

## Climate change effects on multi-taxa pollinator diversity and distribution along the elevation gradient of Mount Olympus, Greece

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### ABSTRACT

Climate change is predicted to dramatically affect mountain biodiversity and especially mountain pollination systems due to the mutual dependence between plants and pollinators. In this work, we investigate climate change effects on pollinator distribution and diversity along the altitudinal gradient of Mt. Olympus, a biodiversity hotspot.

We used a species distribution modelling framework and predicted species richness hotspots, potential distribution and altitude change for 114 pollinator species, comprising bees, butterflies, and hoverflies along the altitudinal gradient (327–2596 m a.s.l.).

We projected potential loss of suitable habitat and upward shift for most pollinator groups, with the exception of bumblebees and hoverflies which were predicted to descend. Pollinator extinctions were not forecasted; instead, we observed a pronounced species-specific response to climate change. Species richness hotspots will be relocated to higher altitudes and to the north-eastern mountain side.

Projections for substantial but not detrimental climate change effects on pollinator fauna may be due to species differential resilience to climate change along with the existence of microrefugia on Mt. Olympus. Divergent response to global warming by bumblebees and hoverflies is probably due to species distribution modelling limitations, resulting in exclusion of the rarest species. We conclude that the predicted climate change impact stresses for the need of urgent conservation measures, including the expansion of the protection status over the whole mountain.

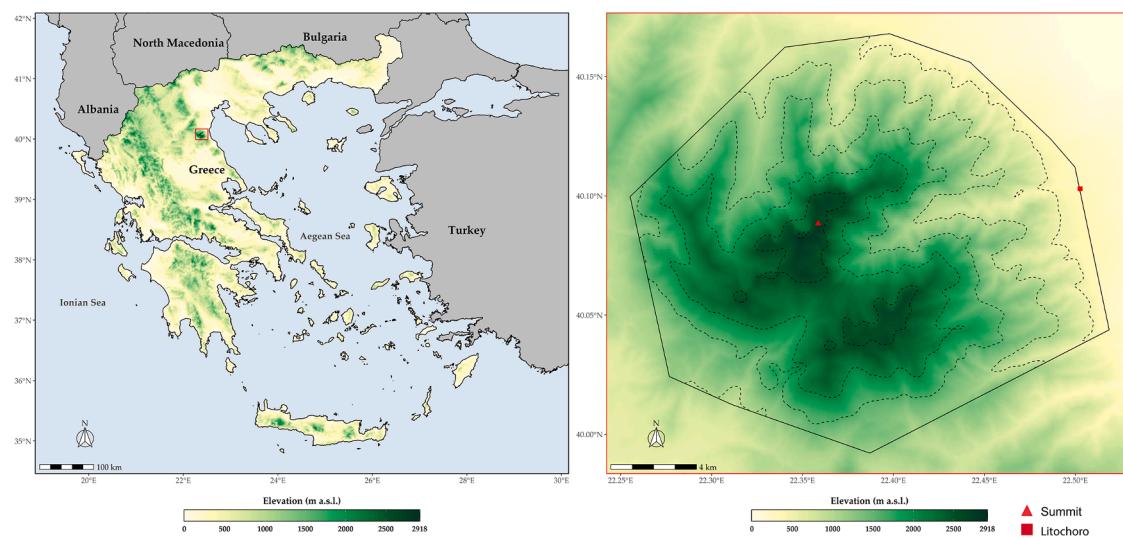
### 1. Introduction

Mountains represent ca. 12% of earth's terrestrial surface (Körner et al., 2017; Körner et al., 2011), sustain the vast majority of mammal, amphibian, and bird species, and nearly one third of the known terrestrial plant species (Körner, 2007; Rahbek et al., 2019). These systems constitute conservation priority areas and excellent models for testing physiological, ecological, and evolutionary hypotheses within small spatial scales due to their high biodiversity and endemism (Körner, 2004; Körner, 2007). Climate change is predicted to affect mountain ecosystems (Seddon et al., 2016) by driving species upslope, enhance species invasion and disrupting ecosystem services, such as pollination (Inouye, 2020; Vasiliev and Greenwood, 2021). Hence, mountains should be placed under the spotlight to predict the future status of pollinator assemblages and plant-pollinator interactions (Lefebvre et al., 2018; Tito et al., 2020).

Climate change is considered as main driver of the historically unparalleled global insect decline (Cardoso et al., 2020; Sánchez-Bayo and Wyckhuys, 2021; Zattara and Aizen, 2021). In this context, the observed decline of insect pollinators and the crucial pollination services they provide to terrestrial ecosystems are especially worrying (Ollerton et al., 2011). Insect pollinator decline in mountain ecosystems will probably have a profound effect on mountain biodiversity, as pollinators ensure reproduction of wild plant species (Inouye, 2020; Potts et al., 2010). Although there is a great interest in climate change impacts on pollinator fauna in mountain and alpine environments (see Inouye, 2020 for a review), studies using species distribution models combined with future climatic projections on mountain environments are still scarce and restricted to specific pollinator groups (Biella et al., 2017; Martínez-López et al., 2021; Rödder et al., 2021). After all, studies along altitudinal gradient could enable prediction of long-term ecological responses to climate change, using space-for-time substitution scenarios (Mayor

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**Fig. 1.** Map showing the study area of Mt. Olympus, Greece. Dashed lines represent the 500-m contour lines.

et al., 2017).

Mediterranean mountains constitute biodiversity hotspots and endemism centres (Blondel et al., 2010; Médail, 2017), a result of their high topographic and climatic heterogeneity, as well as their glacial history during which they served as refugia that conditioned and promoted population differentiation and speciation (Hewitt, 2004; Kougioumoutzis et al., 2021a; Médail and Diadema, 2009). Meanwhile, the Mediterranean Basin and especially its mountains are among the most susceptible regions to climate change, facing the highest desertification risk worldwide (Giorgi and Lionello, 2008; Hill et al., 2008). Consequently, Mediterranean mountain biodiversity will be affected severely (Bravo et al., 2008; Kougioumoutzis et al., 2020; Pauli et al., 2012), especially due to the “escalator to extinction” phenomenon [species moving upslope to track their niche and thus the species now occurring at the highest altitudes will probably become extinct, as e.g., temperature rises beyond what they can tolerate; Urban (2018)]. This will have an immense impact on ecosystem services, like pollination, due to potential extinction of pollinator species, such as the cold – adapted bumblebees (Kerr et al., 2015; Soroye et al., 2020). Indeed, the strong interdependence between pollinators and their host plants results in a complex system where climate change effects could be mitigated or intensified (Inouye, 2020; Vitassee et al., 2021).

Mount Olympus (2918 m a.s.l.), the highest Greek mountain and a legendary landmark, is a circular massif of 25 km diameter on average, situated near the central-east coast of Greece. Hosting > 1700 plant taxa (25% of the Greek flora), including 58 Greek endemics, 25 of which are endemic to Mt. Olympus (Strid, 1980; Strid and Tan, 1986; Strid and Tan, 1991), the mountain is among the Greek extinction risk hotspots (Kougioumoutzis et al., 2021b). Glaciers on Mt. Olympus continued to be present during the Pleistocene interglacial periods and even up to the Holocene (Smith et al., 1997; Styllas et al., 2018). This suggests, that apart from a biodiversity hotspot and endemism centre, population differentiation and speciation went on during the rather recent geological past, when Mt. Olympus constituted a refugium for cold-adapted species (Hewitt, 2004; Kougioumoutzis et al., 2021a; Médail and Diadema, 2009). Because of its high altitude, the rich zonation along its elevation gradient, separation from other mountain ranges, high diversity of flora and fauna, and glacial history, Mt. Olympus is considered a model system for ecological, evolutionary, and biogeographical studies (Strid, 1980).

Mt. Olympus offers the opportunity for extensive research on climate change impacts along the altitudinal gradient of a high mountain. Climate change has already affected the mountain's vegetation: the tree line has shifted ca. 400 m upwards during the last 60 years and the

mountain lost more than one quarter of its forest-bare area, all this attributed to the temperature rise in the growing season due to global warming (Zindros et al., 2020). This is corroborated by dendrochronological data, which showed significant deviations in temperature and precipitation over the last decades, indicating a warming and drying trend since 1975 (Klesse et al., 2015). Therefore, Mt. Olympus is certainly qualified to become a natural laboratory for climate change experiments (Tito et al., 2020), especially considering its geographical position in the Mediterranean Basin, an area predicted to be severely affected by global warming (Giorgi and Lionello, 2008; Hill et al., 2008).

This work is part of a wider research project aiming at investigating pollination ecology along the altitudinal gradient of Mt. Olympus. As documented in an earlier study of some of us, the mountain hosts a very rich bumblebee fauna and some species of potential extinction risk (Minachilis et al., 2020). Here, we employ a species distribution modelling framework and address the following questions:

- (i) Which is the current status in the pollinators' distribution along the altitudinal gradient of Mt. Olympus?
- (ii) How will climate change influence the pollinators' distribution along the altitudinal gradient of Mt. Olympus?
- (iii) Will the climate change impact vary among the different pollinator groups?
- (iv) What are the current and future locations of pollinator species richness hotspots on Mt. Olympus?

## 2. Materials and methods

### 2.1. Study area

The study area is almost circular, with a diameter of ca. 20 km, including most of Mt. Olympus massif with the lowest altitude found at ca. 300 m (Litochoro) and the highest at 2918 m (summit) (Fig. 1). Almost half of this area, specifically its eastern side, is part of the Olympus National Park, historically the first national park ever designated in Greece (1938), part of which constitutes a European Natura 2000 site (GR 1250001). The tree line mean altitude is at 2016 m (Zindros et al., 2020). Mountain climate is Mediterranean at lower altitudes, temperate at intermediate to higher ones, with snow covering areas above 2000 m from late October to late May (Strid, 1980).

### 2.2. Species occurrence data

Insect pollinator surveys were conducted in ten sampling sites with

**Table 1**  
Potential loss of suitable habitat and mean, minimal, maximal altitude and altitudinal range change prediction per pollinator group on Mt. Olympus (average of all GCM and RCP). Species codes denote pollinator species as coded in Table S1. Difference values were calculated by subtracting current from future values.

Pollinator group	Species code	Mean potential loss of suitable habitat (%)	Current Mean Altitude (m)	Future Mean Altitude (m)	Current Minimal Altitude (m)	Future Minimal Altitude (m)	Current Maximal Altitude (m)	Future Maximal Altitude (m)	Current Altitudinal Range (m)	Future Altitudinal Range (m)	Altitudinal Range Difference (m)		
All Pollinators	A139–	29.83	1415	1464	49	619	562	–58	2241	2279	38		
All Bees	A651	31.76	1383	1443	60	635	589	–46	2174	2231	57		
Bumblebees	A540	20.63	1649	1623	–27	636	570	–66	2495	2466	–29		
Non-bumblebee bees	A299	34.22	1325	1404	78	634	593	–41	2104	2180	76		
Hoverflies	A216–	34.22	A271 & A302–	A540	20.97	1625	1614	–11	645	540	–105		
Butterflies	A209	30.93	A599–	A651	31.17	1389	72	489	446	–43	2220	2269	49

average altitudinal difference ca. 250 m on the north-eastern slope of Mt. Olympus. The surveys aimed to collect insect pollinators and were carried out on a monthly basis from May to October during three years: 2013 and 2014, employing both pan traps and hand netting in variable transect walks; and 2016, employing only hand netting. Pan traps were placed as five sets of three plastic bowls (triplets), each pan trap within a triplet painted with a different UV-bright colour (blue, yellow, and white). Each pan trap was filled with a mixture of propylene glycol and water (1:1 in volume) and left open to capture insects for a week. Hand netting was performed in days with fine weather favourable to insect activity, during the active foraging hours (10:00–16:00) and lasted 90 min/site in 2013, and 120 min/site in each of the years 2014 and 2016 (Minachilis et al., 2020). Our database comprised 8803 pollinator specimens belonging to hoverflies (Diptera: Syrphidae), bees (Hymenoptera: Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae) and butterflies (Lepidoptera: Hesperiidae, Lycaenidae, Nymphalidae, Pieridae, Sphingidae). In our analysis we used 8514 specimens identified to species level, with the exception of *Bombus lucorum* s.l. (a complex consisting of three species: *B. lucorum*, *B. cryptarum* and *B. magnus*) and *B. terrestris*; records of all the above four species were pooled together as belonging to one group because they are indistinguishable when observed on the wing (Bossert et al., 2016; Wolf et al., 2010). To enrich our pollinator data, we searched in Global Biodiversity Information Facility (GBIF) for pollinator species occurrence data on Mt. Olympus area, which added to our dataset only 26 pollinator occurrence records.

From the entire number of insect pollinator species collected on the mountain (457 species), our final dataset comprised 114 species since we modelled only those species found in more than three sites (van Proosdij et al., 2016) (Table S1). In this study we considered the following six pollinator groups:

- All pollinators: 114 species.
- All bees (Hymenoptera: Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae): 78 species.
- Bumblebees (Hymenoptera: Apidae: *Bombus*): 13 species and one species group (see above).
- Non-bumblebee bees: other than *Bombus*, as described above: 64 species.
- Hoverflies (Diptera: Syrphidae): 25 species.
- Butterflies (Lepidoptera: Hesperiidae, Lycaenidae, Nymphalidae, Pieridae, Sphingidae): 11 species.

### 2.3. Environmental data

We generated spatially gridded climate data using the ClimateEU v4.63 software (available from [https://springnature.figshare.com/collections/ClimateEU\\_Scale-free\\_climate\\_normals\\_historical\\_time\\_series\\_and\\_future\\_projections\\_for\\_Europe/4846122](https://springnature.figshare.com/collections/ClimateEU_Scale-free_climate_normals_historical_time_series_and_future_projections_for_Europe/4846122)) following the framework described in Hamann et al. (2013), Marchi et al. (2020) and Wang et al. (2012) at ca. 90 m resolution. We estimated monthly climate data for the baseline period 1970–2000, based on altitudinal data obtained from MERIT-DEM [[http://hydro.iis.u-tokyo.ac.jp/~yamadai/MERIT\\_DEM/](http://hydro.iis.u-tokyo.ac.jp/~yamadai/MERIT_DEM/); Yamazaki et al. (2017)] at ca. 90 m resolution. As a next step, using the function “biocars” from the “dismo” 1.1.4 R package (Hijmans et al., 2017), we constructed 19 bioclimatic variables. Afterwards, using functions from the “enviro” 2.2 R package (Title and Bemmels, 2018), we generated 16 additional bioclimatic variables. Then, using functions from the “raster” 2.6.7 (Hijmans, 2019) and the “spatialEco” 1.2–0 R packages (Evans et al., 2019), we estimated supplementary topographical variables (aspect, heat load index, slope, topographic position index and terrain ruggedness index) based on the altitudinal data.

Regarding future projections, we obtained data for 2080 (average for years 2071–2100) for two (CCSM4 and HadGEM2) Global Circulation Models (GCMs) according to McSweeney et al. (2015) and two different Intergovernmental Panel on Climate Change scenarios from the

Representative Concentration Pathways family: RCP4.5 (mild scenario) and RCP8.5 (severe scenario), following the same procedure as described above. We also obtained data from an ensemble of 15 climate models as an extra precautionary measure of climate projections uncertainty.

We used the “vifcor” function from the “usdm” 1.1.18 R package to assess multicollinearity (Naimi et al., 2014). From this initial set of 41 predictors, only five [aspect, heat load index (indicating the temperature of a slope considering solar radiation, aspect and steepness; describes the fact that a southwest facing slope should have warmer temperatures than a southeast facing slope, even though the amount of solar radiation they receive is equivalent), isothermality (i.e., the ratio of mean diurnal range over annual temperature range, with high values indicating stable climatic conditions throughout the year, whereas small values indicating strong seasonality), mean temperature of the wettest quarter, precipitation seasonality] did not have a collinearity problem (Spearman rank correlation < 0.7 and VIF < 10; Table S7) and were thus included in the analyses (Dormann et al., 2013).

## 2.4. Species distribution models

### 2.4.1. Model parameterization and evaluation

We modelled the realized climatic niche of all species included in our analysis under the Ensemble of Small Models (ESM) framework (Breiner et al., 2015; Breiner et al., 2017; Breiner et al., 2018), which is suitable for modelling rare species, using the Random Forest (RF) modelling algorithm [single-technique ESMs perform equally as good as double ensembles; Breiner et al. (2017)], which is robust to overfitting (Lawler et al., 2006). We generated pseudo-absences following Barbet-Massin et al. (2012) at a minimum distance of 1 km from presence locations, which equals to the median autocorrelation distance among the non-collinear environmental variables, using functions from the “blockCV” 1.0.0 R package (Valavi et al., 2019). ESMs were then calibrated by fitting bivariate models, which were then averaged into an ensemble model using weights based on model performances. For all the models, prevalence was equal to 0.5. We evaluated our 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 (Allouche et al., 2006; Fielding and Bell, 1997; Hirzel et al., 2006; Liu et al., 2011; Sofaer et al., 2019) based on a repeated (10 times) split-sampling (calibration data: 80%; evaluation data: 20%) approach, since relying on only one metric may lead to misleading results (Konowalik and Nosol, 2021; Leroy et al., 2018; Somodi et al., 2017). We estimated the aforementioned metrics using functions from the “CalibratR” 0.1.2, “DescTools” 0.99.40, “ecospa” 3.2, “enmSdm” 0.5.3.2, “Metrics” 0.1.4, “MLmetrics” 1.1.1 and “modEvA” 2.0, R packages (Márcia Barbosa et al., 2013; Broennimann et al., 2021; Hamner and Frasco, 2018; Schwarz and Heider, 2018; Signorell et al., 2021; Smith, 2020; Yan, 2016). We used null model significance testing (Raes and ter Steege, 2007) to evaluate the performance of our models. All analyses were run in R 4.0.3 using base R functions and functions from the “biomod2” 3.3.7 and “ecospa” 3.1 R packages (Di Cola et al., 2017; Thuiller et al., 2009).

### 2.4.2. Model projections

We projected the potential suitable area of each species included in our analysis under current and future climate conditions via an ensemble model framework (Araújo et al., 2019), based on calibrated models with TSS  $\geq 0.8$  (to avoid poorly calibrated ones). The contribution of each model to the ensemble forecast was weighted according to its TSS score. While model evaluation was carried out using the above-mentioned data-splitting procedure, the final models used for spatial projections were calibrated using 100% of the data, thus allowing taking advantage of all available data.

We binary transformed the resulting habitat suitability maps based on the metric that maximizes the sum of sensitivity and specificity (Liu

et al., 2005; Liu et al., 2016; Liu et al., 2013) and then compared them to the binary maps obtained for each GCM and RCP. As a conservative approach, the suitability of any cells that had non-zero values in the clamping mask was set to zero (Elith et al., 2010). To assess extrapolation in environmental space and thus model transferability, we estimated two complimentary metrics for each GCM/RCP combination using the “dsmextra” 1.1.4 R package (Bouchet et al., 2020): i) the ExDet metric that calculates Type 1 and Type 2 extrapolation novelty (Fitzpatrick and Hargrove, 2009; Mesgaran et al., 2014; Romero-Alvarez et al., 2017; Zurell et al., 2012) and ii) the proportion of data nearby in multivariate environmental space (%N) (Mannocci et al., 2018). The latter metric quantitatively assesses the extrapolation reliability in multivariate environmental space (Mannocci et al., 2018). Estimating extrapolation based only on ExDet may lead to an unreliable high degree of confidence in model predictions (Bouchet et al., 2019; Mannocci et al., 2018).

### 2.4.3. Area range change

We used functions from the “biomod2” 3.3.7 R package (Thuiller et al., 2009) to infer if our species will contract or expand their future range. All taxa were not assumed to have unlimited dispersal capacity, since this would be overoptimistic.

### 2.4.4. Biodiversity hotspots detection

We followed Kougioumoutzis et al. (2021a) for all spatial analyses regarding biodiversity patterns. We estimated species richness (SR) and its geographically-weighted variant (CWE – Crisp et al., 2001; Linder, 2001a; Linder, 2001b) for each grid cell using functions from Guerin (2020) and Guerin et al. (2015). CWE performs better in detecting biodiversity hotspots, even when SR is high, despite being a range-weighted and scale-dependent metric (Guerin and Lowe, 2015). We defined SR and CWE hotspots as the highest 1% of the cells (i.e., the 1% quantile; L1 hotspots) that had the highest score for each metric, following González-Orozco et al. (2011). We identified these biodiversity hotspots using functions from the ‘phyloregion’ 1.0.4 R package (Daru et al., 2017; Daru et al., 2020a; Daru et al., 2020b).

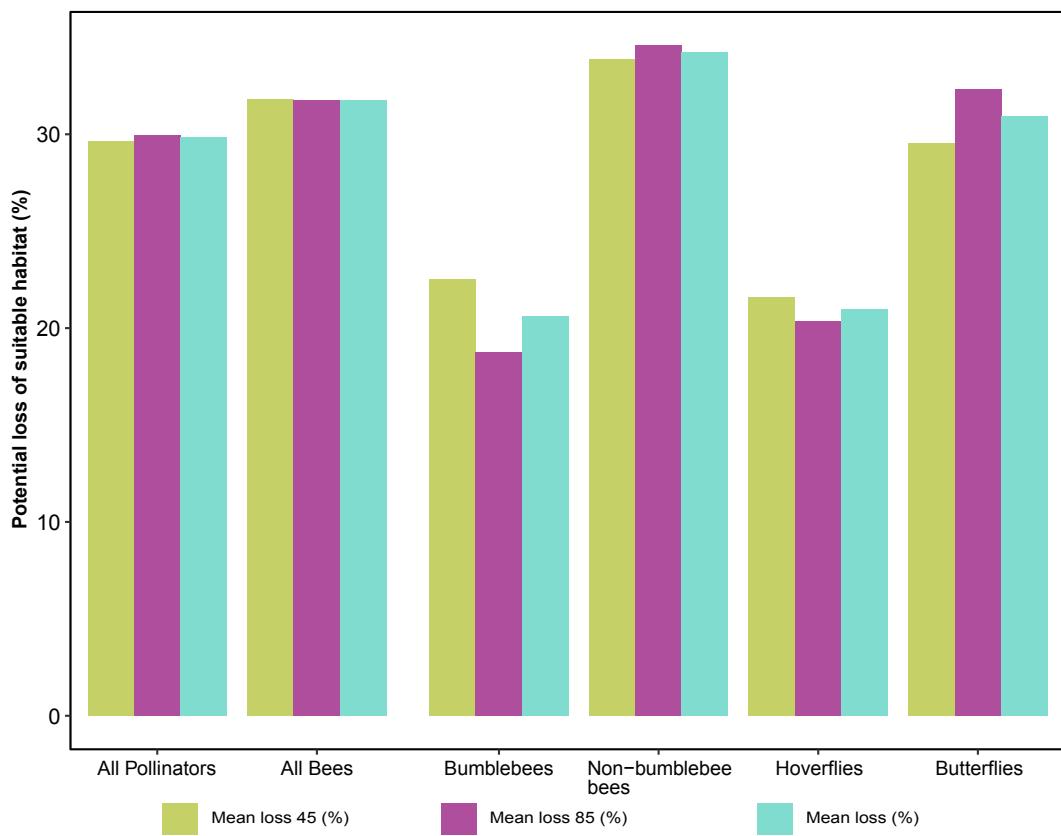
### 2.4.5. Latitudinal and altitudinal shifts of the biodiversity hotspots

We estimated the distribution centroids, as well as the median altitude for both SR and CWE hotspots, in order to test if and how their distribution may shift in the future, using functions from the “raster” 2.6.7 (Hijmans, 2019) and ‘sf’ 0.9.6 (Pebesma, 2018) R packages and via Kruskal-Wallis tests, as well as Watson tests.

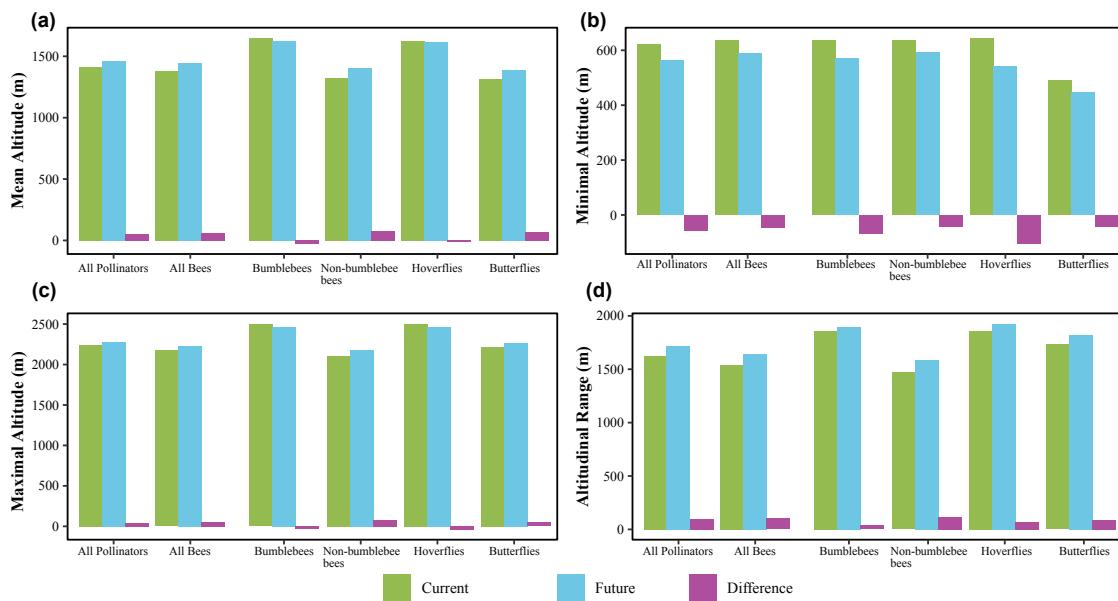
## 3. Results

### 3.1. Species distribution model performance

The vast majority of the ESM predictions had high predictive power ( $AUC \geq 0.97$ ;  $AUC-PR \geq 0.69$ ; Brier’s score  $\leq 0.09$ ; Cohen’s Kappa  $\geq 0.89$ ; CBI  $\geq 1.00$ ; Somer’s D  $\geq 0.95$ ; TSS  $\geq 0.89$  – all values refer to the mean; Table S2) and outperformed the null expectation at  $P < 0.001$  (Table S2). Isothermality (38 species) and heat load index (38 species) had the highest contribution among the environmental variables for most species, followed by aspect (14 species) (Table S3). Univariate and multivariate extrapolation novelty were minimal under any GCM/RCP combination, ranging between 0.63% and 7.58% and 0.00% – 3.64%, respectively (Table S4). The vast majority of the study area displays high similarity of environmental variables under any GCM/RCP combination (88.78% – 100.00%; Table S4, Fig. S1). The proportion of data nearby in the multivariate space was low in the higher and lower altitudes of the study area under any GCM/RCP combination, being more extreme in the HadGEM2 RCP 4.5 combination (Fig. S2).



**Fig. 2.** Potential loss of suitable habitat prediction per pollinator group on Mt. Olympus. Mean loss is the average of all GCM and RCP; Mean loss 45 is the average of CCSM4 4.5, Ensemble 4.5 and HadGEM2 4.5; Mean loss 85 is the average of CCSM4 8.5, Ensemble 8.5 and HadGEM2 8.5.



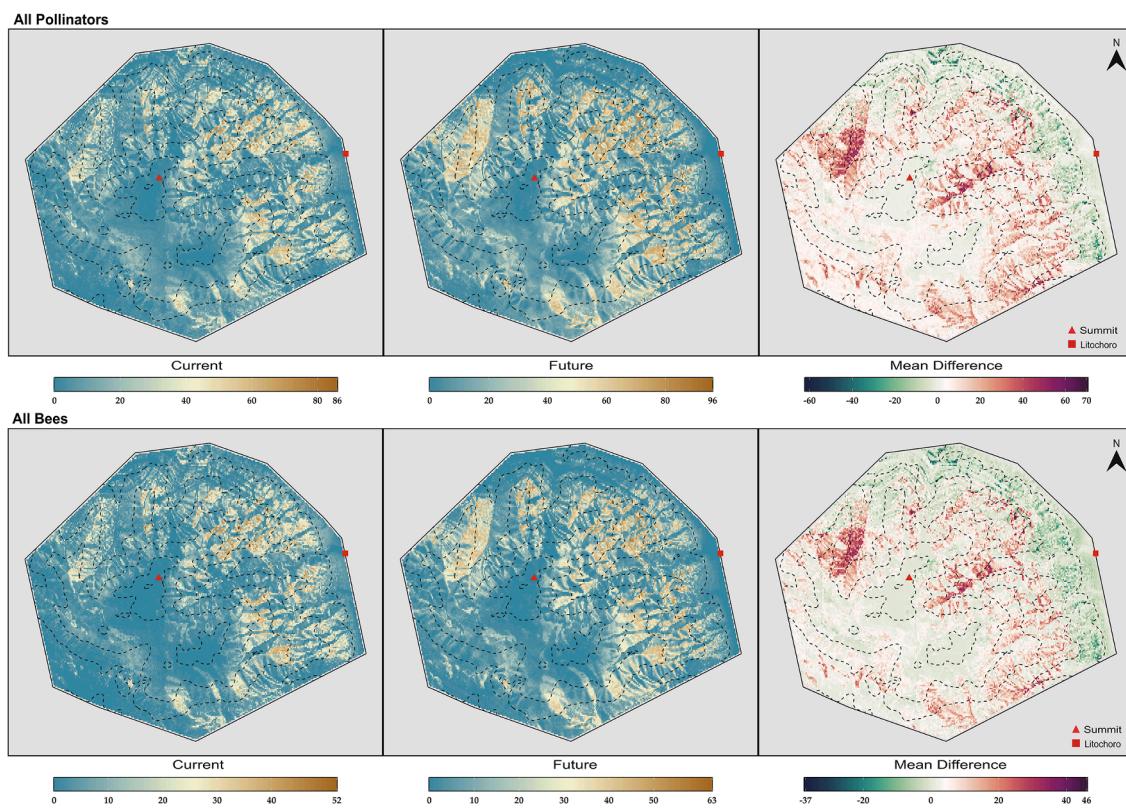
**Fig. 3.** Mean (a), minimal (b), maximal altitude (c) and altitudinal range (d) of current status, future prediction, and difference between them per pollinator group on Mt. Olympus. Future prediction values in all cases are the average of all GCM and RCP.

### 3.2. Habitat suitability range change

All species were projected to lose at least a fraction of their current suitable habitat on Mt. Olympus and this range contraction displayed high variability depending on the species (6.08% – 77.17%; Table S3). The median range contraction was 26.62% and differed significantly

between the different GCMs and RCPs (Kruskal-Wallis ANOVA:  $H = 69.73$ , d.f. = 5,  $p < 0.01$ ), with the HadGEM2 RCP 4.5 and the Ensemble RCP 4.5 combinations showing the highest and lowest mean range contractions, respectively (38.40% and 22.34%, respectively).

The non-bumblebee bees had the highest potential loss of suitable habitat while the bumblebees had the lowest followed by the hoverflies



**Fig. 4.** Species richness hotspots for all pollinators and bees on Mt. Olympus. The three maps regard the entire set of pollinator groups and represent current status, future prediction (based on the Ensemble RCP 8.5), and 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 average of all species). Dashed lines represent the 500-m contour lines.

(Table 1, Fig. 2). Butterflies' average habitat suitability loss was predicted to be among the highest (Table 1, Fig. 2). In general, the predicted area loss of suitable habitat was highly variable among species and thus species-specific (Table S3).

### 3.3. Altitudinal changes

The vast majority of the study species was projected to shift upwards. Specifically, 75 (65.79%) species were projected to increase while 39 (34.21%) species to decrease their mean altitude (Table S5). The same holds true for their altitudinal range, but not for their higher and lower limits of altitude, as most species lower their minimal (78; 68.42%) and maximal altitude (68; 59.65%) (Table S5).

Bumblebees and hoverflies were predicted to move downwards, thus decreasing their mean, minimal and maximal altitude (Table 1; Fig. 3a, b, c). The remaining pollinator groups (all pollinators, all bees, non-bumblebee bees, butterflies), were projected to move upwards and to increase their mean and maximal altitude (Table 1; Fig. 3a, c), but to decrease minimal altitude (Table 1, Fig. 3b). All groups were forecasted to expand their altitudinal range (Table 1, Fig. 3d). There is significant difference of the future altitudes the respective pollinator groups will be located on Mt. Olympus (Kruskal-Wallis ANOVA:  $H = 18.81$ , d.f. = 5,  $p < 0.01$ ), with hoverflies to occur at the lowest altitudes of all remaining pollinator groups and bumblebees to occur at lower altitudes compared to non-bumblebees (Fig. 3). Mean, minimal and maximal altitude, as well as the altitudinal range varied considerably among species in each pollinator group without following any specific trend or associating with specific species (Table S5).

### 3.4. Pollinator biodiversity hotspots

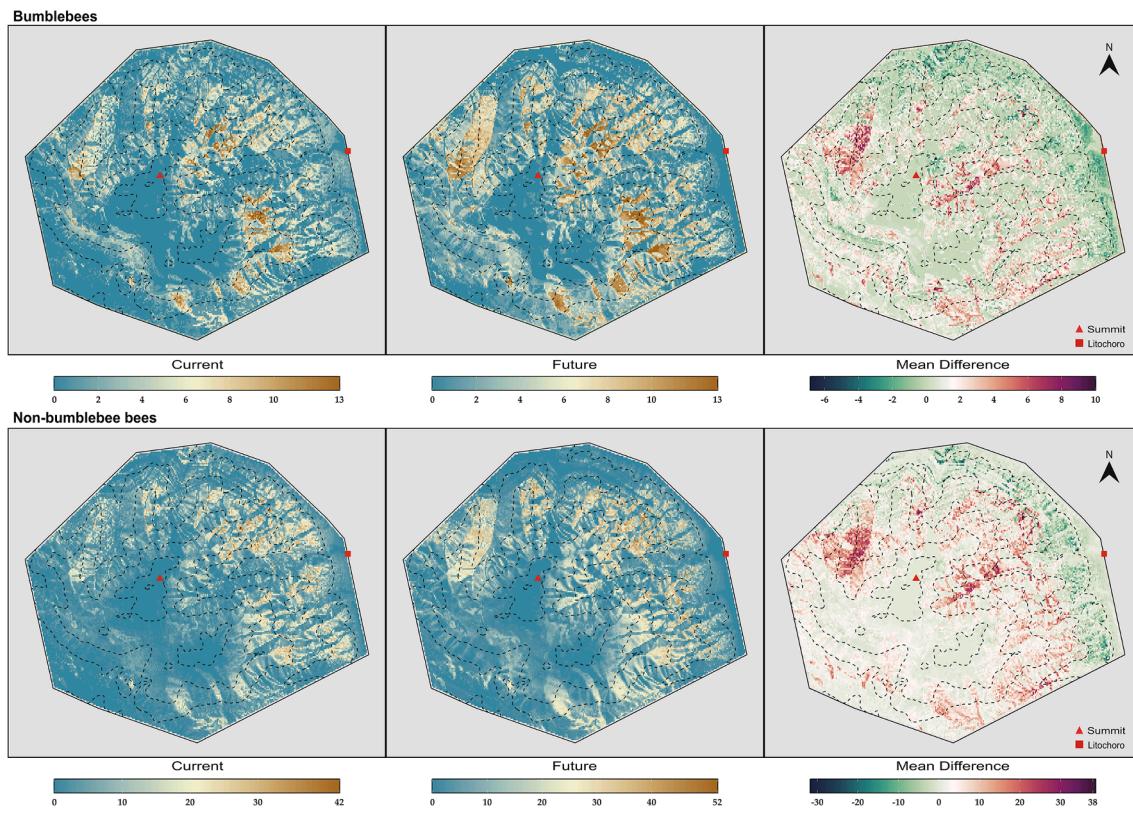
The areas identified as L1 biodiversity hotspots (for either of the two

metrics we used, viz., SR and CWE) are mainly concentrated in the eastern side of Mt. Olympus across all time-slices (Figs. 4–7); however, we detected statistically significant shifts regarding their centroids which were predicted to move to the northeast (Watson tests with  $p$ -values  $< 0.01$  at  $\alpha = 0.05$ ; Fig. 7c). Concurrently, CWE hotspots were projected to shift upwards on Mt. Olympus and to occupy intermediate altitudes in near future (Table S6, Fig. 7b); this trend was blurred regarding SR hotspots (Table S6, Fig. 7a). The mean altitude for the areas that were projected to gain or lose species in the near future equals to 1611 m (gain; range across GCMs and RCPs: 1559 m – 1660 m) and 922 m (loss; range across GCMs and RCPs: 814 m – 1324 m).

## 4. Discussion

Climate change studies along altitudinal gradients could facilitate long-term projections of global warming impact on ecosystem services, like pollination (Gómez-Ruiz and Lacher, 2019; Mayor et al., 2017). However, studies dealing with pollinator richness on a mountain system under climate-change scenarios are scarce and limited to bumblebees [*Bombus alpinus*, Alps: Biella et al. (2017); 18 species, Mesoamerica: Martínez-López et al. (2021)] and to butterflies [37 species, Alps: Rödder et al. (2021)]. On the other hand, studies considering a wider pollinator fauna, although existing (though still restricted to a single pollinator order) do not focus on species distribution along the altitudinal gradient [bees: Giannini et al. (2020); hoverflies: Milićić et al. (2018); butterflies: Settele et al. (2008)]. To our knowledge, this is the first study performed along the altitudinal gradient of a high mountain, using species distribution models, and taking into account a broad pollinator fauna including hoverflies, bees, and butterflies.

For the habitat suitability of most of 114 pollinator species, our approach indicated as fundamental environmental variables both isothermality and heat load index, followed by aspect. Isothermality



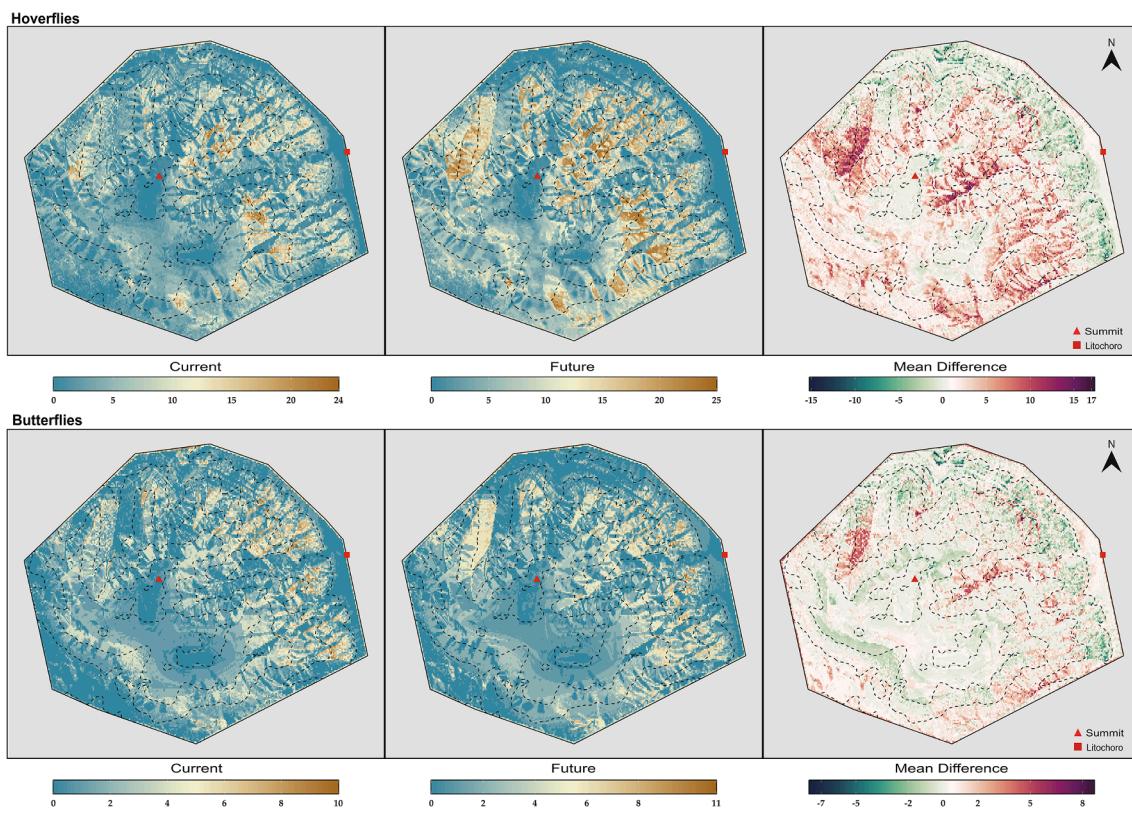
**Fig. 5.** Species richness hotspots for bumblebees and non-bumblebee bees on Mt. Olympus. The three maps regard the entire set of pollinator groups and represent current status, future prediction (based on the Ensemble RCP 8.5), and mean difference of species richness between GCM/RCP and current status (i.e., from each GCM/RCP species richness raster we subtracted the current species richness and then calculated average of all species). Dashed lines represent the 500-m contour lines.

denotes the temperature's importance in insect pollinator performance (Classen et al., 2020; Petanidou et al., 2018). On the other hand, topographical variables like heat load index and aspect are essential in mountain environments, where solar radiation along with slope's orientation and inclination greatly impact species biology, phenology, diversity and distribution (Rahbek et al., 2019; Trew et al., 2021).

Climate change will negatively impact pollinator fauna on Mt. Olympus, as all species were projected to lose a fraction of their current suitable habitat area. Our results indicate substantial effects on pollinator species, and this is in line with the expected high susceptibility of Mediterranean mountains biodiversity due to global warming (Bravo et al., 2008; Kougioumoutzis et al., 2020; Pauli et al., 2012). However, our projections did not indicate extinction of any pollinator species, in line with Guzman et al. (2021), who provided evidence for an overestimation of bumblebee declines by Soroye et al. (2020). Recent studies revealed resilience and even expansion in potential area of suitable habitat for some hoverfly pollinator species in eastern Mediterranean basin (Kaloveloni et al., 2015; Milić et al., 2018) which was attributed to the species' ecological requirements and adaptive capacity. Indeed, Mediterranean pollinator species may be resilient to global warming, due to adaptation to the warm and dry Mediterranean summer, as found for xeric bee species in Australian desert (Dew et al., 2019; Silva et al., 2018). Our results support this view, as pollinators were forecasted not to become extinct, but to lose a portion of their potential suitable habitat while trying to track their (realized) climatic niche. These findings also confirmed Mt. Olympus reputation as a refugium established since glacial periods (Médail and Diadema, 2009). We suggest that the predicted lack of pollinator species extirpations is the result of the adaptive capacity of Mediterranean pollinator species along with the ability of Mt. Olympus to act as shield against climate change (Kougioumoutzis et al., 2021a).

Climate change is predicted to affect altitudinal distribution of pollinator species on Mt. Olympus, with most of them forecasted to shift upwards. Several studies showed an upslope altitudinal shift of pollinators, using either species distribution models (Biella et al., 2017; Martínez-López et al., 2021) or historical records (Chen et al., 2009; Fourcade et al., 2019; Kerr et al., 2015; Mathiasson and Rehan, 2019; Pyke et al., 2016). Additionally, some historical studies provided further information on higher and lower limits shift of species altitudinal range, yet only for bumblebees (Marshall et al., 2020; Ploquin et al., 2013) and butterflies (Wilson et al., 2005). We, too, calculated these altitudinal range limits and found that the detailed description of the altitudinal shift clearly indicates the species-specific response to climate change. Indeed, even when a pollinator group was projected to shift upwards, some species within the group were found to move downslope and this may be the result of either both minimal and maximal altitudes decrease or because one of them decreases more than the other increases. These findings support the view that conservation applications must simultaneously consider taxon-specific forecasts along with focusing on a higher group (Ghisbain et al., 2020; Guzman et al., 2021).

Contrary to the other pollinator groups, bumblebees and hoverflies were predicted to shift downwards and to retain most of their potential suitable habitat area – in brief, to be affected less by climate change. Hoverflies were found to display high resilience but also a differential response on climate change effects: mountainous species are predicted to contract (Milić et al., 2019a; Radenković et al., 2017), while Mediterranean and lowland species to expand their distribution area (Kaloveloni et al., 2015; Milić et al., 2019b; Milić et al., 2018). Furthermore, widespread species are considered less vulnerable to climate change than range-restricted ones (Kaloveloni et al., 2015; Kougioumoutzis et al., 2021b; Thomas et al., 2004). Because most of the 25 hoverfly species studied are chorologically regarded as Mediterranean or



**Fig. 6.** Species richness hotspots for hoverflies and butterflies on Mt. Olympus. The three maps regard the entire set of pollinator groups and represent current status, future prediction (based on the Ensemble RCP 8.5), and 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 average of all species). Dashed lines represent the 500-m contour lines.

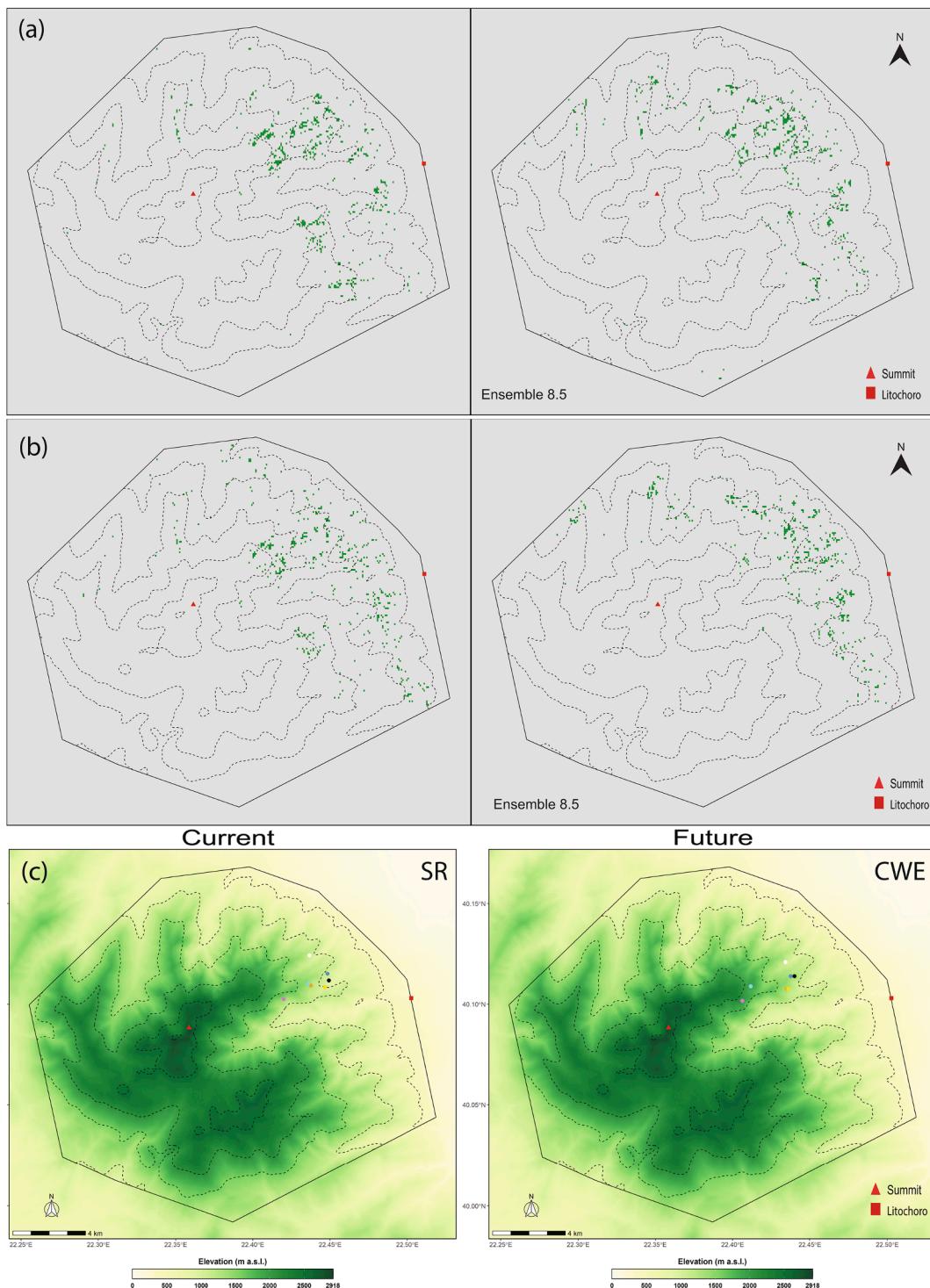
widespread (Table S1), we suggest that their predicted shift to lower altitudes constitutes a positive response to climate change due to their adaptive capacity by being both widespread and Mediterranean species occurring on Mt. Olympus (Vujić et al., 2019).

On the other hand, bumblebees are cold-adapted mountainous species which are expected to move to higher altitudes due to global warming, and this should be more evident in southern Europe (Kerr et al., 2015; Marshall et al., 2020). However, several studies predicted great variability in the bumblebee species' response [Pyrenees, France: Marshall et al. (2020); Mesoamerican mountains: Martínez-López et al. (2021); Cantabrian Range, Spain: Ploquin et al. (2013); Alps, Switzerland: Pradervand et al. (2014)]. Some bumblebee species have been indicated as potentially vulnerable to climate change, specifically *B. quadricolor*, *B. monticola*, *B. hypnorum* and *B. haematurus*, for which Mt. Olympus constitutes their southernmost distribution in Europe (Minachilis et al., 2020). Unfortunately, these species were not included in our analysis, since we modelled only those species found in more than three sites (van Proosdij et al., 2016). It is highly likely that the rarest species with a highly specialized niche will suffer the greatest altitudinal shift upwards (Martínez-López et al., 2021; Pradervand et al., 2014). Hence, we suggest that a possible reason for the observed downward shifting of bumblebees and hoverflies may actually be a statistical artefact (at least partially) due to the exclusion of the rarest species, considering that we included in our analysis only a part of the total number of pollinator species found on Mt. Olympus (bumblebees: 14 species/species groups out of 22 species/species groups; hoverflies: 25 out of 73 species).

Overall, we recorded a pronounced species-specific response to climate change under any GCM and RCP projection. Some studies detected a similar response variability between bumblebee species, which they attributed to bumblebee differential tolerance to climatic conditions (Krechmer et al., 2020; Pradervand et al., 2014). Indeed,

bumblebee tolerance to low temperature was found to differ between short- (higher tolerance) and long-tongue species (Pellissier et al., 2013). Recently, a meta-analysis showed an idiosyncratic altitudinal shift response to climate change among mountainous plant and animal species, resulting in different amount of upslope or downslope movement (Mamantov et al., 2021). The differential response to climate change between pollinator species on Mt. Olympus can also be explained by their different adaptive capacity, due to the fact that these insects include widespread, European, mountainous, and Mediterranean species. After all, a differential climate change effect is likely, especially in areas with a highly heterogeneous microclimatic environment characterised by the existence of microrefugia, like that of Mt. Olympus (Suggitt et al., 2018; Trew et al., 2021).

Despite the variability in species response, climate change impacts on Mt. Olympus are expected to be substantial as the entire pollinator assemblage will face a potential loss of suitable habitat and a shift along the altitudinal gradient in near future. In a recent review, Vitasse et al. (2021) showed a great climate change impact on European Alps terrestrial organisms over the last decades, including an upward shift of 39.9 m/decade for butterflies. Recently, Rödder et al. (2021) found an uphill shift of more than 50 m/decade for butterflies in eastern Alps over the last 60 years. Although we projected a much less upslope shift for butterflies on Mt. Olympus (12 m/decade), we expect a greater impact on pollinators, considering that Zindros et al. (2020) found that the mountain tree line has shifted upwards 66.7 m/decade, while woody plants in Alps shifted upwards 32.7 m/decade (Vitasse et al., 2021). After all, a climatic debt is expected in the European southern part of the Mediterranean Basin (Duchenne et al., 2021) especially due to Mt. Olympus' lower altitude and latitude compared to the Alps. However, no local extinction incident is predicted, and the mountain's high altitudinal range seems to act as a buffer that may prevent or halt the "escalator to extinction" phenomenon (Urban, 2018).



**Fig. 7.** Species richness (SR) and its geographically-weighted variant (CWE) hotspots defined as the highest 1% of the cells (i.e., the 1% quantile; L1 hotspots) for all pollinators on Mt. Olympus. (a) L1 SR hotspots (green cells) for the current and the Ensemble 8.5 RCP time-period, (b) L1 CWE hotspots (green cells) for the current and the Ensemble 8.5 RCP time-period, (c) Distributional centroids for the L1 SR and L1 CWE hotspots. Colour circles represent the distributional centroids of the current time-period (orange), the CCSM4 4.5 RCP (yellow), the CCSM4 8.5 RCP (white), the Ensemble 4.5 RCP (black), the Ensemble 8.5 RCP (blue), the HadGEM2 4.5 RCP (purple), and the HadGEM2 8.5 RCP (azure). Dashed lines represent the 500-m contour lines. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

From another point of view, strong connection between pollinators and host plants may affect species distribution and resilience to climate change: disrupting phenology and differential altitudinal shift between plants and pollinators or, worst, plant extinctions, will severely impact pollinator capital (Inouye, 2020; Pyke et al., 2016; Vitassee et al., 2021),

especially considering predictions for a severe climate change impact on Mediterranean plants (Giménez-Benavides et al., 2018; Kougioumoutzis et al., 2020). Moreover, competition with lowland invaders, generalisation or specialisation in host plant range and migration ability are important factors for pollinator adaptation (Inouye, 2020; Schweiger

et al., 2010). Evidently, biotic interactions effects on future pollinator status may be positive or negative, but always important. Nonetheless, we believe that our projections robustly reveal the general trend of pollinator species distribution under the climate change impact and indicate their resilience along with the great value of Mt. Olympus as a refugium.

Regarding the future pollinator species richness hotspots on the mountain, we observed a shift upwards and to the northeast (the latter refers to the hotspots' centroids). Taking into account the current protection status on Mt. Olympus, with only its eastern side being part of both the Olympus National Park and the European Natura 2000 site, we predict here that pollinator diversity hotspots in the near future will be outside the currently protected area. Mt. Olympus is not exceptional in this, however, as there are other protected areas worldwide with similar conditions, requiring swift actions to be taken (Kougioumoutzis et al., 2021b; Martínez-López et al., 2021; Radenković et al., 2017). We argue, therefore, that the Olympus National Park area and/or the Natura 2000 site should be extended to cover the entire mountain, encompassing all mountain sides and altitudes or, at least, the intermediate to high altitudes (>1500 m) including the north-eastern side of the mountain. Special conservation and protection plans should be applied on future pollinator hotspots areas to improve ecosystem stability (viz. host-plant diversity and abundance), also considering the overgrazed highly degraded part of the mountain that is non-protected (Minachilis et al., 2020).

## 5. Conclusions

Our study predicted the potential habitat suitability area and the altitudinal range for a broad pollinator fauna and forecasted the climate change effects on 114 pollinator species status. Climate change will affect the entire pollinator assemblage along the altitudinal gradient of Mt. Olympus, restricting species into smaller areas in the highlands. Pollinator species present a prominent idiosyncratic response to climate change both in habitat suitability area and in altitudinal shift probably owing to differential adaptive capacity. Contrary to expectations and to predictions for the other pollinator groups, bumblebees and hoverflies are projected to move downslope probably due to species distribution modelling framework limitation that resulted in exclusion of the rarest species. Pollinator richness hotspots are predicted to move to higher altitudes and to the north-eastern side of the mountain, outside of the actual Olympus National Park protected area.

Under these projections, we suggest that actions for pollinator conservation should be taken urgently. As there are no local measures that could be effectively taken against the climate change impact, we recommend conservation and protection measures against threats and anthropogenic pressures that may exacerbate climate change effects. Such measures could comprise: inclusion of pollinators in monitoring and conservation schemes of Olympus National Park; expanding the Olympus National Park area, i.e., against the government planning to reduce the protected area in order to construct a ski resort; protecting against species invasion from the lowland; mitigating tourism disturbance in the mountain ecosystem (Biella et al., 2017; Miličić et al., 2018); forbidding any land use change. Finally, future research is urgently needed to disentangle effects of microclimatic variation and biotic factors on pollinator resilience to global warming, both on Mt. Olympus and on other mountains of the Mediterranean.

## CRediT authorship contribution statement

**Konstantinos Minachilis:** Data curation, Methodology, Investigation, Writing – original draft, Writing – review & editing, Project administration. **Konstantinos Kougioumoutzis:** Formal analysis, Writing – original draft, Writing – review & editing. **Theodora Petanidou:** Conceptualization, Methodology, Resources, Writing – review & editing, Supervision, Funding acquisition.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2021.108335>.

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