493.

Liu, C., Newell, G. & White, M. (2016) On the selection of thresholds for predicting species occurrence with presence-only data. *Ecology and Evolution*, 6, 337–348.

Lyons, J.E., Runge, M.C., Laskowski, H.P. & Kendall, W.L. (2008) Monitoring in the context of structured decision-making and adaptive management. *The Journal of Wildlife Management*, 72, 1683–1692.

Marchi, M., Castellanos-Acuña, D., Hamann, A., Wang, T., Ray, D. & Menzel, A. (2020) ClimateEU, scale-free climate normals, historical time series, and future projections for Europe. *Scientific Data*, 7, 428.

Marini, L., Fontana, P., Battisti, A. & Gaston, K.J. (2009) Response of orthopteran diversity to abandonment of semi-natural meadows. *Agriculture, Ecosystems & Environment*, 132, 232–236.

Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R.K. & Thuiller, W. (2009) Evaluation of consensus methods in predictive species distribution modelling. *Diversity and Distributions*, 15, 59–69.

May, F., Rosenbaum, B., Schurr, F.M. & Chase, J.M. (2019) The geometry of habitat fragmentation: effects of species distribution patterns on extinction risk due to habitat conversion. *Ecology and Evolution*, 9, 2775–2790.

McCain, C.M. & Colwell, R.K. (2011) Assessing the threat to montane biodiversity from discordant shifts in temperature and precipitation in a changing climate. *Ecology Letters*, 14, 1236–1245.

McGarigal, K. (2002) *FRAGSTATS: spatial pattern analysis Prog-ram for categorical maps*. Amherst: Computer software program produced by the authors at the University of Massachuse-tts. Available at: www.umass.edu/landeco/research/fragstats/fragstats.html

Menéndez, R., González-Megías, A., Jay-Robert, P. & Marquéz-Ferrando, R. (2014) Climate change and elevational range shifts: evidence from dung beetles in two European mountain ranges. *Global Ecology and Biogeography*, 23, 646–657.

Miller-Rushing, A.J., Primack, R.B., Devictor, V., Corlett, R.T., Cumming, G.S., Loyola, R. et al. (2019) How does habitat fragmentation affect biodiversity? A controversial question at the core of conservation biology. *Biological Conservation*, 232, 271–273.

Mucina, L., Bültmann, H., Dierßen, K., Theurillat, J.-P., Raus, T., Čarni, A. et al. (2016) Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. *Applied Vegetation Science*, 19, 3–264.

NOA. (2024) National Observatory of Athens. Available at: https://www.noa.gr [Accessed on 27 May 2024].

Noriega, J.A., Hortal, J., Azcárate, F.M., Berg, M.P., Bonada, N., Briones, M.J.I. et al. (2018) Research trends in ecosystem services provided by insects. *Basic and Applied Ecology*, 26, 8–23.

O'Neill, K.M. & Rolston, M.G. (2007) Short-term dynamics of behavioral thermoregulation by adults of the grasshopper *Melanoplus sanguinipes*. *Journal of Insect Science*, 7, 1–14.

Papavasileiou, G. & Giannaros, T.M. (2022) The catastrophic 2021 wildfires in Greece: an outbreak of pyroconvective events. *Environmental Sciences Proceedings*, 17, 7.

Parr, S.J., Naveso, M.Á. & Yarar, M. (1997) Habitat and potential prey surrounding lesser kestrel *Falco naumanni* colonies in central Turkey. *Biological Conservation*, 79, 309–312.

Peduzzi, P., Concato, J., Kemper, E., Holford, T.R. & Feinstein, A.R. (1996) A simulation study of the number of events per variable in logistic regression analysis. *Journal of Clinical Epidemiology*, 49, 1373–1379.

Peterson, A.T. (2001) Predicting species' geographic distributions based on ecological niche modeling. *The Condor*, 103, 599–605.

Poniatowski, D. & Fartmann, T. (2008) The classification of insect communities: lessons from orthopteran assemblages of semi-dry calcareous grasslands in central Germany. *European Journal of Entomology*, 105, 659–671.

Pörtner, H., Roberts, D., Masson-Delmotte, V., Zhai, P., Poloczanska, E., Mintenbeck, K. (2019) In: A. Alegría, M. Nicolai, A. Okem, J. Petzold, B. Rama, N.M. Weyer (eds.) *IPCC, 2019: technical summary. IPCC special report on the ocean and cryosphere in a changing climate*. Cambridge, UK and New York, NY, USA: Cambridge University Press, 755 pp. Available at: https://doi.org/10.1017/9781009157964

R Core Team, R. (2024) *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Available at: https://www.R-project.org/

Rada, S., Mazalová, M., Šipoš, J. & Kuras, T. (2014) Impacts of mowing, grazing and edge effect on Orthoptera of submontane grasslands: perspectives for biodiversity protection. *Polish Journal of Ecology*, 62(123–138), 16–138.

RAE. (2024) Geospatial map for energy units and requests. Available at: https://geo.rae.gr/?lang=EN [Accessed 28 May 2024].

Rahbek, C., Borregaard, M.K., Antonelli, A., Colwell, R.K., Holt, B.G., Nogues-Bravo, D. et al. (2019) Building mountain biodiversity: geological and evolutionary processes. *Science*, 365, 1114–1119.

Reinhardt, K., Köhler, G., Maas, S. & Detzel, P. (2005) Low dispersal ability and habitat specificity promote extinctions in rare but not in widespread species: the Orthoptera of Germany. *Ecography*, 28, 593–602.

Richards, S.A. (2005) Testing ecological theory using the information-theoretic approach: examples and cautionary results. *Ecology*, 86, 2805–2814.

Robertson, M.P., Visser, V. & Hui, C. (2016) Biogeo: an R package for assessing and improving data quality of occurrence record datasets. *Ecography*, 39, 394–401.

Samietz, J., Salser, M.A. & Dingle, H. (2005) Altitudinal variation in behavioural thermoregulation: local adaptation vs. plasticity in California grasshoppers. *Journal of Evolutionary Biology*, 18, 1087–1096.

Sánchez-Bayo, F. & Wyckhuys, K.A.G. (2019) Worldwide decline of the entomofauna: a review of its drivers. *Biological Conservation*, 232, 8–27.

Saura, S., Bodin, Ö. & Fortin, M.-J. (2014) EDITOR'S CHOICE: stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. *Journal of Applied Ecology*, 51, 171–182.

Scherrer, D., Schmid, S. & Körner, C. (2011) Elevational species shifts in a warmer climate are overestimated when based on weather station data. *International Journal of Biometeorology*, 55, 645–654.

Schickhoff, U., Singh, R.B. & Mal, S. (2021) *Mountain landscapes in transition: effects of land use and climate change*. Switzerland: Springer Nature, Ed. 1, 656. Available at: https://doi.org/10.1007/978-3-030-70238-0

Schirmel, J., Mantilla-Contreras, J., Blindow, I. & Fartmann, T. (2011) Impacts of succession and grass encroachment on heathland Orthoptera. *Journal of Insect Conservation*, 15, 633–642.

Schori, J.C., Steeves, T.E. & Murray, T.J. (2020) Designing monitoring protocols to measure population trends of threatened insects: a case study of the cryptic, flightless grasshopper *Brachaspis robustus*. *PLoS One*, 15, e0238636.

Schtickzelle, N., Mennechez, G. & Baguette, M. (2006) Dispersal depression with habitat fragmentation in the bog fritillary butterfly. *Ecology*, 87, 1057–1065.

Schumaker, N.H. (1996) Using landscape indices to predict habitat connectivity. *Ecology*, 77, 1210–1225.

SDF. (2020) Natura 2000—Standard Data Form: GR2450005. Notioanatolikos Parnassos-Ethnikos Drymos Parnassou-Dasos Tithoreas, Spilaio Varathro. Available at: https://natura2000.eea.europa.eu/Natura2000/SDF.aspx?site=GR2450005

Senior, A.F., Chapple, D.G., Atkins, Z.S., Clemann, N., Gardner, M.G., While, G.M. et al. (2021) Agonistic behavioural asymmetry in two species of montane lizard that exhibit elevational replacement. *Landscape Ecology*, 36, 863–876.

Shepard, I.D., Wissinger, S.A. & Greig, H.S. (2021) Elevation alters outcome of competition between resident and range-shifting species. *Global Change Biology*, 27, 270–281.

Smith, A.B. (2020) enmSdm: tools for modeling species niches and distributions. R package version 0.5.1.5. Available at: http://github.com/adamlilith/enmSdm

Spehn, E., Rudmann-Maurer, K., Korner, C. & Maselli, D. (2010) *Mountain biodiversity and global change*. Basel: GMBA-DIVERSITAS.

Stefanidis, A., Fotiadis, G., Willemse, L., Tzortzakaki, O. & Kati, V. (2024) *Parnassiana parnassica and Oropodisma parnassica (Orthoptera) dataset*. DRYAD. Available at: https://doi.org/10.5061/dryad.xd2547ds6

Stork, N.E. (2018) How many species of insects and other terrestrial arthropods are there on earth? *Annual Review of Entomology*, 63, 31–45.

Strid, A. (1986) Mountain flora of Greece. Cambridge University Press.

Theron, K.J., Pryke, J.S. & Samways, M.J. (2022) Identifying managerial legacies within conservation corridors using remote sensing and grasshoppers as bioindicators. *Ecological Applications*, 32, e02496.

Thomaes, A., Kervyn, T. & Maes, D. (2008) Applying species distribution modelling for the conservation of the threatened saproxylic stag beetle (*Lucanus cervus*). *Biological Conservation*, 141, 1400–1410.

Thuiller, W., Georges, D., Engler, R. & Breiner, F., Lafourcade B., Patin R. (2023) biomod2: ensemble platform for species distribution modeling. R package version 4.2-4. Available at: https://CRAN.R-project.org/package=biomod2

Tibshirani, R. (1996) Regression shrinkage and selection via the lasso. *Journal of the Royal Statistical Society: Series B (Methodological)*, 58, 267–288.

Title, P.O. & Bemmels, J.B. (2018) ENVIREM: an expanded set of bioclimatic and topographic variables increases flexibility and improves performance of ecological niche modeling. *Ecography*, 41, 291–307.

Troumbis, A.Y., Gaganis, C.M. & Sideropoulos, H. (2023) Probabilistic wildfire risk assessment and modernization transitions: the case of Greece. *Fire*, 6, 158.

Unnisa, Z., Govind, A., Lasserre, B. & Marchetti, M. (2023) Water balance trends along climatic variations in the Mediterranean Basin over the past decades. *Water*, 15, 1889.

Velazco, S.J.E., Rose, M.B., de Andrade, A.F.A., Minoli, I. & Franklin, J. (2022) Flexsdm: an r package for supporting a comprehensive and flexible species distribution modelling workflow. *Methods in Ecology and Evolution*, 13, 1661–1669.

Velazco, S.J.E., Rose, M.B., De Marco, P., Jr., Regan, H.M. & Franklin, J. (2024) How far can I extrapolate my species distribution model? Exploring shape, a novel method. *Ecography*, 2024, e06992.

Vrahnakis, M. & Kazoglou, Y. (2022) Mountain habitats dynamics under changing grazing management schemes in Greece. In: Schickhoff, U., Singh, R.B. & Mal, S. (Eds.) *Mountain landscapes in transition: effects of land use and climate change*. Cham: Springer International Publishing, pp. 575–591.

Walker, E.J. & Gilbert, B. (2023) Extinction dynamics: the interplay of species traits and the spatial scales of metapopulation declines. *Ecology*, 104, e3840.

Wang, T., Hamann, A., Spittlehouse, D.L. & Murdock, T.Q. (2012) ClimateWNA—high-resolution spatial climate data for western North America. *Journal of Applied Meteorology and Climatology*, 51, 16–29.

Weyer, J., Weinberger, J. & Hochkirch, A. (2012) Mobility and microhabitat utilization in a flightless wetland grasshopper, *Chorthippus montanus* (Charpentier, 1825). *Journal of Insect Conservation*, 16, 379–390.

Willemse, L., Hochkirch, A., Heller, K.-G., Kati, V., Papapavlou, K. & Tzirkalli, E. (2016) *Parnassiana parnassica*. The IUCN Red List of threatened species 2016: e.T68450303A70624784. https://doi.org/10.2305/IUCN.UK.2016-1.RLTS.T68450303A70624784.en

Willemse, L., Hochkirch, A., Kati, V., Papapavlou, K., Tzirkalli, E. & Heller, K.-G. (2016) *Oropodisma parnassica*. The IUCN Red List of threatened species 2016: e.T16084516A70566636. https://doi.org/10.2305/IUCN.UK.2016-1.RLTS.T16084516A70566636.en

Willemse, L., Kleukers, R. & Odé, B. (2018) The grasshoppers of Greece. EIS Kenniscentrum Insecten & Naturalis Biodiversity Center, Leiden.

Wingerden, W.V., Kreveld, A.V. & Bongers, W. (1992) Analysis of species composition and abundance of grasshoppers (Orth., Acrididae) in natural and fertilized grasslands. *Journal of Applied Entomology*, 113, 138–152.

Wipf, S., Rixen, C., Fischer, M., Schmid, B. & Stoeckli, V. (2005) Effects of ski piste preparation on alpine vegetation. *Journal of Applied Ecology*, 42, 306–316.

Yang, L.H. & Gratton, C. (2014) Insects as drivers of ecosystem processes. *Current Opinion in Insect Science*, 2, 26–32.

Zizka, A., Silvestro, D., Andermann, T., Azevedo, J., Duarte Ritter, C., Edler, D. et al. (2019) CoordinateCleaner: standardized cleaning of occurrence records from biological collection databases. *Methods in Ecology and Evolution*, 10, 744–751.

Zou, H. & Hastie, T. (2005) Regularization and variable selection via the elastic net. *Journal of the Royal Statistical Society Series B: Statistical Methodology*, 67, 301–320.

SUPPORTING INFORMATION

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

Figure S1. The extent of occurrence (EOO) for *Parnassiana parnassica* and *Oropodisma parnassica*.

Figure S2. Target species occurrences in relation to the ski centre area (1.57 km^2: 200 m buffer around infrastructures and ski slopes) and the roadless area of Mt. Parnassos (66.88 km^2: Kati et al., 2023).

Figure S3. Habitat suitability binary maps (presence–absence) for the target species within their potential distribution areas, as defined by the IUCN. Panels (a) and (b) illustrate the habitat suitability for *P. parnassica*, with an extrapolation threshold of 35.1. Panels (c) and (d) show the habitat suitability for *O. parnassica*, with an extrapolation threshold of 28.8. The maps depict only the ensemble small models with a value of True Skill Statistic (TSS) ≥0.4.

Table S1. The full dataset of 27 variables considered for the Species Distribution Modelling, indicating the 12 variables selected. The table presents the time period of reference and the resolution data were available from respected sources. All the variables were created at 100 × 100 m resolution, using ClimateEU Software for bioclimatic variables.

Table S2. The dominant plant species (>70% cover) and their frequency (%) in the quadrats sampled for Parnassiana parnassica (33 quadrats) and Oropodisma parnassica (36 quadrat).

Table S3. Best-ranked GLMs for P. parnassica and O. parnassica, showing the number of parameters (k), the AIC corrected for small-sample size (AICc), the differences in AICc (ΔAICc = AICci − AICcbest), model's Akaike weight (wi) and Maximum-Likelihood Pseudo-R^2. Only models with ΔAICc <2 were considered in model averaging (Ghmean: mean height of herbaceous vegetation, Rpcover: shrubby vegetation cover, Alt: altitude, Sl: slope, So: soil cover, R: rock cover).

How to cite this article: Stefanidis, A., Kougioumoutzis, K., Zografou, K., Fotiadis, G., Tzortzakaki, O., Willemse, L. et al. (2024) Mitigating the extinction risk of globally threatened and endemic mountainous Orthoptera species: *Parnassiana parnassica* and *Oropodisma parnassica*. *Insect Conservation and Diversity*, 1–15. Available from: https://doi.org/10.1111/icad.12784