Bumblebee diversity and pollination networks along the elevation gradient of Mount Olympus, Greece

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Abstract
Aim: We studied bumblebee diversity and bumblebee pollination networks along the altitudinal gradient of Mt. Olympus, a legendary mountain in Central Greece, also known for its exceptional flora.

Location: Mt. Olympus, Central Greece.

Taxon: Bombus (Latreille, 1802).

Methods: We explored 10 study sites located on the north-eastern slope of the mountain, from 327 to 2,596 m a.s.l. Bumblebee surveys were carried out on a monthly basis using pan traps (years 2013 and 2014) and random transect observations assisted by hand netting (years 2013, 2014, and 2016); visited flowering plants and their diversity were recorded during the transect observations.

Results: With a total of 22 recorded bumblebee species and one species complex, Mt. Olympus is one of the richest mountains in Mediterranean Europe regarding bumblebee diversity. Bombus quadricolor was recorded as a new species for Greece, whereas four species were recorded at their southernmost distribution limit, therefore possibly vulnerable to climate change. Species richness of both bumblebees and plants in flower followed a unimodal pattern along the altitudinal gradient, the former peaking at high altitudes (1,900–2,200 m a.s.l.), the latter at lower to intermediate altitudes (500–1,500 m a.s.l.). Bumblebee–plant visitation networks were larger, more diverse and more generalized in the between intermediate altitudes (1,500–1,800 m a.s.l.), while nestedness peaked at low and high altitudes.

Main conclusions: Our results disclose the differential significance of the altitudinal zones of Mt. Olympus for the conservation of the diversity of bumblebees and their host plants, as well as of the interactions among them. Furthermore, they highlight the importance of this mountain, because of its South-European location, regarding climate change impacts on the bumblebee fauna of Europe. All in all, they point towards more reinforced conservation measures to be taken including the expansion of the protection status to the entire mountain.

KEYWORDS
altitudinal gradient, Bumblebee diversity, global warming, Mount Olympus, mountain system, pollination network
Mountain ecosystems constitute excellent model systems for testing physiological, ecological and evolutionary hypotheses within small spatial scales (Körner, 2000, 2003, 2007). Air temperature, atmospheric pressure and available land area decrease with altitude, whereas solar radiation levels rise, resulting in increasingly challenging abiotic conditions with far-reaching impacts on the survival and reproduction of organisms, especially at the extremes (Körner, 2007). Studies performed along altitudinal gradients have provided valuable insights on the effects of climate change on the diversity and distribution of species, using space-for-time substitution scenarios (Mayor et al., 2017). There is little doubt that mountain ecosystems should be placed under the spotlight, mainly because the expected climatic changes in the 21st century are projected to disrupt species distribution, with cascading effects on ecosystem services, such as pollination (Lefebvre, Villemant, Fontaine, & Daugeron, 2018; Rahbek et al., 2019).

Mediterranean mountains are of pivotal importance for biodiversity conservation, for two main reasons. First, because they are key biogeographical elements in the Basin, having shaped species distribution and diversity during glacial periods (Blondel, Aronson, Bodiou, & Boeuf, 2010). During the Pleistocene glacial periods, major mountain ranges in the Iberian, Italian and Balkan peninsulas constituted refugia for northern species, which, during the subsequent interglacial periods, including the Holocene, recolonized northern Europe (Hewitt, 1999). Consequently, temperate species constricted their range to the southern peninsulas, to expand it later to northern Europe or/and retreat to higher altitudes of Mediterranean mountains (Hewitt, 2011). Cold-adapted species, such as bumblebees (Hymenoptera: Apidae), expanded their range during the glacial periods to the south and, in interglacial periods, returned to the north or reached refugia at high mountain altitudes (Martinet et al., 2018; Stewart, Lister, Barnes, & Dalen, 2010). It is well accepted that such climatic oscillations set the ideal conditions for population differentiation and speciation (especially in the refugia), and are responsible for the high levels of biodiversity and endemism in the Mediterranean Basin (Blondel et al., 2010; Hewitt, 2004).

The second reason why Mediterranean mountains are of pivotal importance for biodiversity conservation is because the Mediterranean area is one of the most susceptible regions of the world to climate change (Giorgi, 2006; Giorgi & Lionello, 2008). Predictions suggest that over this century, widespread drought events will affect the Basin (Dai, 2012; Giorgi & Lionello, 2008), resulting in the highest desertification risk in the near future, worldwide (Hill, Stellmes, Udelhoven, Röder, & Sommer, 2008). In turn, it is expected that such a pronounced change in climatic conditions could affect the Mediterranean mountain systems more dramatically, and likely sooner, compared to montane systems of higher latitudes. Under this view, vital ecosystem services, such as pollination, should be thoroughly studied, both to cover knowledge gaps, which are prominent in the region (Petanidou et al., 2013), and to be able to make projections for the future status of pollination services under different climatic scenarios (e.g. Kaloveloni, Tscheulin, Vujic, Radenkovic, & Petanidou, 2015).

Among all pollinator groups, bumblebees (Bombus Latreille 1802) constitute a fundamental resource in mountain ecosystems. This is mainly because they are cold-adapted, endothermic species, remaining active in cool conditions when other pollinators are inactive (Heinrich, 1979). As a result, bumblebees are often the most important pollinators in cool environments, such as the Arctic (Løken, 1973), montane (Bingham & Orthner, 1998) and temperate (Ricketts et al., 2008) regions. Bumblebees are present at altitudes even above 4,000 m a.s.l., providing invaluable pollination services to the alpine flora (Williams, 1991). A rise of the ambient temperature may act against their adaptive advantage to exploit floral resources at higher altitudes by increasing competition with other pollinators, with unknown consequences for the current species distributions (Martinet et al., 2015). This is particularly likely in the eastern Mediterranean, because although it has long been considered a hotspot for wild bee diversity (Michener, 1979, 2000), the diversity of bumblebees is comparatively low (Balzan et al., 2016; Nielsen et al., 2011; Petanidou & Ellis, 1993; Varnava et al., 2020). Research on bumblebee diversity in Mediterranean mountains is therefore paramount in order to assess the role of the genus in structuring mountain communities at different elevations and disclose the conservational importance of these habitats for the genus.

Here, we study the patterns of diversity and pollination networks of bumblebees along an altitudinal gradient of Mt. Olympus (2,918 m), a legendary landmark. The mountain constitutes a circular massif of 25 km diameter on average, situated relatively near the central-east coast of Greece, and separated from other Balkan mountains by plains, lower mountains and deep river valleys. Its flora consists of >1,700 plant species, encompassing ca. 25% of the Greek flora, including 58 Greek endemics of which 25 are endemic to Mt. Olympus itself (Strid, 1980; Strid & Tan, 1986, 1991). The mountain retained a certain level of glaciation in Pleistocene interglacial periods and even up to the Holocene (Smith, Damian Nance, & Genes, 1997; Styllas et al., 2018), thus constituting a refuge for glacial relics (Médail & Diadema, 2009), such as the local endemic Jankaea heldreichii (Boiss.) Boiss. (Gesneriaceae) characterized as a “living fossil” (Vokou, Petanidou, & Bellos, 1990). 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). High biodiversity and endemism suggest population differentiation and speciation in past geological times when Mt. Olympus was a species refuge (Hewitt, 2004; Médail & Diadema, 2009). Until today, mainly plant-focused studies have been conducted on the mountain, with at most partial consideration of plant-pollinator interactions, pollinator diversity, and community structure, and only at particular altitudes (Blonis & Vokou, 2005 and references cited therein; Makrodimos, Blonis, Krigas, & Vokou, 2008; Vokou et al., 1990).

Pollination networks constitute a sophisticated tool to describe and visualize the structure of interactions among plants and
pollinators within a community, allowing comparisons among communities through specific metrics that can be computed. The tool has been employed to document such variation along altitudinal gradients worldwide (Adedoja, Kehinde, & Samways, 2018; Cuartas-Hernandez & Medel, 2015; Hoiss, Krauss, & Steffan-Dewenter, 2015; Lara-Romero, Segui, Pérez-Delgado, Nogales, & Traveset, 2019; Maglianesi, Blüthgen, Böhning-Gaese, & Schleuning, 2015; Miller-Struttmann & Galen, 2014; Ramos-Jiliberto et al., 2010; Trejelsgaard & Olesen, 2013), but only once within the wider Mediterranean area: Lara-Romero et al. (2019) for Mt. Teide in Tenerife Island. The last study, however, was conducted only at four different high altitudes (between 2,350–3,520 m a.s.l.) and not at the entire altitudinal range of the mountain.

In this study, we aim to explore the bumblebee patterns of diversity and function, that is involvement in pollination services within communities occurring along the entire altitudinal gradient of Mt. Olympus. This approach helps to disclose the present and historical biogeography of the bumblebees in the Mediterranean, and highlights conservation priorities regarding both species and habitat types. It is noteworthy that among all studies investigating both pollinator distribution/diversity and function along a mountain’s altitudinal gradient, only two focused on bumblebees: Egawa and Itino (2019), who studied the elevation gradient 700–2,600 m a.s.l. of Mt. Norikura, Japan; and Miller-Struttmann and Galen (2014), who analysed data from the Colorado Rocky Mountains collected by Macior (1974), limited, however, to only high altitudes, viz. >1,600 m a.s.l.. There are two additional studied areas of Mediterranean-type climate, albeit focusing on all insect groups: Adedoja et al. (2018), a W. Cape Province study, South Africa; and Lara-Romero et al. (2019), a study in the infra-Mediterranean/Canaries, limited to the highest altitudes, >2,350 m a.s.l. Other studies focused solely on bumblebee distribution along an altitudinal gradient, including Williams (1991) and Goulson, Lye, and Darvill (2008b) who studied Mt. Apharwat (maximum study altitude 4,143 m, Kashmir) and Gorce and Tatra mountains (maximum study altitude 1,580 m, Poland), respectively. Our study is unique in that it explores bumblebee diversity patterns and involvement in pollination networks along the entire altitudinal gradient of a mountain.

In particular, we address the following questions:

1. How the composition and diversity of bumblebees and plants vary along the altitudinal gradient of Mt. Olympus?
2. Whether any bumblebee species are associated with specific altitudinal ranges?
3. Whether plant-bumblebee visitation network properties are altitude-dependent and how this varies along the gradient?

2 | METHODS

2.1 | Study area

The study was conducted on the north-eastern slope of Mt. Olympus, following the path route from Litochoro town to Mousses Plateau (Figure 1). Along this route and at different altitudes and vegetation zones (see below), we established ten sampling sites with a NNE aspect, including both open areas and forest openings when inside a forest; between successive sites, the average altitudinal difference was ca. 250 m and average distance in straight line ca. 1.5 km; in the two cases the distance between sites was <1 km (in fact between 500 and 600 m), these sites were taken by necessity as the only ones available (Figure 1, Table S1). Almost half of the mountain, 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). Our study sites cover all four major vegetation zones of Mt. Olympus, according to Strid (1980): (a) evergreen–sclerophyllous (Mediterranean) scrub (300–600 m), (b) mixed beech and montane coniferous forests (700–1,500 m), (c) cool temperate coniferous forests (1,500–2,500 m) and (d) alpine meadows (2,500–2,917 m). The climate is Mediterranean at lower altitudes and temperate at intermediate to higher ones, with snow covering areas above 2,000 m from late October to late May (Strid, 1980). Afternoon thunderstorms are common in summer, and sudden snowstorms or hail may also occur. There is no permanent water source above 1,100 m; thus, humidity from fog or low clouds is of crucial importance. North-eastern slopes are more humid due to their vicinity to the sea (Strid, 1980).

2.2 | Sampling of insects and their flowering plant hosts

Insect surveys were carried out within an area of ca. 0.1 ha at each site; they consisted of a collection of all insects using pan traps (years 2013 and 2014) and additional random transect observations assisted by hand netting collection of unknown bumblebees (years 2013, 2014 and 2016). Pan traps were placed as sets of three plastic bowls (triplets), each pan trap painted with a different UV-bright colour: blue, yellow and white (Nielsen et al., 2011; Westphal et al., 2008). Triplets, five in each site and set at a distance of >5 m from each other, were placed on height-adjustable metal stands in order to be levelled with the height of the continuously growing vegetation during the sampling season, and thus being always visible to flying insects. Each pan trap was filled with a mixture of propylene glycol and water (1:1 in volume) and was left open to capture insects for a week. The use of propylene glycol was adopted for two reasons: to minimize evaporation and to preserve the collected specimens, thereby allowing a longer operational time of the pan traps.

Bumblebee surveys were carried out using hand netting in variable transect walks during which both bumblebees and the visited flowering plants were recorded (Nielsen et al., 2011; Westphal et al., 2008). Specimens of unknown bumblebees were collected together with the respective forage plants for later identification. Hand netting lasted 90 min in 2013, and 120 min in the 2014 and 2016 surveys.

All insect observations and collections were carried out on a monthly basis from May to October of both 2013 and 2014 (both
by pan trapping and hand netting), as well as of 2016 (only by hand netting). Thus, the planning was to conduct a total of six sampling rounds per year. Due to snow cover or harsh weather conditions in certain years, a number of sites were inaccessible before June and after September, resulting in fewer sampling rounds conducted at these sites. They were the following: S-1838, S-1936, S-2262, S-2424 and S-2596 that were not sampled in 2013; and S-2262, S-2424 and S-2596 not sampled in both 2014 and 2016. Yet, in September 2014 pan traps at site S-2424 were destroyed by a heavy hailstorm.

The observation and collection of specimens was conducted in days with fine weather favourable to bee activity and during the active bumblebee foraging hours (10:00–16:00). During the survey, we tried to collect and observe bumblebees as thoroughly as possible and to disturb them as little as possible. If occasional disturbances may have occurred and some interactions missed, we trust this was evenly distributed over all sites along the altitudinal gradient. As some bumblebee species are long-distance flyers, movement between sites could potentially have occurred, although we believe this was most unlikely to happen due to the topology and the existing dense forests between sites. Several factors, like difficult accessibility (all sites above 1,200 m had to be accessed on foot), accommodation restrictions (only one refuge along the path) and the erratic mountain weather, influenced the data collection, affected both the choice of sampling methods and the sampling effort employed within a year (once per month) and in different years (variation between years). To have comparable results, such differences (viz. different sampling methods and duration) were taken into account in the analyses. Finally, because sites were selected not far from the hiking path, carefully prepared bilingual informational signs were set to minimize disturbance by hikers.

All collected insect specimens were processed in the laboratory and identified to species level, except for Bombus lucorum s.l., a complex consisting of three species that are indistinguishable with a microscope: B. lucorum, B. cryptarum and B. magnus; yet, because B. terrestris was also difficult to distinguish under field conditions, visit records of all the above species were pooled together as belonging to the same group (Bossert, Gereben-Krenn, Neumayer, Schneller, & Krenn, 2016; Wolf, Rohde, & Moritz, 2009). Bumblebee specimens are kept at the Melissotheque of the Aegean (Laboratory of Biogeography and Ecology, Department of Geography, University of the Aegean, Greece) (Petanidou et al., 2013). Voucher plant specimens are kept at the Herbarium of the Laboratory of Systematic Botany, Agricultural University of Athens, Greece.

### 2.3 Plant diversity and flower cover

Number of plants in flower and their flower cover were measured within 1 × 1 m squares (n = 25) randomly selected at each site and round (Lázaro, Tscheulin, Devalez, Nakas, & Petanidou, 2016). Flower cover was measured by counting the number of flowers or inflorescences per plant species within the squares. Flower abundance for each plant species was calculated as the average number of flowers/
were calculated: the total number of species within a community. (ii) Shannon-Wiener diversity index ($H'$): a widely used metric of $\alpha$-diversity, which accounts both for the diversity and evenness of species within a community. (iii) Effective Number of Species (ENS): defined as the number of species in a community with equal abundances that would give the same as the observed value of $\alpha$-diversity, and considered as the true species diversity within a community (Jost, 2007).

Metrics (ii) and (iii) were calculated using the R package vegan 2.5-2.

2.5 | Network properties

We calculated the following network properties, using all hand netting data recorded, each year considered separately (viz. years 2013, 2014 and 2016), in order to describe the interacting bumblebees and the plants observed to be visited by them in each of the ten communities sampled (see Figures S1–S3). Namely, the following properties were calculated:

(i) Network size: the number of bumblebee–plant (b–p) links observed in each community.
(ii) Nestedness: the weighted NODF was used, which describes the degree to which specialist species tend to interact with generalist ones (Almeida-Neto & Ulrich, 2011).
(iii) Linkage density: it represents the mean number of links per species, weighted by the number of interactions (Bersier, Banašek-Richter, & Cattin, 2002). Following (Lázaro, Tscheulin, Devalez, Nakas, Stefanaki, et al., 2016), we used this metric to estimate generalization, particularly where the networks differed in size.
(iv) Shannon’s diversity of interactions: the Shannon index calculated for the different links of the network.
(v) Selectiveness: we used the $H'_2$ index, which describes the selectiveness in the network, that is to which extent observed interactions deviate from random selection of partners. The more selective the species in the network, the higher the $H'_2$ index (Blüthgen, Menzel, & Blüthgen, 2006).

All the above metrics were calculated using the R package bipartite 2.11.

2.6 | Statistical analysis

To test the relationship between altitude and bumblebee community composition, we used multivariate-response generalized linear mixed models (MGLM) (R package mvabund 3.13.1). This approach fitted a separate GLM (binomial family with “cloglog” link) to the distribution matrix of each insect of the network, using altitude as explanatory variable, and a resampling-based hypothesis testing (Wang, Naumann, Wright, & Warton, 2012), and was used to indicate those species whose distribution showed a significant effect to altitudinal change. The multidimensional response variable was the presence/absence matrix of bumblebee species distribution among the ten sites, compiled by using the combined data from pan trapping and hand netting of the years 2013 and 2014. The statistical significance of the fitted model was assessed with ANOVA (likelihood ratio tests) using 999 bootstrap iterations via PIT-trap residual resampling. We used AIC to compare the best-fitted model with the null model ($y = 1$). Univariate tests were subsequently performed to determine which response variables (bumblebee species) showed significant effects in response to altitude.

To test the relationship between altitude and the diversity of bumblebees on Mt. Olympus, we used Generalized Linear Mixed-effects Models (R package lme4 1.1-18-1) considering all pan trapping and hand netting data combined. To avoid pseudoreplication, we used “site ID” nested within “year” as categorical random variables. As dependent variables, we used (i) the bumblebee species richness, (ii) the Shannon–Wiener diversity index and (iii) the Effective Number of Species (ENS), calculated for each of the sampled sites. For Shannon–Wiener index and ENS, we used models with Gaussian distribution, while for the bumblebee species richness, we used Poisson distribution and log link function (in the latter case, the model was not overdispersed; that is, the ratio between the residual deviance and residual degrees of freedom was <1.1 [Zuur, Ieno, Walker, Saveliev, & Smith, 2009]). As fixed variables (predictors), we included both the linear and the quadratic term of the altitude of each site. To avoid collinearity, we standardized the variable “altitude” ($\bar{x}=0, \sigma = 1$) before calculating its quadratic term. In addition, we used plant Shannon–Wiener index as a predictor. To select the best combination of predictors (including the interaction terms of plant diversity and altitude), we used a backward selection process based on AICc (R package AICcmodavg 2.1-1). We also used the $\Delta$AICc in order to compare the best-fitted model with the null model ($y = 1$).

The same modelling approach (GLMMs) was used to test the relationship between altitude and species richness of the plants in flower. “site ID” nested within “year” as categorical random variables, and the linear and the quadratic term of the altitude of each site, as predictors. We used Poisson distribution and log link function (in the latter case, the model was not overdispersed; that is, the ratio between the residual deviance to residual degrees of freedom was <1.1 [Zuur et al., 2009]). To test the relationship between altitude and the b–p visitation network properties, we considered the hand netting data alone and
applied GLMMs. To do so, we used the abovementioned network properties (viz. network size, $H_2'$ index, weighted NODF, linkage density and Shannon's diversity index) as dependent variables. As predictors, we used the linear and the standardized (see above) quadratic term of altitude, and flower abundance. As random factors, we used site ID, nested within year (2013, 2014, 2016). We performed analyses using (a) the Gaussian distribution for Shannon's diversity and linkage density, (b) binomial distribution (link “logit”) for NODF and $H_2'$, and (c) Poisson distribution for network size (link “log”) (the model was not overdispersed). To determine whether there was a significant altitudinal trend in the network properties, we used the $\Delta$AICc between the best-fitted model and the null model ($y \sim 1$).

3 | RESULTS

During the three study years, we recorded 5,255 bumblebees belonging to 22 species and one species complex (Table S2 in which species identification is of the lowest taxonomic level), which visited the flowers of 94 plant species (Table S3).

Bumblebee species occurrence on Mt. Olympus varied with altitude (MGLM; $\Delta$AIC = 36, $\chi^2 = 104.4$, $p = .003$; combined data of pan trapping and hand netting of the years 2013 and 2014). The distribution of seven species correlated with altitude: Bombus mesomelas (MGLM; $\chi^2 = 8.6$, $p = .020$), B. niveatus (MGLM; $\chi^2 = 13.8$, $p = .005$), B. pratorum (MGLM; $\chi^2 = 12.0$, $p = .011$), B. ruderarius (MGLM;...
\( \chi^2 = 7.0, p = .025 \), B. rupestris (MGLM; \( \chi^2 = 12.0, p = .011 \)), B. so -
roensis (MGLM; \( \chi^2 = 11.9, p = .011 \)) and B. vestalis (MGLM; \( \chi^2 = 6.2, p = .046 \)). The specific altitudinal ranges these species are related
with are shown in Figure 2.

Based on combined data (pan trapping and hand netting; separate sampling years 2013 and 2014), bumblebee diversity was found to be associated with high to very high altitudes (Figure 3a–c). Specifically, species richness peaked at 2,200 m (GLM; \( \chi^2_{2,4} = 13.3, p < .001 \)), Shannon–Wiener at 1,900–2,000 m (LM; \( F_{1,14} = 80.4, p < .0001 \)) and ENS at 1,900–2,000 m (LM; \( F_{1,16} = 25.0, p < .0001 \)). All diversity indices had higher values in 2014 vs. 2013, partly due to
the lower sampling effort in 2013 (see Section 2), but also most likely attributable to year-to-year significant variations occurring in nature (Petanidou, Kallimanis, Tzanopoulos, Sgardelis, & Pantis, 2008).

Plant species richness was highest at low to intermediate altitudes, that is between 500 and 1,500 m in all three sampling years (GLM; \( \chi^2_{2,4} = 13.6, p = .001 \)) (Figure 4). Again, plant richness was lowest in 2013, probably due to the lower sampling effort in that year (see Section 2). The bumblebee Shannon–Wiener index correlated
with the plant Shannon–Wiener index (LM; \( F_{1,14} = 8.3, p = .012 \)), and
with the interaction between altitude and plant Shannon–Wiener index (altitude \( \times \) plant Shannon–Wiener: \( F_{1,14} = 6.7, p = .021 \)).

**FIGURE 3** Predictors of bumblebee diversity on Mt. Olympus. a–c: Altitude as predictor of bumblebee (a) species richness, (b) Effective
Number of Species (ENS) and (c) Shannon–Wiener index; (d) Plant diversity as predictor of bumblebee diversity (viz. Plant Shannon–Wiener
index vs. bumblebee Shannon–Wiener index). Plots (c) and (d) show the partial residuals of the best-fitted model that included both altitude
and plant Shannon–Wiener index. The two fitted lines in each plot correspond to different sampling years, which represent random-effect
factors in the fitted models (*\( p \leq .050 \), **\( p \leq .001 \))
Interestingly, bumblebee diversity correlated negatively with plant diversity (Figure 3d), probably as a result of the inverse diversity trends of the two groups along the altitudinal gradient (i.e., diversity of plants peaked at lower to intermediate altitudes, while that of bumblebees at high ones [cf. above and Table S4]).

The structure of b–p networks varied along the altitudinal gradient for each of the three years of sampling (2013, 2014, 2016) (Figure 5). Networks were larger (i.e. included more links) between 1,500 and 1,800 m in all sampling years (GLM; $\chi^2_{1,3} = 18.4$, $p < .0001$). (Note that 2013 networks were overall smaller than the other two years, probably due to the lower sampling effort in that year; see Section 2). Linkage density also peaked at ca. 1,800 m (LM; $F_{1,24} = 20.0$, $p < .0001$); year 2014 did not follow this trend, probably because metrics for the lowest altitude site (S-327) could not be computed (only one bumblebee species was recorded, viz. $B$. terrestris/lucorum s.l. group) (cf. Figure 5). Shannon’s link diversity peaked at around 1,800 m (LM; $F_{1,24} = 13.5$, $p = .001$). Finally, the b–p networks were more nested at the extreme altitudes of the mountain, that is <600 m and >2,400 m, showing an opposite trend than the other properties (GLM; $\chi^2_{1,3} = 7.1$, $p = .008$). The selectiveness index ($H'_{s}$) was found to correlate neither with altitude nor with flower abundance. In fact, no property was correlated with flower abundance in the study sites: based on AICc, flower abundance was not included in any of the best-fitted models.

4 | DISCUSSION

4.1 | Bumblebee diversity and faunistics

Three years of systematic survey in ten sites along the altitudinal gradient of Mt. Olympus yielded 22 identified species and one species complex of bumblebees, consisting of three cryptic species. Such a rich bumblebee diversity is comparative with that recorded in a much variable set of temperate habitats in NW Greece surveyed for a wider period of time, which encompassed a total of 29 species out of the 33 currently known for Greece (Anagnostopoulos, 2005, 2009, 2017; cf. Table 1). Mediterranean systems are notorious for their paucity in bumblebee diversity (Balzan et al., 2016; Nielsen et al., 2011; Petanidou & Ellis, 1993; Varnava et al., 2020) as compared with temperate regions in the European continent (Table 1). Nonetheless, the Mediterranean mountains, characterized by multiple climate zones and rich glacial history that favoured the preservation of bumblebee populations (Martinet et al., 2018; Médail & Diadema, 2009), host a high diversity of bumblebees as it is the case of Susa Valley, Italy (Manino, Patetta, Boglietti, & Porporato, 2010), the French and Spanish sides of the Pyrenees (Iserbyt, 2009; Iserbyt, Durieux, & Rasmont, 2008; Ornosa, Torres, & Rua, 2017) and the Cantabrian Mountains, Spain (Obeso, 1992; Floquin, Herrera, & Obeso, 2013; Table 1). Mt. Etna, in Sicily, stands as an exception, with only 12 bumblebee species resulted, however, from a partly surveyed mountain just up to 1,900 m a.s.l. (Mazzéo, Bella, Seminara, & Longo, 2015).

The present study discovered one new species for Greece, viz. $B$. quadricolor which is a rare parasite specialist of $B$. soroeensis. This parasitic species has a wide distribution range from the Cantabrian Mountains and the Pyrenees through to the Balkan mountains and Fennoscandia, with Mt. Olympus constituting its southernmost distribution area (Rasmont et al., 2015). Furthermore, this study documented the range expansion of another three bumblebee species, for which Mt. Olympus constitutes their southernmost distribution in Europe: $B$. monticola, whose range extends from the Pyrenees to Fennoscandia, including the Alps and some Balkan mountains (Martinet et al., 2018); $B$. hypnorum, a species with a wide distribution, from the Pyrenees and Balkan mountains in the south, to the Barents Sea in the north (Rasmont et al., 2015); and $B$. haeomatus, a species that reaches Slovakia and Romania in the north (Bossert & Schneller, 2014; Rasmont et al., 2015). Given their altitudinal restriction, the above four species can be considered as vulnerable to climate change, especially $B$. monticola being restricted to the highest sites of Mt. Olympus (>2,400 m a.s.l., cf. Table S2) (Kerr et al., 2015; Rasmont et al., 2015).

Seven of the species of Mt. Olympus ($B$. mesomelas, $B$. niveatus, $B$. pratorum, $B$. ruderarius, $B$. rupestris, $B$. soroeensis and $B$. vestalis) are significantly associated with specific altitudinal ranges on this mountain (Figure 2). This is in agreement with what is found in other mountains where bumblebee species have, however, much wider altitudinal ranges than on Mt. Olympus (Figure 6). This might be the result of (a) the non-sampling over all the sides of Mt. Olympus, (b) the mostly non-systematic sampling approach of most previous studies (usually done as entomological surveys), following a less strict place and time schedule (Table 1), (c) the limited altitudinal range of Mt. Olympus as compared to other higher mountains and its low latitude, and (d) climatological factors, for example the influence of the Atlantic to Cantabrian Mountains.

![Figure 4](https://via.placeholder.com/1573)

**Figure 4** Altitude as predictor of plant species richness on Mt. Olympus. The three fitted lines correspond to different sampling years, which represent random-effect factors in the fitted models (***$p < .001$)
Six of the above seven species (viz. *B. mesomelas*, *B. pratorum*, *B. ruderalis*, *B. rupestris*, *B. soroeensis*, *B. vestalis*) are associated to high altitudes of Mt. Olympus (cf. Figure 2, Table S2 showing the abundances of these species in different altitudes). Among all these species, however, only *B. mesomelas* is exclusively associated with very high altitudes. Furthermore, as shown in Figure 6, our records of *B. campestris* signpost the highest altitudes this species has been ever recorded at. We have to emphasize the uniqueness of Mt. Olympus by highlighting that, among the three mountains in Mediterranean Europe close to the 40th parallel north with altitude ca. 3,000 m a.s.l. (the others are Sierra Nevada and Mt. Etna), Mt. Olympus is the least isolated, and certainly not fully isolated from the Balkan mountain ranges, which explains not only the importance of this mountain as established species refuge but also why it constitutes the southernmost distribution limit for the aforementioned bumblebee species.

There is hard evidence on the decline of bumblebee species worldwide (Cameron et al., 2011; Kosior et al., 2007) which is associated not only with climate change, but also with land use change, pesticide use, pathogens, invasive species and combinations among these factors (Cameron & Sadd, 2020; Goulson, Lye, & Darvill, 2008a). Within the Olympus National Park protected area,
where this study was carried out, the most important threat bumblebees are likely to be impacted by in the near future is climate change. And because climate change is considered as the main cause of bumblebee decline by most recent studies (Kerr et al., 2015; Soroye, Newbolt, & Kerr, 2020), we justifiably expect the impact of climate change on Mt. Olympus to be significant.

Communities are more vulnerable to loss of generalists, and bumblebees are generalist pollinators offering pollination services to numerous plant species (Memmott, Waser, & Price, 2004). This implies that the consequences in communities will be critical in case of bumblebee species extinction. We assume, however, global warming effects to vary among communities along the altitudinal gradient, not only because of the existence of microrefugia hosted within a highly heterogeneous microclimatic environment (Suggitt et al., 2018), but also because of the communities’ diverse resilience related to a variety of different factors. Such a factor, for instance, is nestedness, which was found to increase community’s resilience (the speed at which the community returns to the equilibrium following a disturbance) (Dalsgaard et al., 2013; Thébault & Fontaine, 2010), suggesting that in our case communities at low and high altitudes may be more resilient against global warming impacts (see pollination networks below).

Bumblebees respond to global warming by either restricting their southern (Kerr et al., 2015) or shifting uphill their lower (Ploquin et al., 2013) distribution limits. Therefore, the observed range expansion of bumblebees, both latitudinal (B. quadricolor, B. monticola, B. hypnorum and B. haematurus) and altitudinal (B. campesi- tris), is either the result of a recent colonization due to present climate change or these species have been established since the last glacial age. Unfortunately, past historical records of bumblebee distribution are lacking, so no firm conclusion can be drown at the moment. Theoretical models predict a severe reduction in suitable distribution area for most of the bumblebee species not only on Mt. Olympus but also for the entire Greece, as only four of the Greek species are predicted to retain their present distribution (viz. B. argillaceus, B. niveatus, B. terrestris and B. vestalis: Rasmont et al., 2015).

Such predictions pinpoint towards the utter need of a regular bumblebee monitoring scheme to track future changes in bumblebee distribution in the country, especially on Mt. Olympus. In this respect, it is worth mentioning that of all species recorded on the mountain, only one, B. laesus, has been included in the Red Data List under the status Near Threatened at European level (Nieto et al., 2014).

Our results indicate that the altitudes between 1,900 and 2,200 m a.s. l. are the most important for conserving the highest diversity of bumblebee species on Mt. Olympus. Such a predominance of high-elevational peak in bumblebee diversity agrees with other studies published so far. In some of them, bumblebee diversity was found to peak at relatively lower altitudes than on Mt. Olympus (at 900–1100 m, Gorce and Tatra mountains, maximum study altitude 1,580 m high, Poland [Goulson et al., 2008b]; at 1,300–1,900 m, Mt. Norikura, maximum study altitude 2,600 m high, Japan [Egawa & Itino, 2019]). But Williams (1991) found bumblebee diversity to occur even higher, between 3,000 and 3,800 m (Mt. Aphasvat, maximum study altitude 4,143 m, Kashmir). As it happens on Mt. Olympus, the diversity in alpine zone is generally lower than subalpine and montane (cf. also Miller-Struttmann & Galen, 2014 exploring elevations >1,600 m of the Colorado Rocky Mountains). These studies on bumblebee diversity, however, were carried out at mountain

| Region              | # Species | Study area (km2) | Study purpose                                      | Source                                      |
|---------------------|-----------|------------------|---------------------------------------------------|---------------------------------------------|
| Entire Europe       | 68        | 10.4 × 10⁶       | Compilation of existing studies                    | Nieto et al. (2014)                        |
| UK (entire country) | 22        | 242,495          | Compilation of existing studies                    | Goulson (2010)                             |
| Florina District, Greece | 29     | 1,924            | 5-year bumblebee survey, 550–1,800 m a.s.l.       | Anagnostopoulos (2005, 2009, 2017)         |
| Turkey (entire country) | 47      | 783,562          | Bumblebee survey, 0–3,500 m a.s.l.                 | Rasmont et al. (2009)                      |
| Susa Valley, Italy  | 30        | 1,261            | 10-year bumblebee survey, 124 locations, 340–1,310 m a.s.l. | Manino et al. (2010)                      |
| Mt. Etna, Sicily, Italy | 12      | 581              | 10-year bumblebee survey, 9 locations, 0–1,900 m a.s.l. | Mazzeo et al. (2015)                      |
| Pyrenees, Eyne Valley, France | 33  | 21               | 5-year bumblebee survey, 457 locations, 1,450–2,850 m a.s.l. | Iserbyt et al. (2008)                     |
| Pyrenees National Park, France | 30  | 2,521            | 3-year bumblebee survey, 703 locations, 296–3,298 m a.s.l. | Iserbyt (2009)                             |
| Pyrenees, Spain     | 28        | 19,000           | 10-year bumblebee survey, 78 locations, 670–2,600 m a.s.l. | Ornosa et al. (2017)                      |
| Cantabrian Range, Spain | 28     | 10,600           | 2-year bumblebee survey, 80 locations, 0–2,200 m a.s.l. | Obeso (1992)                              |
| Cantabrian Range, Spain | 21      | 10,600           | 3-year bumblebee survey, 53 locations, 0–2,200 m a.s.l. | Ploquin et al. (2013)                      |

Further information and data sources:
- Memmott et al. (2004): Bumblebees and their role in pollination services to wildflower plant species.
- Ploquin et al. (2013): The role of bumblebees in alpine ecosystems.
- Anagnostopoulos et al. (2005, 2009, 2017): The impact of climate change on bumblebee species distribution and diversity.
- Rasmont et al. (2015): The influence of climate change on the distribution of bumblebee species in Europe.
- Iserbyt et al. (2008): The role of climate change in bumblebee species richness.
- Nieto et al. (2014): The effect of climate change on bumblebee species richness and diversity in the Mediterranean region.
regions with different latitude, biogeography and geological history than Mt. Olympus, so a comparison restricted to altitude is certainly incomplete. As we already mentioned, the unique characteristics of Mt. Olympus establish the mountain as refuge and southernmost distribution limit for several bumblebee species, and this situation probably influences the altitudinal pattern of bumblebee diversity observed on the mountain.

Studies looking at all pollinator species or different pollinator guilds did not all come to the same conclusion as those focusing on bumblebees. Some found that, like in our case, insect pollinators displayed a hump-shaped relationship with altitude: Alps, Germany: Hoiss et al. (2015); Jonaskop Mountain, W. Cape Province, South Africa: Adedoja et al. (2018); El Teide, Tenerife, Canary Islands: Lara-Romero et al. (2019), presenting only data above 2,350 m. The results concerning Geometrid moths were similar (meta-analysis on 26 global elevational gradients: Beck et al., 2017). On the other hand, several studies found a clear linear decline with altitude not only for the entire pollinator group (Andes, Chile: Ramos-Jiliberto et al., 2010 based on data from Arroyo, Primack, & Armesto, 1982; Trøjelsgaard & Olesen, 2013, a meta-analysis using 54 global data sets; Antioquia, Colombia: Cuartas-Hernandez & Medel, 2015), but also for bees (Alps, Germany: Hoiss, Krauss, Potts, Roberts, & Steffan-Dewenter, 2012) and for butterflies alone (Mt. Olympus, Greece: Kaltsas et al., 2018); interestingly, the last study also reports no significant altitudinal variation of butterflies on Rhodope Mountains.

4.2 | The host plants

Plants displayed a low- to mid-elevational richness on Mt. Olympus, at much lower altitudes than bumblebees (500–1,500 vs. 1,900–2,200 m, respectively; cf. Figure 4, Table S4). This implies that altitude functions as an ecological filter which is harsher to plants than it is to bumblebees, indicating that on Mt. Olympus the ecotone signifying the transition from woods to open alpine grasslands (coinciding, in fact, with the maximal bumblebee diversity) favours bumblebee rather than plant diversity. This suggests that bumblebees’ ability to thermoregulate and the resulting advantages at higher altitudes, potentially leading to competitive release from other pollinator groups, may outweigh the disadvantage of a decreased food-plant diversity.
Trojelsgaard and Olesen (2013). To the above contrasting patterns, it is interesting to add the only study reporting a continuous increase of plant host diversity along the altitudinal gradient of the Rocky Mountains carried out by Miller-Struttmann and Galen (2014) that reported 8, 12 and 15 plant species interacting with 19, 15 and 15 bumblebee species in montane, subalpine and alpine zones, respectively.

### 4.3 | Pollination networks

We found bumblebee–plant interaction networks on Mt. Olympus to be larger, more diverse, and more generalized at intermediate altitudes (1,500–1,800 m), which is also reflected in the lowest nestedness values (NODF) found for the same altitudes (Figure 5, Table S5). This elevation range is higher than the range of plant diversity maxima (viz. 500–1,500 m) and lower than that of bumblebee diversity maxima (viz. 1,900–2,200 m) (cf. Figures 3a, b and 4; Table S4). Evidently, the resulting larger, more diverse and more generalized b–p networks are encountered within the gradient where the highest diversity of both bumblebee and plant groups tends to overlap. This result highlights that the assessment of species diversity alone does not allow conclusions regarding the trends of interaction diversity (i.e., the diversity and architecture of plant–pollinator interactions) along the altitudinal range of the mountain. To extend this thought, studies of biodiversity, along environmental gradients, should include not only the taxonomic, but also the interaction diversity, for example interspecific interactions, within the communities (Kaiser-Bunbury & Blüthgen, 2015) in order to (a) elucidate community biogeography, (b) predict responses to environmental change and, ultimately, (c) help set solid and targeted conservation objectives about for specific species or habitat types.

Nestedness (NODF), an indicator of asymmetry in b–p networks, had its lowest values at intermediate altitudes on Mt. Olympus, where networks are larger (Figure 5b), implying that at the lower and higher altitudes b–p networks consist of many specialist species that are more likely to interact with generalist partners (Bascompte, Jordano, Melián, & Olesen, 2003). The high nestedness value at the altitudinal extremities can be explained by the higher asymmetry of b–p resources, as resulting from the low diversity ratio of bumblebees:plants in the lower altitudes and the low diversity ratio of plants:bumblebees at higher altitudes (cf. Figure 3a–c, Table S4); this is corroborated by the low linkage density at either altitude (Figure 5d). In general, larger networks tend to have smaller values of nestedness (Kantsa et al., 2018; Trojelsgaard & Olesen, 2013), which may also explain the observed trend at intermediate altitudes where networks are the largest along the entire gradient. Like on Mt. Olympus, nestedness in b–p networks was found to increase at high elevations (Miller-Struttmann & Galen, 2014). Being the only studies focusing on b–p networks along an altitudinal gradient, their convergent results imply that communities at high altitudes are more resilient against global warming impacts (cf. above). However, in studies including all pollinators, nestedness was found to decrease with altitude (Ramos-Jiliberto et al., 2010) or to be altitude-independent (Cuartas-Hernandez & Medel, 2015).

Network specialization (selectiveness index $H_{ij}^\prime$) did not correlate with altitude in our study. In contrast, Hoiss et al. (2015) reported decreased $H_{ij}^\prime$ values with elevation, which agrees with Lara-Romero et al. (2019) who also found network specialization to decrease with altitude. However, the results of both these studies are based on networks including all pollinator guilds. On the other hand, bumblebees are considered generalist pollinators (Goulson, 2010), consisting, however, of both long- and short-tongued species that both occur throughout the range of the mountain. As a result, b–p interaction networks are largely influenced by the differential bumblebee behaviour, and the availability of floral resources that follows a somewhat different altitudinal trend. All in all, we believe that the lack of specialization trend along the altitudinal gradient of Mt. Olympus versus other published studies may be the result of either having employed the full altitudinal range of Olympus versus a few sites at particular altitudes (mainly the highest ones) employed in other studies, or because other studies present results of meta-analysis consisting of tens of different mountain studies in which particularities are masked.

### 5 | CONCLUSIONS

We found bumblebee community structure on Mt Olympus to be strongly altitude-dependent: (a) bumblebee species richness and diversity maximize at high altitudes; (b) bumblebee–plant networks are larger, more diverse and more generalized at intermediate altitudes, whereas nestedness peaks at low and high altitudes; and (c) seven bumblebee species have a significant connection to certain altitudinal ranges.

Thus far, the conservation and protection measures applied in the Olympus National Park (covering, however, only half the mountain area) focus primarily on plants, birds and mammals. Our results provide evidence that conservation strategies should also include pollinators, with emphasis on bumblebees, which represent major providers of pollination services, especially at higher altitudes. Furthermore, our findings disclose the need to focus on multiple elevation zones regarding conservation priorities: high altitudes (1,900–2,200 m) harbour the richest bumblebee diversity; at lower to intermediate altitudes (500–1,500 m), flowering plants display their highest diversity; and at intermediate altitudes (1,500–1,800 m), b–p communities include the most diverse interactions.

Based on our results, we recommend the Olympus National Park area should be extended to cover the entire mountain co-considering all mountain sides and altitudes, and the conservation and protection schemes should comprehensively include measures against future threats to the bumblebee fauna, for example land use change and invasive species; authorities considerations to reduce the protected area to construct ski resort and the observed degradation of the non-protected area of the mountain justify our proposition as the only measure against human activities. Regular
monitoring, including especially pollination network properties and pollination services, should be established to track possible adverse effects of climate change on communities along the altitudinal gradient and to allow for timely conservation actions (Kaiser-Bunbury & Blüthgen, 2015). For the time being, there are no local measures that could be effectively taken against the impact of global warming. Certainly, future research will fill this gap in order to advise us on the key species, specific measures and management schemes including assisted migration, on Mt. Olympus (Hällfors et al., 2018).

Overall, this first systematic study regarding the bumblebees of Mt. Olympus highlights the need for future research in order to deepen our understanding of the diversity and particularities of pollinators and their host plants of this divine mountain. This is to enhance our knowledge regarding not only the present and past status of its biota, including the effects of Pleistocene glaciations, but also how to treat habitat conservation on this mountain in view of global warming.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the Supplementary material of this article.

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**BIOSKETCH**

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**SUPPORTING INFORMATION**

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

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