



# Article Climate-Change Impacts on the Southernmost Mediterranean Arctic-Alpine Plant Populations

Konstantinos Kougioumoutzis <sup>1,\*,†</sup>, Ioannis P. Kokkoris <sup>1,†</sup>, Arne Strid <sup>2</sup>, Thomas Raus <sup>3</sup>, and Panayotis Dimopoulos <sup>1,\*</sup>

- <sup>1</sup> Laboratory of Botany, Department of Biology, University of Patras, 26504 Patras, Greece; ipkokkoris@upatras.gr
- <sup>2</sup> Bakkevej 6, DK-5853 Ørbæk, Denmark; arne.strid@youmail.dk
- <sup>3</sup> Botanischer Garten und Botanisches Museum Berlin-Dahlem, Freie Universität Berlin, 14195 Berlin, Germany; t.raus@bo.berlin
- \* Correspondence: kkougiou@aua.gr (K.K.); pdimopoulos@upatras.gr (P.D.)
- + These authors contributed equally to this work.

Abstract: Human-induced climate- and land-use change have been affecting biogeographical and biodiversity patterns for the past two centuries all over the globe, resulting in increased extinction and biotic homogenization rates. High mountain ecosystems are more sensitive to these changes, which have led to physiological and phenological shifts, as well as to ecosystem processes' deformation. Glacial relicts, such as arctic-alpine taxa, are sensitive indicators of the effects of global warming and their rear-edge populations could include warm-adapted genotypes that might prove-conservationwise-useful in an era of unprecedented climate regimes. Despite the ongoing thermophilization in European and Mediterranean summits, it still remains unknown how past and future climate-change might affect the distributional patterns of the glacial relict, arctic-alpine taxa occurring in Greece, their European southernmost distributional limit. Using species distribution models, we investigated the impacts of past and future climate changes on the arctic-alpine taxa occurring in Greece and identified the areas comprising arctic-alpine biodiversity hotspots in Greece. Most of these species will be faced with severe range reductions in the near future, despite their innate resilience to a multitude of threats, while the species richness hotspots will experience both altitudinal and latitudinal shifts. Being long-lived perennials means that there might be an extinction-debt present in these taxa, and a prolonged stability phase could be masking the deleterious effects of climate change on them. Several ex situ conservation measures (e.g., seed collection, population augmentation) should be taken to preserve the southernmost populations of these rare arctic-alpine taxa and a better understanding of their population genetics is urgently needed.

**Keywords:** biodiversity conservation; extinction risk; GIS analysis; Greece; Mediterranean flora; species distribution modelling

# 1. Introduction

Arctic-alpine taxa are a biogeographically interesting group and are considered glacial relicts [1–6] that exhibit niche conservatism [7]. They are weak competitors, especially for light and against woody vegetation [8]. Arctic-alpine taxa are also among the most sensitive indicators of the effects of global warming, especially at the southern limit of their range [9]. They are also considered locally extinction-prone in a warming environment [10–12], even though they persisted the transition from the Last Glacial Maximum (LGM) to the current interglacial [8].

Most arctic-alpine taxa have a disjunct and extrazonal distribution—especially in Europe, which hosts 140 such taxa [1]—and they mainly occur in the highest mountain summits ([13] and references therein). Arctic-alpine species-rich areas are mainly found in high-latitude regions, such as Fennoscandia [12], but the three Mediterranean (i.e., the



Citation: Kougioumoutzis, K.; Kokkoris, I.P.; Strid, A.; Raus, T.; Dimopoulos, P. Climate-Change Impacts on the Southernmost Mediterranean Arctic-Alpine Plant Populations. *Sustainability* **2021**, *13*, 13778. https://doi.org/10.3390/ su132413778

Academic Editor: Panayiotis Dimitrakopoulos

Received: 26 November 2021 Accepted: 9 December 2021 Published: 14 December 2021

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**Copyright:** © 2021 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). Iberian, the Italian and the Balkan) peninsulas also host a significant number of arcticalpine taxa ([1] and references therein), owing to the presence of a number of climatic refugia [14–17], with the Alps being the most important European centre of the Arcticalpine flora [1].

Greece, one of the most species-rich European countries [18], apart from hosting more than 1400 endemic taxa, many of which are threatened [19] and occur in several endemism centres [20], constitutes the southernmost range margin for 29 arctic-alpine taxa [1,18,21]. These taxa occur in high altitudes mainly in the Pindos mountain range and other mountains of northern Greece, reaching as far south as the Lefka Ori mountain range in western Crete (Figure 1). In general, Greek mountains have provided shelter to several cold-adapted species [22–25], with large areas in NE Greece and in Crete being climatically stable for the past 4 Mya (see Figure S5 in [20] and Figure 6 in [26]) and thus acted as local refugia due to their higher microclimatic buffering capacity for some relict, microthermic taxa [27,28].



Figure 1. Distribution of the arctic-alpine taxa occurring in Greece.

Climate change is undoubtedly already altering biogeographical and biodiversity patterns all over the globe, at various spatial scales, leading—in conjunction with land-use change—to elevated extinction and biotic homogenization rates [29–40]. Even though several studies have dealt with the phylogeography, molecular ecology and population genetics of arctic-alpine taxa (e.g., [41–46]) and many other have dealt with the effects of climate change on arctic-alpine taxa in Central Europe and Fennoscandia (e.g., [12,13,47–50]), none has ever investigated how arctic-alpine taxa occurring at the lowest Mediterranean latitudes might respond to changing temperature and precipitation regimes. This is ever more important in the Anthropocene, an era of unprecedented pressures to biodiversity [32,51],

since low latitude populations of cold-adapted plants occurring at high altitudes probably exhibit adaptive plasticity, highly efficient physiological responses to harsh environmental conditions and unique genetic diversity that might prove valuable regarding the persistence in a warming climate [52,53]. Despite the ongoing thermophilization in European and Mediterranean summits that is already altering high-altitude beta-diversity patterns [26,54] and the growing interest in forecasting the potential climate-change impacts on plants occurring in Greece [26,39,55–59], none has ever investigated how past and future climate-change might affect the distributional patterns of the glacial relict, arctic-alpine taxa occurring in Greece. Understanding the vulnerability drivers of these resilient and ecologically marginal populations of arctic-alpine taxa is pivotal for biodiversity conservation in a time of unprecedented changes and elevated threats and including past climate projections in species distribution modelling might pave the way to lay out more systematic and elaborate conservation plans [60].

Thus, after employing a species distribution modelling framework, we aim to address the following questions:

- (a) How will climate-change influence the plant diversity patterns of the arctic-alpine taxa occurring in Greece?
- (b) Where are currently located the arctic-alpine species richness hotspots in Greece?
- (c) Will these hotspots shift in the future and have they shifted since the Last Glacial Maximum?
- (d) Which conservation measures need to be taken for the efficient protection and management of these glacial relicts?

# 2. Materials and Methods

### 2.1. Species Occurrence Data

Twenty-none arctic-alpine taxa (Table S1) occur in Greece [18,21]. Following [18,21], taxa are defined as (a) subspecies and (b) species that have no subspecies, i.e., when a species has subspecies, then only its subspecies are counted. We followed the nomenclature suggested by [18,21] regarding the synonymity check for all the arctic-alpine taxa occurring in Greece. Henceforth, we based all of our analyses on the Flora Hellenica Database, Strid (ongoing), which comprises ~1.2 M occurrences regarding the plant taxa found in Greece. After removing any duplicate records, we spatially thinned the occurrence data following [61,62], using functions from the 'spThin' 0.1.0 [62] R package. Our final dataset comprised 902 records for 21 taxa (Table S2), since we included in our analyses only those taxa that had 5 or more occurrences, following [63].

## 2.2. Environmental Data

We obtained current, future and past (Last Glacial Maximum—LGM) climatic data from the CHELSA [64] and ENVIREM [65] databases and soil variables from the SoilGrids database [66] at a 30 sec resolution. Altitudinal data were obtained from the CGIAR-CSI data-portal (http://srtm.csi.cgiar.org—[67]). Since altitudinal data had a finer resolution than the climatic data we obtained, we ensured that their resolution matched that of the other abiotic variables, using functions from the 'raster' 3.3.13 R package [68]. We calculated five additional abiotic (topographical) variables (slope, aspect, heat load index, topographic position index and terrain ruggedness index) based on the aggregated and resampled altitudinal data using functions from the 'raster' 3.3.13 [68] and 'spatialEco' 1.2-0 R packages [69].

As for future climatic data, these were extracted for 2070 for two different Global Circulation Models (GCMs—BCC and CCSM4) following [70] and two different Intergovernmental Panel on Climate Change scenarios from the Representative Concentration Pathways family: RCP2.6 (mild scenario) and RCP8.5 (severe scenario).

We retained in our analyses only ten predictors that were not highly correlated (Spearman rank correlation <0.7 and VIF < 10—[71]) to reduce multicollinearity and thus minimize model overfitting (Table S2), using functions from the 'usdm' 1.1.18 [72] R package.

#### 2.3. Species Distribution Models

We used the random forest (RF) modelling algorithm under the ensemble of small models (ESM) framework [73–75] for any taxon with an occurrence to predictors ratio lower than 10:1 [76], to model their realized niche with the 'ecospat' 3.1 [77] R package. For the remaining taxa (n = 5), we used Bayesian additive regression trees (BARTs) as implemented in the 'embarcadero' [78] R package, using the 'bart.step' and 'retune' functions to fine-tune the models following [79]. We used the 'EOO.computing' function from the 'ConR' 1.1.1 package [80] to approximate the background area of all the arctic-alpine taxa included in our analyses based on the alpha-hull method ([81] and references therein), as their exact distribution in Greece is incompletely known. Subsequently, we followed [82,83] to create taxon-specific pseudo-absences. The models' predictive performance was first evaluated on a repeated (10 times) 80–20 split-sampling approach based on several metrics—AUC, AUC-PR, (Brier score, Cohen's kappa, Continuous Boyce Index (CBI), Somer's D, TSS) [84-88]using functions from the 'CalibratR' 0.1.2, 'DescTools' 0.99.40, 'ecospat' 3.2, 'enmSdm' 0.5.3.2, 'Metrics' 0.1.4, 'MLmetrics' 1.1.1 and 'modEvA' 2.0, R packages [89–95]. Finally, we evaluated if our models performed better than chance via null model significance testing, following [96].

The reconstruction of each taxon's potential past, current and future suitable habitat was accomplished via ensemble modelling [97], based on well-calibrated models (TSS  $\geq$  0.5) for taxa modelled under the ESM framework. We used the TSS score to weight each model's contribution to the ensemble forecast. As for the models produced by 'embarcadero', this was achieved via the 'predict2.bart' function, using only the predictors that were retained in the final tuned model. We estimated variable importance for the BART models via the 'varimp' function of the 'embarcadero' R package.

We constructed binomial presence/absence maps from the habitat suitability maps we generated in the previous step for each GCM, RCP and time-slice, by using the metric that maximizes the sum of sensitivity and specificity [98–100]. The suitability of any cells that had non-zero values in the clamping mask was set to NA in R as a precautionary measure [76] for ESMs. Regarding models produced by 'embarcadero', the suitability of any cells that had an uncertainty value equal to or higher than the 90% of the cells was set to NA in R.

Finally, we used the 'BIOMOD\_RangeSize' function from the "biomod2" 3.3.7 R package [101] to assess the projected range change of all taxa. Taxa were not assumed to have unlimited dispersal capacity, since this would be overoptimistic in our case, considering these taxa constitute glacial relicts in Greece and the Balkans [1–3]. The unlimited dispersal scenario provides optimistic predictions, similar to static models and is more suited for the Arctic and alpine areas of northern Europe and Fennoscandia [12,102–104].

#### 2.4. Biodiversity Hotspots Detection

We followed [20] for all spatial analyses regarding biodiversity patterns. We estimated species richness (SR) and the corrected weighted endemism metric (CWE—[105–107]) using the R code from [108,109], as the latter metric is considered more robust and reliable compared to SR when trying to locate biodiversity hotspots [110]. L1 SR and CWE hotspots are herein delineated as the cells belonging to the 1% quantile for each metric [111] and were located via the 'phyloregion' 1.0.4 R package [112–114]. The biodiversity hotspots as defined here refer to regional biodiversity hotspots [115].

## 2.5. Latitudinal and Altitudinal Shifts of the Biodiversity Hotspots

We investigated if the distribution centroids of the SR and CWE hotspots might have shifted spatiotemporally and altitudinally through Kruskal–Wallis and Watson tests, using base R functions, as well as functions from the "raster" 2.6.7 [68] and 'sf' 0.9.6 [116] R packages.

## 3. Results

# 3.1. Species Distribution Models

All models outperformed the null expectation at p < 0.001 and performed sufficiently well (median AUC:  $0.96 \pm 0.06$ ; AUC-PR:  $0.90 \pm 0.06$ ; Brier score:  $0.07 \pm 0.03$ ; CBI:  $0.95 \pm 0.22$ ; Cohen's kappa:  $0.83 \pm 0.14$ ; Somer's D:  $0.92 \pm 0.12$ ; TSS:  $0.83 \pm 0.14$ ; Figure 2A; Table S3). Prediction uncertainty was generally low across all taxa analysed via 'embarcadero', with relatively high uncertainty values observed mainly in mid-altitude areas (Figures 3 and S1–S4). The mean temperature of the wettest quarter (MTWQ) had the highest contribution among the response variables for the majority of taxa (66.67%; Tables S3 and S4), followed by the potential evapotranspiration of the coldest quarter (PETCQ). Table S3 contains all of the details and analysis of the models' performance. Since the trends for the future potential distribution of all the arctic-alpine taxa occurring in Greece and included in our analyses were identical across all sources of uncertainty, we present only the SR/CWE richness and area range change for the BCC GCM and the RCP 8.5 scenario in the following sections (all other GCM/RCP combinations are presented in the Supplementary Materials).

All arctic-alpine taxa in Greece are projected to experience severe range contraction irrespective of the GCM and RCP analysed (median range contraction: 98.69%; Table S5; Figure 2B). As for the range change during the transition from the Last Glacial Maximum towards the present time-period, most taxa retained their extent, apart from six species that experienced severe range contraction (Table S5).

#### 3.2. Biodiversity Hotspots Detection

LGM SR was highest at the areas surrounding lakes Kastoria, Vegoritida and Petron, as well as at the lowland plains near Velventos (Figure 4A). The northern tips of Pindos mountain range together with Mt. Vermio currently display the highest SR, as most species retreated to higher altitudes and latitudes during the transition from the LGM to the Mid- to Late Holocene (Figures 4B and S5). Regarding the future projections, in all cases, SR is expected to be drastically reduced, being highest in the north-eastern Greek lowlands, since most arctic-alpine species are projected to become extirpated in the coming decades (Table S5; Figures 4C and S6). LGM L1 CWE hotspots occurred in Mts. Parnassos, Kajmakcalan and Pinovon, in the Gramos and Rodhopi mountain ranges, the areas surrounding lakes Kastoria, Vegoritida, Prespes and Petron, as well as at the lowland plains near Velventos (Figure 5A). Current L1 CWE hotspots are found in Mts. Olympus, Vermion, Falakron, Volakas, Kajmakcalan, Giona and Vardousia, as well as the northern tips of Pindos mountain range (Figures 5B and S7-S9). Future SR and CWE L1 hotspots are rather identical, as large swathes of the north-eastern Greek lowlands, with some small pockets appearing in Mt. Olympus and at the northern edges of Pindos mountain range, emerged as SR and CWE L1 hotspots under any GCM/RCP combination (Figures 5C and S7–S13).



Figure 2. Raincloud plot [117] of the (A) discrimination (AUC, AUC-PR, TSS) and calibration (Brier score, Cohen's kappa, continuous Boyce index (CBI), Somer's D) metrics for all the taxa included in our analyses and (B) projected proportion of area range loss for all the taxa included in our analyses under any global circulation model (GCM) and representative pathway concentration (RCP) combination.



**Figure 3.** Bivariate map of the habitat suitability values and the corresponding prediction uncertainty for *Euphrasia salisburgensis* in Greece. The dashed line denotes the species' potential distributional area in Greece, using the alpha-hull method. *Euphrasia salisburgensis* is one of the five arctic-alpine taxa occurring in Greece that we analysed via the 'embarcadero' R package and the one with the widest distribution among the arctic-alpine taxa occurring in Greece. Dark blue cells indicate areas with the highest habitat suitability and the lowest prediction uncertainty.



Figure 4. (A) Last Glacial Maximum (LGM) species richness (SR), (B) current SR and (C) Future SR based on the BCC 8.5 GCM/RCP combination of the arctic-alpine taxa occurring in Greece.



Figure 5. L1 (top 1%) CWE hotspots (green cells) for the (A) LGM, (B) current and (C) the BCC 8.5 RCP time-periods, respectively.

### 3.3. Latitudinal and Altitudinal Shifts of the Biodiversity Hotspots

We detected statistically significant latitudinal shifts regarding the time-slices' L1 centroids for both metrics, which were predicted to move to the northeast and migrated to the north after the LGM ended (Watson tests with *p*-values < 0.01 at  $\alpha$  = 0.05; Figure 6). The mean altitude for the L1 hotspots for both metrics is statistically significantly different between all time-slices (Kruskal–Wallis ANOVA: H = 13567, d.f. = 11760, *p* < 0.001), with current hotspots occurring in higher altitudes, while LGM hotspots were found at lower altitudes (LGM SR hotspots were found at sea level; Table S6).

As the trends for the future and past potential distribution were similar across species and all uncertainty sources, we selected to present the range change for two emblematic arctic-alpine species occurring in Greece, Dryas octopetala and Euphrasia salisburgensis [1]. Dryas octopetala has a narrow distribution in northern Greece, while Euphrasia salisburgensis has the widest distribution among the arctic-alpine taxa occurring in Greece, reaching as far south as the Lefka Ori mountain range in Crete (see Table S3 for the EOO of these taxa). Both of these taxa were more widespread during the Last Glacial Maximum, with Dryas octopetala being seemingly more resilient to the climatic changes that manifested during the transition to the current interglacial compared to Euphrasia salisburgensis, which seems to have lost a large fraction of its past distribution (Figure 7). Most of the other arctic-alpine taxa responded similarly to Dryas octopetala, while five taxa (Phleum alpinum, Polystichum lonchitis, Saxifraga paniculata, Sedum annuum and Veronica serpyllifolia subsp. humifusa) had a response similar to that of Euphrasia salisburgensis (Table S5). Both Dryas octopetala and Euphrasia salisburgensis are predicted to lose a significant portion of their range in the coming decades (Table S5; Figures 8 and S14–S19). Euphrasia salisburgensis, Oxyria digyna, Phleum alpinum and Saxifraga paniculata are projected to become locally extirpated in the coming decades, while the rest of the arctic-alpine taxa occurring in Greece are projected to experience severe range reductions until the end of the 21st century (Table S5).



Figure 6. Distributional centroids for the L1 (A) CWE and (B) SR hotspots. Colour circles represent the distributional centroids of the current (orange), the CCSM4 2.6 RCP (red), the CCSM4 8.5 RCP (pink), the BCC 2.6 RCP (black), the BCC 8.5 RCP (dark green) and the LGM (dark blue) time-periods.



**Figure 7.** Projected potential distribution map for the LGM time-period for (**A**) *Dryas octopetala* and (**B**) *Euphrasia salisburgensis*. Light grey grid cells: The species was projected to have been present in these areas during the LGM but does not currently occur there. Red grid cells: The species is currently projected to be present in these areas and had occupied them during the LGM. The black solid line delineates the species' potential distributional area in Greece based on the alpha-hull method.



**Figure 8.** Projected potential distribution map for 2070 and the BCC GCM and the RCP 8.5 scenario for (**A**) *Dryas octopetala* and (**B**) *Euphrasia salisburgensis*. Red grid cells: The species is currently projected to occur there but will not occur there in the future. Blue grid cells: The species is currently projected to occur there and will continue to occur there in that time-slice. Light grey grid cells: The species is not currently projected to occur there in that time-slice. The black solid line delineates the species' potential distributional area in Greece based on the alpha-hull method.

## 4. Discussion

The rugged topography of the southern Mediterranean mountain ranges offered shelter to numerous cold-adapted, arctic-alpine species [17,22,118,119]. These extirpation-prone [10–12], glacial relicts reach their southernmost distributional limits in Greece [1,18,21]. Several studies exist regarding the molecular ecology of these species and the climate-change impacts on their distribution in the Alps and Fennoscandia [12,13,41–47], yet how the southernmost populations of the arctic-alpine taxa might respond to the ongoing and future thermophilization still remains unknown. Here, we (a) conducted the first ever climate-change assessment of the southernmost populations of the arctic-alpine biodiversity hotspots in Greece and (c) investigated whether these hotspots might shift in the future, aiming to provide adequate scientific evidence to timely support conservation decisions and policy making towards climate change mitigation and adaptation measures regarding mountain biodiversity, following the objectives of the UN Sustainable Development Goals [120].

## 4.1. Climate-Change Impacts

Climate change affects high mountain ecosystems at a galloping rate, resulting in extensive—observed or anticipated—range changes, abrupt beta-diversity fluctuations and elevated vulnerability to a multitude of stressors, such as invasive/neonative species and land-use changes (e.g., habitat alteration due to forest expansion or increased urbanization; [121] and references therein). This has already led to physiological and phenological shifts, as well as to modifications of ecosystem processes ([121] and references therein). Rear-edge populations of cryophilic species are expected to experience more pronounced range declines and will most probably be unable to track their niche [122]. In addition, the pressure imposed due to altering climate regimes, high-altitude specialists, such as the arctic-alpine taxa, are faced with the upward migration of more common, competitive, thermophilic species, which will quite likely dislocate the former from the lower end of their altitudinal distribution, thus constraining even more their already available niche space ([121] and references therein). This phenomenon will be further aggravated by the low dispersal ability, slow dispersal rates and limited phenotypic plasticity that higher-elevation plants usually exhibit ([121] and references therein). Arctic-alpine plants occurring in Greece-irrespective of their EOO, life-form and reproduction strategy-seem to be also facing dire prospects, since they are projected to experience substantial range contractions and will be faced with an increased extinction risk in the near future (Table S5), despite persisting so far south from their core distribution for ca. 20 Ky. This is especially worrying, since rear-edge populations are considered to harbour high levels of standing genetic variation and their local extirpation might lead to excessive evolutionary history loss [9,123,124]. Plant population genetic data for rare or endangered species are rather scant in Greece (e.g., [55,56,58,125–128]) and our knowledge is rather limited as well regarding the population genetics of the arctic-alpine taxa occurring there [128]. Dryas octopetala displays moderate genetic diversity in Greece, which is probably a result of a driving genetic drift effect, clonality and longevity [128]. Longed-lived perennial dwarfs, such as Dryas octopetala and the other arctic-alpine taxa occurring in Greece, usually display slow evolutionary responses and thus evolutionary adaptation seems unlikely to forestall their anticipated range reductions, even if these taxa had higher genetic diversity than high latitude populations, which at least for *D. octopetala* is not true [129]. Thus, for one, we need to better understand the population genetics of the arctic-alpine taxa in Greece, since we are unaware if these southern populations are sufficiently intraspecifically genetically and ecologically diverse [130] (especially those that have experienced little to none range decline since the LGM, such as most of the arctic-alpine taxa occurring in Greece; Table S5), so that they can actually genetically 'rescue' their northern counterparts via the introduction of warm-adapted genotypes ([131] and references therein) and second, there seems to be an extinction-debt present in these taxa, due to their reproduction strategy and life-form history, as long-lived perennials can withstand harsh conditions for an extended

period of time, yet display limited adaptive capacity ([132] and references therein), meaning that there might be a prolonged stability phase masking the deleterious effects of climate change on these taxa [133]. We should note that our forecasts are conservative, since we did not incorporate in our models any potential biotic interactions (e.g., uphill-moving strong competitors) which are more influential in species' warm-limits [134] or take into account the effects of land-use change, which is expected to be a major driver of biotic homogenization in mountain ecosystems globally ([121] and references therein).

#### 4.2. Species Richness Hotspots

Greek mountains are species-rich areas, serving as diversity museums, while constituting long-lasting refugia [19,20]. They seem to have fostered the persistence of the arctic-alpine taxa occurring in Greece, as most of these taxa are located in the northern tips of the Pindos mountain range and in other northern Greek mountains, such as Mt. Olympus, Vermio, Mt. Falakron and Mt. Kajmakcalan (Figures 4B and 5B). These areas comprise low-latitude safe-havens due to their increased topographical complexity and have acted as buffers against the rising temperature and aridity during the transition from the LGM to Late Holocene, hosting apart from several cold-adapted species, numerous range-restricted Greek endemics and displaying phylogenetic clustering [135]. LGM hotspots were probably located at significantly lower altitudes (Table S6) near several lakes and damp, lowland plains in northern Greece (Figures 4A and 5A), as arctic-alpine taxa have a cold-wet ecological optimum [136,137] and precipitation/aridity related variables seem to drive the potential distribution of most of the arctic-alpine plants occurring in Greece (Tables S3 and S4). Climate-change will undoubtedly alter these biodiversity patterns, since many taxa are projected to become locally extinct (Table S2; Figures 4C and 5C). Consequently, we anticipate an abrupt latitudinal and altitudinal shift in the next decades regarding the location of arctic-alpine biodiversity hotspots in Greece, with these migrating downwards and to the north-east (Figure 6). Mt. Olympus, the highest Greek mountain, will presumably act as a buffer against the impacts of climate-change for some of these species (i.e., those not projected to become locally extinct; Table S5), as it seems it will also serve as such for several pollinators [138], which are equally sensitive to climate oscillations. Our findings corroborate earlier studies dealing with the projected demise of arctic-alpine taxa all over the globe, such as Spain [139,140], the Alps [141], Central Europe and Fennoscandia [12,13,47,48], the Carpathians [13], Korea [142], Mexico [143] or elsewhere [144,145]. As arctic-alpine taxa are weak competitors, locally rare, comprising small populations, facing a multitude of threats and presumably act as agents of the entire biome they occur [143], they might provide insight regarding the climate-driven extinction risk forecast of the rarest or most endangered Greek mountain endemics, since range reductions are projected to be more pronounced for high-mountain endemic taxa [26,39,103].

## 4.3. Conservation Implications

According to our results, arctic-alpine taxa in Greece will be faced with a severe shrinkage or even loss of their habitat, a condition that sets any efforts for the protection of their populations at stake, since the escalator to extinction effect and other climate-change induced factors such as the upslope-shifting of lowland species, will determine their fate of survival over the next decades. However, all arctic-alpine taxa that migrated as far south as Greece during the LGM, are still found in Greek mountains, a fact underlining the conservation significance of mountain landscapes and their habitats that confer resilience to climate change, particularly for arctic-alpine taxa [8]. This highlights the need to assess marginal, high altitude mountainous areas for extinction threat evidence of relict, arctic-alpine taxa and their habitats, especially where topographic buffering capacity is limited [8]. The identification and mapping of resilient to past climate and land-use changes hotspots provides a valuable tool for setting conservation priorities at the scale of areas and ecosystems instead of focusing only on endangered species [8]. Moreover, these outcomes support scientifically informed decision making for management, zonation, area

prioritization and licensing actions, especially within protected areas or at mountainous sites where e.g., development projects are designed.

According to the UN Sustainable Goals [120], national conservation strategies need to incorporate mountain biodiversity assessments, as mountain species and ecosystems are especially sensitive to climate- and land-use changes. Thus, regarding Greece, conservation measures could initially include a cost-effective monitoring of arctic-alpine taxa under the periodically conducted Habitat's Directive reporting scheme, where all of their habitats within Sites of Community Importance are also assessed. By this, a baseline of current pressures and threats will be developed that will guide specific future steps for conservation measures and actions for arctic-alpine taxa, their habitats and all other taxa found in similar environments (e.g., high-altitude Greek endemics), adding another resource to the decision-makers' toolbox regarding the conservation management implementations in Greece [19].

In parallel, ex situ conservation measures should be designed and implemented, to minimize the risk of losing a vast amount of the genetic diversity included in the Greek arctic-alpine populations, thus making a step forward towards the Aichi Biodiversity Target 8, i.e., the ex situ conservation of the most threatened plant species [146]. These ex situ conservation measures could include the following: (i) seed collection and deposition in seed banks, (ii) germplasm collection and curation and (iii) population augmentation from populations grown in botanical gardens. The aforementioned ex situ conservation interventions could be supplemented with an array of in situ conservation actions to further alleviate the potential extinction risk of the arctic-alpine taxa occurring in Greece, such as long-term population monitoring, assisted colonization and reproduction, mitigation translocations, micro-reserve establishment and control/eradication of invasive alien plants, according to the IUCN Guidelines [147].

## 5. Conclusions

Arctic-alpine taxa in Greece have survived climatic oscillations and biotic stressors for several millennia in a rather inhospitable environment, so they are no strangers to adverse conditions. However, despite their innate resilience, their future prospects do not seem so bright in their southernmost distributional limit in the coming decades. Most of the cold-adapted arctic-alpine taxa in Greece will most probably become locally extinct or face significant range reductions, due to the synergistic effects of land-use and climate-change, as well as due to the increased interspecific competition and other negative biotic interactions (e.g., herbivory, disease; [148]) from upslope-shifting lowland species, which are bound to intensify in the near future in the southern Mediterranean [26,35,149]. It thus seems there is an 'extinction-lag' present in the Greek high mountains, which is in line with the trend revealed for cold-adapted species elsewhere [150] and with recent findings for the Greek endemic flora [19]. The repercussions of this apparent extinction-debt may be further exacerbated by the low seed viability and recruitment arctic-alpine species often display [151], which in turn are negatively affected by short and warm winters [152], such as the ones the southern Mediterranean mountains are expected to experience in the foreseeable future (e.g., [137,153] and references therein). Consequently, several conservation actions are urgently warranted, such as precise, long-term demographic monitoring and an analysis of the arctic-alpine species' population genetic diversity, since phenotypic plasticity may act as a short-term buffer against climate-change for isolated, rare and genetically depauperate species [154,155]. Arctic-alpine taxa could serve as beacons for climate risk-assessment models for other rare and range-restricted species [143], such as the threatened Greek endemics, due to the sensitivity of their rear-edge populations to climate-related changes [9].

**Supplementary Materials:** The following are available online at https://www.mdpi.com/article/ 10.3390/su132413778/s1, Figure S1: Bivariate map of the habitat suitability values and the corresponding prediction uncertainty for *Phleum alpinum* in Greece. The dashed line delineates the species' potential distributional area in Greece based on the alpha-hull method, Figure S2: Bivariate map of the habitat suitability values and the corresponding prediction uncertainty for *Polystichum lonchitis* in Greece. The dashed line delineates the species' potential distributional area in Greece based on the alpha-hull method, Figure S3: Bivariate map of the habitat suitability values and the corresponding prediction uncertainty for Saxifraga paniculata in Greece. The dashed line delineates the species' potential distributional area in Greece based on the alpha-hull method, Figure S4: Bivariate map of the habitat suitability values and the corresponding prediction uncertainty for Sedum annuum in Greece. The dashed line delineates the species' potential distributional area in Greece based on the alpha-hull method, Figure S5: Mean difference of species richness between the present time-period and the Last Glacial Maximum (LGM; i.e., from the LGM species richness raster we subtracted the current species richness and then calculated the average of all the arctic-alpine taxa occurring in Greece and included in our analyses), Figure S6: Mean difference of species richness between GCM/RCP and current status (i.e., from each GCM/RCP species richness raster we subtracted the current species richness and then calculated the average of all the arctic-alpine taxa occurring in Greece and included in our analyses), Figure S7: L1 (top 1%) CWE hotspots (green cells) for the BCC 2.6 RCP time-period, Figure S8: L1 (top 1%) CWE hotspots (green cells) for the CCSM4 2.6 RCP time-period, Figure S9: L1 (top 1%) CWE hotspots (green cells) for the CCSM4 8.5 RCP time-period, Figure S10: L1 (top 1%) SR hotspots (green cells) for the BCC 2.6 RCP time-period, Figure S11: L1 (top 1%) SR hotspots (green cells) for the BCC 8.5 RCP time-period, Figure S12: L1 (top 1%) SR hotspots (green cells) for the CCSM4 2.6 RCP time-period, Figure S13: L1 (top 1%) SR hotspots (green cells) for the CCSM4 8.5 RCP time-period, Figure S14: Projected potential distribution map for 2070 and the BCC GCM and the RCP 2.6 scenario. Red grid cells: Dryas octopetala is currently projected to occur there but will not occur there in that time-slice. Blue grid cells: Dryas octopetala is currently projected to occur there and will continue to occur there in that time-slice. Light grey grid cells: Dryas octopetala is not currently projected to occur there and is not projected to occur there in that time-slice, Figure S15: Projected potential distribution map for 2070 and the CCSM4 GCM and the RCP 2.6 scenario. Red grid cells: Dryas octopetala is currently projected to occur there but will not occur there in that time-slice. Blue grid cells: Dryas octopetala is currently projected to occur there and will continue to occur there in that time-slice. Light grey grid cells: Dryas octopetala is not currently projected to occur there and is not projected to occur there in that time-slice, Figure S16: Projected potential distribution map for 2070 and the CCSM4 GCM and the RCP 8.5 scenario. Red grid cells: Dryas octopetala is currently projected to occur there but will not occur there in that time-slice. Blue grid cells: Dryas octopetala is currently projected to occur there and will continue to occur there in that time-slice. Light grey grid cells: Dryas octopetala is not currently projected to occur there and is not projected to occur there in that time-slice, Figure S17: Projected potential distribution map for 2070 and the BCC GCM and the RCP 2.6 scenario. Red grid cells: Euphrasia salisburgensis is currently projected to occur there but will not occur there in that time-slice. Blue grid cells: Euphrasia salisburgensis is currently projected to occur there and will continue to occur there in that time-slice. Light grey grid cells: Euphrasia salisburgensis is not currently projected to occur there and is not projected to occur there in that time-slice, Figure S18: Projected potential distribution map for 2070 and the CCSM4 GCM and the RCP 2.6 scenario. Red grid cells: *Euphrasia salisburgensis* is currently projected to occur there but will not occur there in that time-slice. Blue grid cells: Euphrasia salisburgensis is currently projected to occur there and will continue to occur there in that time-slice. Light grey grid cells: Euphrasia salisburgensis is not currently projected to occur there and is not projected to occur there in that time-slice, Figure S19: Projected potential distribution map for 2070 and the CCSM4 GCM and the RCP 8.5 scenario. Red grid cells: Euphrasia salisburgensis is currently projected to occur there but will not occur there in that time-slice. Blue grid cells: Euphrasia salisburgensis is currently projected to occur there and will continue to occur there in that time-slice. Light grey grid cells: Euphrasia salisburgensis is not currently projected to occur there and is not projected to occur there in that time-slice, Table S1: The arctic-alpine taxa occurring in Greece, Table S2: The uncorrelated predictor variables used in the main analyses, along with their abbreviations, Table S3: Evaluation of models' predictive performance via several discrimination (AUC, AUC-PR, TSS) and calibration [Brier score, Cohen's kappa, Continuous Boyce Index (CBI), Somer's D] metrics based on a repeated (10 times) split-sampling (calibration data: 80%; evaluation data: 20%) approach. The abbreviations of the predictor variables are as in Table S2. EOO: Extent of Occurrence (in sq. km), Table S4: Variable importance for each of the arctic-alpine taxa occurring in Greece and included in our analyses. The abbreviations of the predictor variables are as in Table S2, Table S5: Proportion of potential area loss for each of the arctic-alpine taxa occurring in Greece and included in our analyses for every time-period and climate change model/scenario. GCM: Global Circulation Model. LGM: Last Glacial Maximum. RCP: Representative Concentration

Pathway, Table S6: Median, mean, minimal and maximal altitude (in m) for species richness (SR) and the corrected weighted endemism (CWE) hotspots. L1 SR and CWE hotspots are delineated as the cells belonging to the 1% quantile for each metric for each GCM/RCP combination. GCM: Global Circulation Model. IQR: Interquartile range. LGM: Last Glacial Maximum. RCP: Representative

**Author Contributions:** Conceptualization: K.K., I.P.K. and P.D.; investigation: K.K. and I.P.K.; methodology: K.K. and I.P.K.; formal analysis: K.K.; resources: A.S., T.R. and P.D.; supervision: P.D.; writing—original draft preparation: K.K., I.P.K., T.R., A.S. and P.D.; writing—review and editing: K.K., I.P.K., T.R., A.S. and P.D.; visualization: K.K. and I.P.K. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Concentration Pathway. SD: Standard deviation.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

**Conflicts of Interest:** The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

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