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High species turnover and unique plant–pollinator interactions make a hyperdiverse mountain

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Abstract

1. We studied α- and β-diversity of pollinators, flowering plants and plant–pollinator interactions along the altitudinal gradient of Mt. Olympus, a legendary mountain and biodiversity hotspot in Central Greece.

2. We explored 10 study sites located on the north-eastern slope of the mountain, from 327 to 2596 m a.s.l. Insect surveys were conducted once a month using hand netting (years 2013, 2014 and 2016), and they were combined with recordings of flowering plant diversity (species richness and flower cover). We then calculated α- and β-diversity of pollinators, plants in flower and plant–pollinator interactions, and explored their demographic response along the altitudinal gradient.

3. Alpha diversity of pollinators, plants and plant–pollinator interactions were altitude dependent; α-diversity of all pollinators, bees, non-bumblebee bees, bee flies and butterflies showed linear declines with altitude, whereas those of hoverflies and bumblebees showed unimodal patterns. Beta diversity and its turnover component of all pollinators, hoverflies, bees, bumblebees, non-bumblebee bees, butterflies and plants showed linear increases, whereas those of bee flies and of plant–pollinator interactions varied independently from the pairwise altitudinal difference.

4. The high dissimilarity and uniqueness of pollination networks, which is probably a result of the high biodiversity and endemism of Mt. Olympus, is driven by species turnover and the formation of new interactions between new species. Contrasting to the monotonic decline of the remaining groups, the unimodal patterns of hoverfly and bumblebee α-diversity are probably the effect of a higher tolerance of these groups to high-altitude environmental conditions. Our findings highlight that the high turnover of species and of pollination interactions along the altitudinal gradient are the mainstay of hyperdiverse mountains, a fact that conveys important historical, ecological and conservational implications.

KEYWORDS
altitudinal gradient, Mount Olympus, pollination networks, pollinator guilds, α-diversity, β-diversity

1 | INTRODUCTION

Mountains occupy only ca. 12% of earth's land area (Körner et al., 2011, 2017), sustaining however, nearly one third of the known terrestrial plant species (Barthlott et al., 2007; Körner, 2007), high rates of endemism (Rahbek et al., 2019) and ca. 10-fold higher number of invertebrates versus plants (Körner, 2004; Spehn et al., 2010). Considering that >80% of wild plant species rely for reproduction on animal pollinators (Ollerton et al., 2011; Potts et al., 2010), mountain diversity is highly dependent on pollinator services. Therefore, studies on mountain pollination systems are pivotal for monitoring biodiversity and for predicting community responses in view of the risks associated with pollinator declines (Inouye, 2020; Potts et al., 2010).

In this context, comprehensive research approaches emerge, considering the local diversity (α-diversity) of pollinators, plants and their interactions (e.g. Adedoja et al., 2018; Hoiss et al., 2015; see Table 1 for a review), as well as the (dis)similarity (β-diversity) of all the above along altitudinal gradients (Simanonok & Burkle, 2014; Sponsler et al., 2022; see Table 1 for a review). Indeed, the detailed examination of the different components of mountain biodiversity can disclose the patterns of community change and their drivers and reveal how similar or unique pollination systems along the altitudinal clines are (Cuartas-Hernández & Gómez-Murillo, 2015; Luna et al., 2020). Apart from their significance for conservation, such approaches may provide important information both for the past and for the future of mountain biomes.

First, clinal changes of β-diversity and its components can unveil the mountains' glacial histories reflected into plant and pollinator distributions, patterns of endemism or the uniqueness of pollination systems (Baselga, 2010; Cuartas-Hernández & Gómez-Murillo, 2015; Luna et al., 2020). To that end, the assessment of the fundamental components of β-diversity, viz. nestedness and turnover, can be particularly useful for disclosing ecological processes because they relate to different ecological mechanisms (Soininen et al., 2018). For example, according to Baselga (2010), the nestedness (indicating the degree to which species occurring in one site are a subset of the species assemblage in another site) and the turnover component of β-diversity (indicating species replacement by new ones across sites) denote two different biogeographical processes: the first one prevails in regions with past extinctions and recolonizations (e.g. in high latitudes); therefore it is higher in regions with a later deglaciation, and concerns organisms with lower dispersal ability and temperature tolerance (Dobrovolski et al., 2012). On the other hand, the turnover component prevails in regions with high species diversity and endemism, which served as refugia and speciation centres during the recent geological past, like the south-European (Mediterranean) region (Baselga, 2008, 2010).

Second, the analysis of α- and/or β-diversity, using space-for-time substitution, is pivotal for predicting the future impact of climate change on mountains (Luna et al., 2020; Mayor et al., 2017; Sundqvist et al., 2013; Tito et al., 2020). Apart from driving species upslope, promoting species invasions, and disrupting pollination services (Inouye, 2020; Vasiliev & Greenwood, 2021), climate change-induced extinctions may result in homogenization, low dissimilarity and low β-diversity along altitudinal clines (Fourcade et al., 2021; Vasiliev & Greenwood, 2021). To that end, the study of β-diversity of interactions along the altitudinal gradients may indicate whether a change is mainly due to species turnover (i.e. new interactions between new species) or to rewiring (i.e. new interactions between same species) (Poisot et al., 2012); in the first case, pollination networks (i.e. plant–animal interaction communities) are expected to be more vulnerable to secondary species extinctions, as species are less flexible to form new interactions (Simanonok & Burkle, 2014).

Third, a comprehensive analysis of the different components of mountain biodiversity can reveal differential patterns in altitudinal distribution between pollinator groups. This information may elucidate the thermal ecology of different pollinating animals and, importantly, allow predictions on the future responses of populations in warmer climates. Studies considering α-diversity of different pollinator groups along altitudinal gradients have shown either unimodal patterns or linear declines, depending on the focal pollinator group and mountain range (cf. Table 1, lines 8–19). For example, bumblebees and hoverflies are known to show tolerance to high-altitude conditions, especially temperature (McCabe & Cobb, 2021; Peters et al., 2016); this behaviour explains their shared unimodal clinal patterns of their α-diversity found in previous studies on mountains around the world (Table 1, lines 10–14, 18–19).

In this study, we aimed at exploring in detail the patterns of α- and β-diversity of pollinators, of flowering plants and of plant–pollinator interactions along the entire altitudinal range of Mt. Olympus, Greece (327–2596 m a.s.l.). In this context, we made the following predictions:

(i) Considering the α-diversity of different pollinator groups along altitudinal gradients, different patterns were found (Table 1, lines 8–19). We predict similar results in Mt. Olympus, specifically unimodal clinal patterns for bumblebees and hoverflies due to their ability to cope with high-altitude low temperatures (McCabe & Cobb, 2021; Peters et al., 2016); this is in line with their α-diversity patterns found in previous studies on mountains around the world (Table 1, lines 10–14, 18–19).

(ii) Studies on elevational patterns of β-diversity of pollinators have always shown a linear increase, usually deriving from the high turnover component (Table 1, lines 2, 6, 8, 13; but see line 4 for the prevalence of nestedness component); besides, a meta-analysis considering different organisms and ecosystems also showed prevalence of the turnover component (Soininen et al., 2018). In addition, studies on β-diversity of interactions were also found high turnover component (Encinas-Viso et al., 2022; Simanonok & Burkle, 2014; Sponsler et al., 2022). We predict that this will be also the case in Mt. Olympus, in accordance with the cases of ecosystems of southern Europe (Mediterranean), as a main result of the glacial history of the region (Baselga, 2008, 2010), given that Mt. Olympus has acted as a species refugium with continuous speciation taking place during its recent geological past (Kougioumoutzis et al., 2021; Médail & Diadema, 2009). Moreover,

TABLE 1 Studies on α- and β-diversity of pollinators and pollinator groups along the altitudinal gradient studied on mountains around the world. Icons inside the cells indicate: ∩, unimodal; /, linear increase; \, linear decrease.

#	Pollinator group	# of species and/or morphospecies	Altitudinal range (m)	Mountain	Country	α-diversity pattern with altitude	β-diversity pattern with altitudinal difference	Prevailing β-diversity component	Reference
1	All pollinators	71	550–1640	Jonaskop	South Africa	∩			Adedoja et al. (2018)
2	All pollinators	73	2200–2900	Andes	Colombia		/	Turnover (β_{SIM})	Cuartas-Hernández and Gómez-Murillo (2015)
3	All pollinators	333	600–2000	Alps	Germany	∩			Hoiss et al. (2015)
4	All pollinators	119	2350–3520	El Teide	Canary Islands	∩	/	Nestedness (β_{SNE})	Lara-Romero et al. (2019)
5	All pollinators	110	1800–3600	Andes	Chile	\			Ramos-Jiliberto et al. (2010)
6	All pollinators	126	2975–3310	Beartooth Plateau	USA		/	Turnover (β_{SIM})	Simanonok and Burkle (2014)
7	All pollinators	6–840, mean 146		Meta-analysis using 54 global datasets		\			Trøjelsgaard and Olesen (2013)
8	Bees and Wasps	137	1000–2000	Caraça	Brasil	\	/	Turnover (β_{SIM})	Perillo et al. (2017)
9	Bees	87	600–2000	Alps	Germany	\			Hoiss et al. (2012)
10	Bumblebees	9	700–2600	Norikura	Japan	∩			Egawa and Itino (2019)
11	Bumblebees	23	370–1580	Gorce, Tatra	Poland	∩			Goulson et al. (2008)
12	Bumblebees	25	327–2596	Olympus	Greece	∩			Minachilis et al. (2020)
13	Bumblebees	16	641–2032	German Alps	Germany	∩	\	Turnover (β_{SIM})	Sponsler et al. (2022)
14	Bumblebees	24	1800–4143	Apharwat	Kashmir	∩			Williams (1991)
15	Butterflies	55	800–2480	Olympus	Greece	\			Kaltsas et al. (2018)
16	Butterflies	67	600–2000	Alps	Germany	\			Leingärtner et al. (2014)
17	Butterflies	67	620–2040	Sierra de Guadarrama	Spain	∩			Wilson et al. (2007)
18	Hoverflies	93	972–2659	Alps	France	∩			Lefebvre et al. (2018)
19	Hoverflies	68	780–2130	Dolomites	Italy	∩	/	Turnover (β_{SIM})	Sommaggio et al. (2022)
	Bees	67				\	/	Turnover (β_{SIM})	

we expect different β-diversity patterns between some pollinator guilds due to their association with specific altitudinal range, arising from different environmental needs (Perillo et al., 2017).

All in all, the prospect for high dissimilarity in pollinator species and their interactions, would imply unique pollination systems existing along the altitudinal gradient of Mt. Olympus and thus pose important implications for designing future ecosystem conservation schemes (Cuartas-Hernández & Gómez-Murillo, 2015; Luna et al., 2020; Sommaggio et al., 2022).

2 | MATERIALS AND METHODS

2.1 | Study area

Mount Olympus (2918 m), a legendary landmark, constitutes a circular massif of 25-km diameter on average, situated near the central-eastern coast of Greece. Its flora consists of >1700 plant species, encompassing ca. 25% of the Greek flora, including 58 Greek endemics of which 25 are endemics to Mt. Olympus itself (Strid, 1980; Strid & Tan, 1986, 1991). Almost the entire mountain is part of the Olympus National Park, part of which constitutes a European Natura 2000 site (GR 1250001). The study was conducted on the north-eastern slope of the mountain, following the path route from Litochoro town to Mousses Plateau. Along this route and at different altitudes, we established 10 sampling sites having a north north-eastern aspect and an average altitudinal difference ca. 250 m (Minachilis et al., 2020). Fieldwork in the Olympus National Park was permitted by the Ministry of the Environment and Energy (licence number 128258/743/28-03-2013).

2.2 | Sampling of insects and visited plants

Insect surveys were carried out within an area of ca. 0.1 ha at each site; they consisted of recording of all insects that touched the reproductive organs of flowering plants, using random transect observations assisted by hand netting collection (Minachilis et al., 2020). Both pollinators and the visited plants were recorded; specimens of unknown insects and visited plants were collected for later identification. The surveys were conducted on a monthly basis from May to October during years 2013, 2014 and 2016. Hand netting was performed in days with weather favourable to insect activity, during the active foraging hours (10:00–16:00) and lasted for 90 min/site in 2013, and for 120 min/site in each of the years 2014 and 2016 (Minachilis et al., 2020). Although our study did not require ethical approval to work with insect pollinators, we minimized collection of insect specimens considering impact on mountain ecosystem and species conservation.

We collected 2779 insect pollinator specimens belonging to 333 species (Table S1), which were found to visit 153 plant species (Table S2). Most pollinator specimens were identified to species level (2671 specimens; 96.1%), few specimens to genus level (108

specimens; 3.9%), whereas the specimens of *Bombus terrestris* and *B. lucorum* s.l. (i.e. a complex consisting of three species: *B. lucorum*, *B. cryptarum* and *B. magnus*) were pooled together into one group because they are indistinguishable when observed on the wing (Bossert et al., 2016; Wolf et al., 2009).

For the analysis, the collected/observed insects were grouped as follows:

- Bee flies (Diptera: Bombylidae): 20 species
- Hoverflies (Diptera: Syrphidae): 53 species
- Bees (Hymenoptera: Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae and Melittidae): 205 species (*Apis mellifera* was not considered in our study, even it might occur in the sites)
- Bumblebees (Hymenoptera: Apidae: *Bombus*): 18 species, plus one species group (see above)
- Non-bumblebee bees: bees other than *Bombus*, as described above: 186 species
- Butterflies (Lepidoptera: Hesperiidae, Lycaenidae, Nymphalidae, Papilionidae, Pieridae, Sphingidae and Zygaenidae): 55 species.

2.3 | Flowering plant diversity and flower cover

Flower cover was measured per plant species in flower during our fieldwork visits, by counting the number of flowers or inflorescences within 1×1 m squares (n = 25) randomly selected at each site and round. Flower abundance for each plant species in flower was the average number of flowers/m^2 of the 25 squares within a site (Minachilis et al., 2020). We recorded 142 plant species in flower (Table S2) and used the flower abundance of each plant to calculate α- and β-diversity of plants in flower (hereafter referred simply as 'plants').

2.4 | Alpha diversity of pollinators, plants and plant–pollinator interactions

Using flower cover data for plants (#flowers/m^2) for the years 2013, 2014 and 2016 separately, and hand-net weighted data for pollinators (insect abundance/collection duration) and for plant–pollinator interactions for the same years, we computed two metrics of α-diversity of pollinators, of plants and of plant–pollinator interactions in the study communities (Table S3):

(i) *Shannon–Wiener diversity index (H′)*: a widely used metric of α-diversity, which accounts both for species diversity and evenness within a community.
(ii) *Shannon's diversity of interactions*: the α-diversity Shannon index calculated for the links existing within a network (Dormann et al., 2009).

Metrics (i) and (ii) were calculated using the R packages VEGAN 2.5-7 (Oksanen et al., 2020) and BIPARTITE 2.17 (Dormann et al., 2008) respectively.

2.5 | Beta diversity of pollinators and of plants

Using the species occurrence data for pollinators (hand net) and for plants (flower cover) for the years 2013, 2014 and 2016 separately, we computed three metrics that describe pollinator and plant species β-diversity as pairwise dissimilarity between the study communities (Table S4):

(i) β_{SOR}: the total species β-diversity, measured as compositional dissimilarity between sites, using the Sørensen dissimilarity index (Baselga, 2010). The β_{SOR} is partitioned into two components ($\beta_{SOR} = \beta_{SIM} + \beta_{SNE}$):

(ii) β_{SIM} (turnover component): the dissimilarity in species composition between sites due to species turnover (replacement by new species) from one site to another,

(iii) β_{SNE} (nestedness component): the dissimilarity in species composition between sites due to species loss from site to site, meaning that species of one site are a subset of species of the other site (nestedness).

The values of these metrics vary between 0 (when species composition of focal sites is identical) and 1 (when species composition of focal sites is completely different). Metrics were calculated using the R package BETAPART 1.5.4 (Baselga & Orme, 2012).

2.6 | Beta diversity of plant–pollinator interactions

Using the hand-net weighted data for plant–pollinator interactions for the years 2013, 2014 and 2016 (separately), we computed three metrics that describe the β-diversity of interactions as pairwise dissimilarity, among the pollination networks of the study communities (Table S4):

(i) β_{WN}: the total β-diversity of interactions measured as dissimilarity of interactions between pollination networks (Poisot et al., 2012). The β_{WN} is partitioned into two components ($\beta_{WN} = \beta_{ST} + \beta_{OS}$):

(ii) β_{ST} (turnover component): the dissimilarity of interactions due to changes in species composition between pollination networks (turnover),

(iii) β_{OS} (rewiring component): the dissimilarity of interactions due to changes in realized interactions between pollination networks shared species (rewiring).

The values of these metrics vary between 0 (when interactions of focal networks are identical) and 1 (when interactions of focal networks are completely different). All the above metrics were calculated using the framework available in the R package BETALINK 2.2.1 (Poisot et al., 2012) as changed and incorporated in the R package BIPARTITE 2.17 (Dormann et al., 2008).

We also calculated the proportion of turnover component with total β-diversity of species or of interactions (β_{SIM}/β_{SOR} or β_{ST}/β_{WN},

respectively; Table S4) to conclude if turnover contributed the most to β-diversity (when proportion values >0.5) (Dobrovolski et al., 2012; Poisot et al., 2012).

2.7 | Statistical analysis

To test the relationship between altitude and the α-diversity of pollinators, plants and plant–pollinator interactions on Mt. Olympus, we used linear mixed effects models (R package LME4 1.1-27.1) considering weighted hand netting data (pollinators, plant–pollinator interactions) or flower cover (plants) data for each year separately. To avoid pseudoreplication, we used 'site ID' nested within 'year' as categorical random variables. As dependent variables, we used (i) the pollinators Shannon–Wiener diversity index, (ii) the plants Shannon–Wiener diversity index and (iii) Shannon's diversity of interactions index, calculated for each of the sampled sites. For these three indices we used models with Gaussian distribution. 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' ($\bar{x} = 0$, $s = 1$) before calculating its quadratic term. To select the best combination of predictors we used a backward selection process based on AICc (Akaike's information criterion with correction for small sample size; R package AICcMODAVG 2.3-1). We also used the AIC weights in order to compare the best-fitted model with the null model ($Y_i = \beta_0 + \varepsilon_i$). All the aforementioned analyses were performed for all pollinators and for each pollinator group separately.

To investigate the relationship between altitude and the β-diversity of pollinators, plants and plant–pollinator interactions on Mt. Olympus, we used generalized linear mixed effects models (R package LME4 1.1-27.1) with binomial distribution (link='logit'; the models were not overdispersed), considering weighted hand netting data (pollinators, plant–pollinator interactions) or flower cover (plants) data separately for each sampling year, using 'year' as categorical random variable. As dependent variables, we used (i) the pairwise compositional dissimilarities of pollinator and plant species (β_{SOR} and its components) and, (ii) the pairwise dissimilarities of plant–pollinator interactions (β_{WN} and its components), calculated for each pair of the sampled sites. As fixed variables (predictors), we included both the linear and the quadratic term of the pairwise differences of altitude. To select the best combination of predictors, we used a backward selection process based on AICc (R package AICcMODAVG 2.3-1). We also used the AIC weights in order to compare the best-fitted model with the null model ($Y_i = \beta_0 + \varepsilon_i$). All the aforementioned analyses were performed for all pollinators and for each pollinator group separately.

To further examine the dissimilarity of interactions of pollination networks along the altitudinal gradient of Mt. Olympus, we calculated the uniqueness (local network uniqueness–LNU) and commonness of interactions (shared interactions frequency–SIF) using the framework and the R code proposed by Luna et al. (2020) (Table S5). To investigate the relationship between altitude and these two

metrics (LNU, SIF) we used generalized linear mixed effects models (R package LME4 1.1-27.1) with binomial distribution (link='logit'; the models were not overdispersed), using 'year' as categorical random variable. As fixed variables (predictors), we included both the linear and the quadratic term of the altitude of each site. To select the best combination of predictors, we used a backward selection process based on AICc (R package AICCMODAVG 2.3-1). We also used the AIC weights in order to compare the best-fitted model with the null model ($Y_i = \beta_0 + \varepsilon_i$).

3 | RESULTS

3.1 | Alpha diversity

The α-diversity of pollinators, plants and plant–pollinator interactions was found to be altitude dependent on Mt. Olympus (Figure 1; Table S6). Among them, only pollinators showed a significant dependency pattern with altitude, in fact a linear decline in all three sampling years ($p = 0.003$; Figure 1a). Pollinator groups were also

found to be altitude dependent as to their α-diversity, showing a significant trend: hoverflies and bumblebees showed a unimodal pattern (Figure 2b,d), while the remaining groups (bee flies, bees, non-bumblebee bees and butterflies) showed a linear decline (Figure 2a,c,e,f).

3.2 | Beta diversity

Beta diversity of pollinators, of plants (β_{SOR}) and of plant–pollinator interactions (β_{WN}) was high in all cases and the same holds true for their turnover component (β_{SIM} and β_{ST} respectively; Table S4). Beta diversity of pollinators and plants (β_{SOR}) was positively related (linear increase) to the pairwise altitudinal difference along the gradient, and the same applied for the turnover component (β_{SIM}), considering each year separately (Figure 3a,b,d,e; Table S7). Both the pollinators' and the plants' nestedness component (β_{SNE}) were not related with altitudinal difference (Figure 3c,f respectively). Beta diversity of interactions (β_{WN}), turnover (β_{ST}) and rewiring (β_{OS}) components were not related to the altitudinal difference;
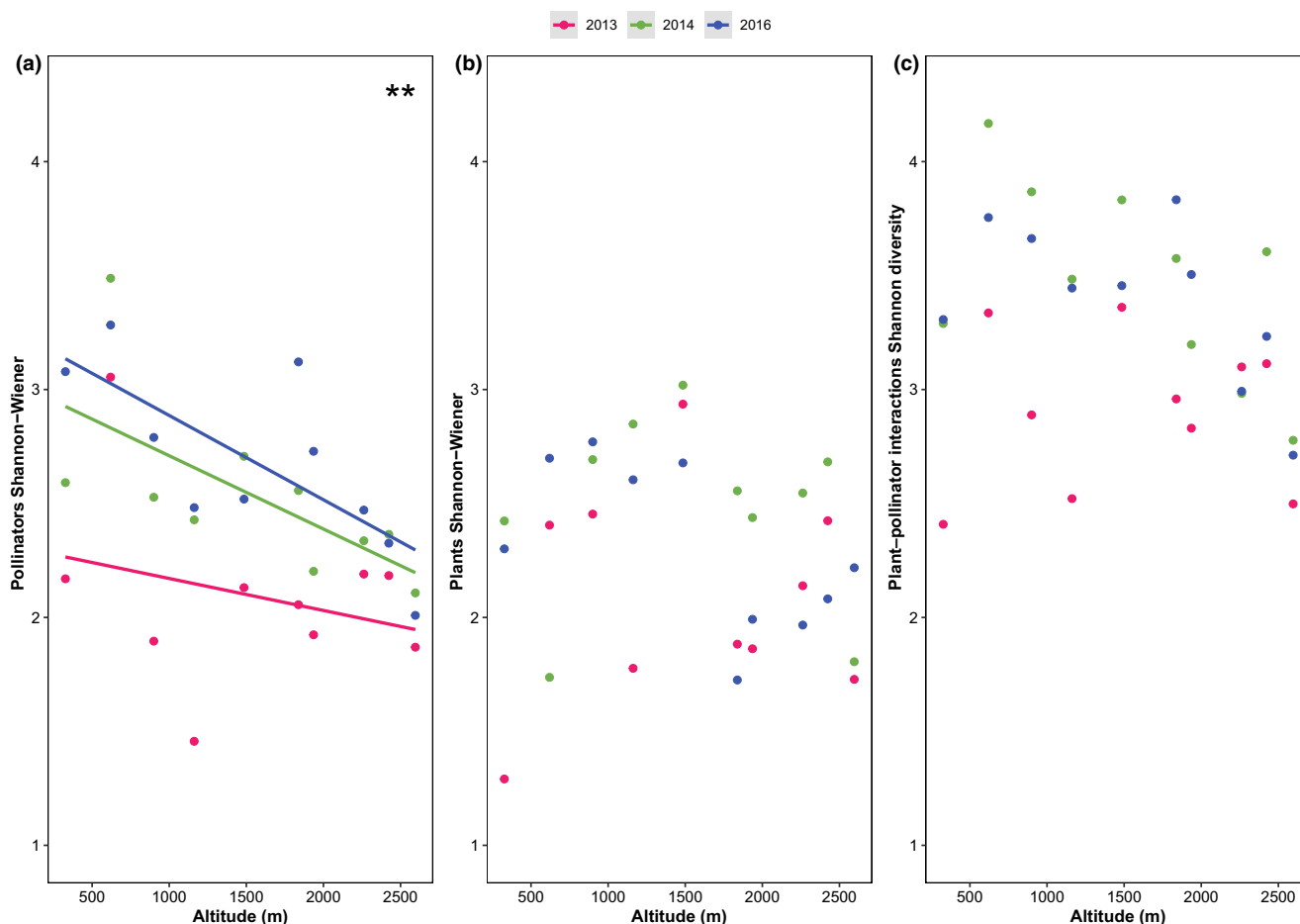

FIGURE 1 Altitude as predictor of α-diversity of pollinators, plants in flower and plant–pollinator interactions on Mt. Olympus, depicted using Shannon–Wiener of species index (a, b), and Shannon's diversity of interactions index (c). The colours correspond to different sampling years, representing random effect factors in the fitted models, while fitted lines are shown only for the statistically significant relationships (**$p \leq 0.010$).

however, an increase for β_{WN} and β_{ST} and decrease trend for β_{OS} was observed up until 1000m altitudinal difference between sites (Figure 3g–i; Table S7).

Considering the different pollinator groups, both pairwise dissimilarity (β_{SOR}) and turnover component (β_{SIM}) of all groups were related to pairwise altitudinal difference (Figure 4; Table S7), except for bee flies' β_{SOR} and β_{SIM} (Figure 4a,b) and non-bumblebee bees' β_{SOR} (although marginally, $p = 0.057$; Figure 4i). Particularly, hoverflies, bees, bumblebees, non-bumblebee bees and butterflies showed a linear increase in β-diversity with the altitudinal pairwise

difference between sites (Figure 4c–h,j,k), except for the turnover component (β_{SIM}) of butterflies which showed a unimodal pattern (Figure 4l).

The proportion of turnover component with total β-diversity of pollinators, of plants and of plant–pollinator interactions (β_{SIM}/β_{SOR} or β_{ST}/β_{WN}) was in most cases higher than 0.5 (with the exception of some alpine site pairs in 2014), indicating that species (β_{SIM}) or interaction turnover component (β_{ST}) was the main dissimilarity driver as the altitudinal difference between sites increased (Table S4).
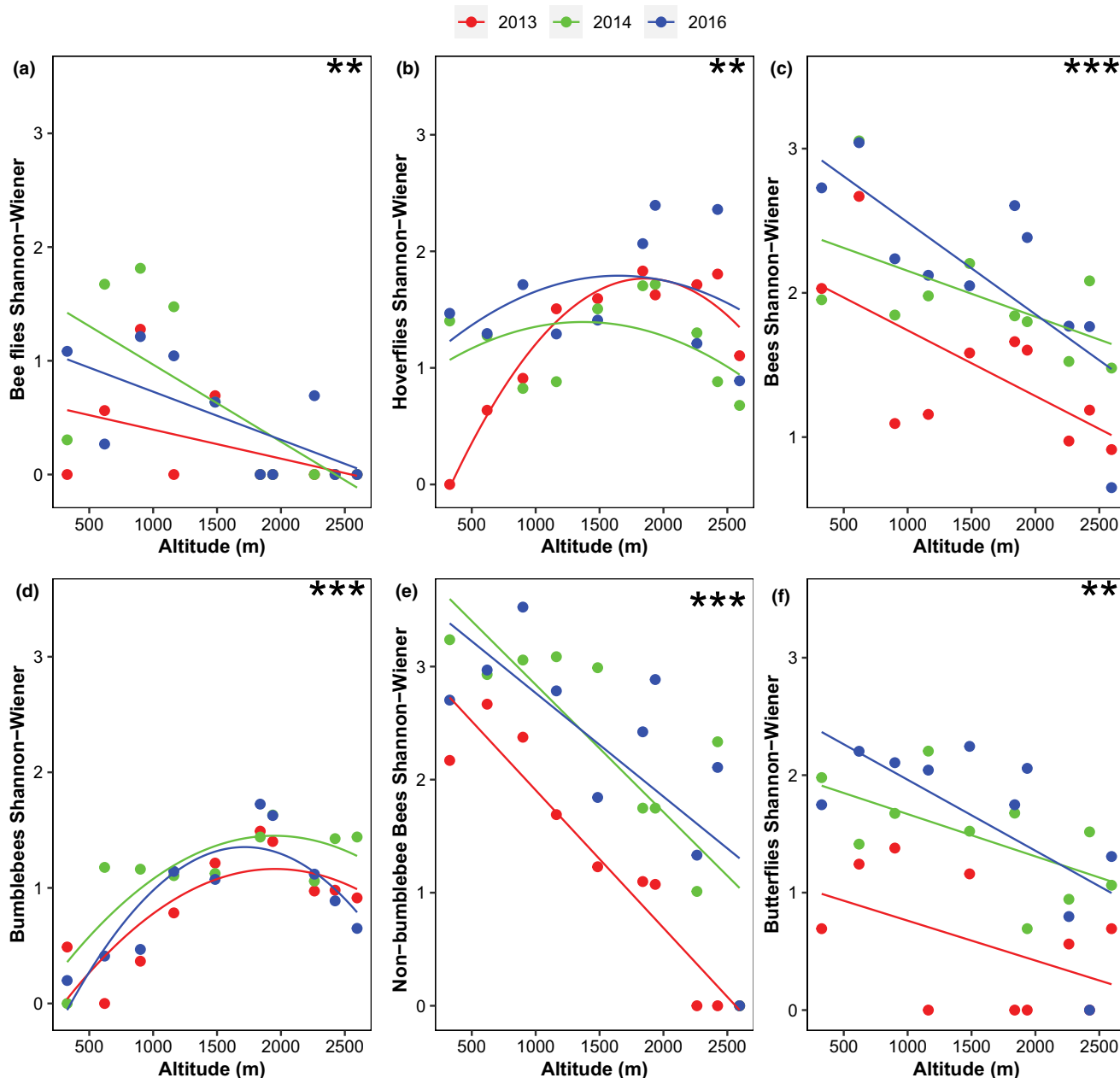

FIGURE 2 Altitude as predictor of α-diversity of pollinator groups on Mt. Olympus, described with Shannon–Wiener index for bee flies (a), hoverflies (b), bees (c), bumblebees (d), non-bumblebee bees (e) and butterflies (f). The colours correspond to different sampling years, representing random effect factors in the fitted models, while fitted lines are shown only for the statistically significant relationships (**$p \leq 0.010$; ***$p \leq 0.001$).
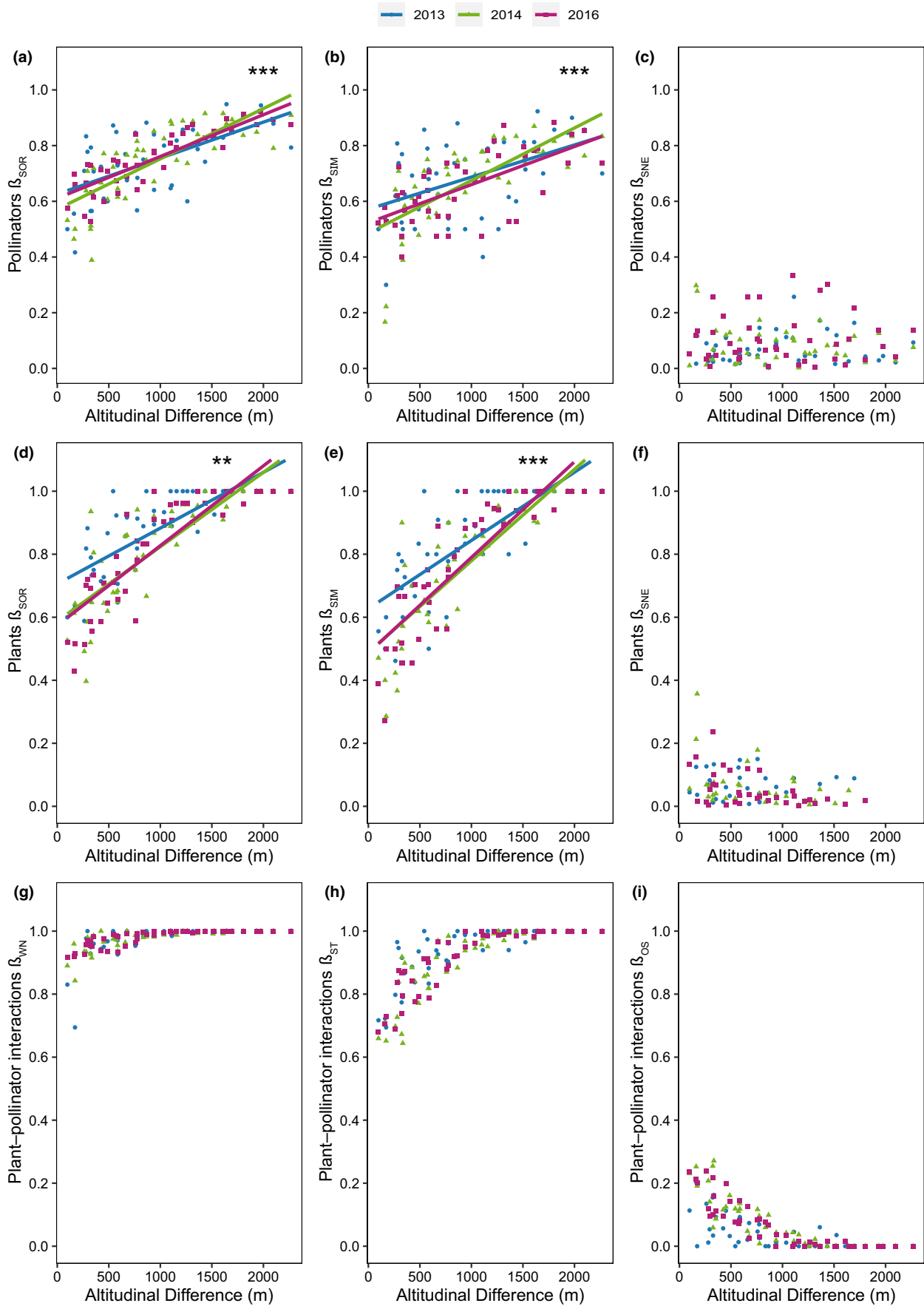
FIGURE 3 Pairwise altitudinal difference as predictor of β-diversity of pollinators, plants in flower and plant–pollinator interactions on Mt. Olympus, described with β_{SOR} index and its components β_{SIM} and β_{SNE} for pollinators (a–c) and plants in flower (d–f), and with plant–pollinator interactions β_{WN} index and its components β_{ST} and β_{OS} (g–i). The colours correspond to different sampling years, representing random effect factors in the fitted models, while fitted lines are shown only for the statistically significant relationships (**$p \leq 0.010$; ***$p \leq 0.001$).

Uniqueness (LNU) of interactions remained high along the altitudinal gradient, while commonness (SIF) was low (Table S5). Neither metric was related to altitude (Table S7).

4 | DISCUSSION

To our knowledge, this is the first study carried out along the entire altitudinal gradient of a high mountain (sensu Karagulle et al., 2017) co-considering: (i) α-diversity of all pollinators and pollinator groups, of flowering plants, and of plant–pollinator interactions, (ii) β-diversity of all pollinators and pollinator groups, of flowering plants and of plant–pollinator interactions. In this context, we described the elevational patterns of α-diversity, highlighting the special roles of hoverflies and bumblebees especially for high altitudes, and showed that both for species and for interspecific interactions the turnover component of β-diversity prevailed over nestedness and rewiring respectively, implying remarkably high rates of uniqueness of pollination systems. Given the fundamental role of plant–pollinator interactions for maintaining biodiversity and the continuity of ecosystems, we argue that our approach unravelled and quantified the biodiversity patterns lying behind a known 'hyperdiverse' mountain. In the following paragraphs, we discuss the possible drivers of biodiversity patterns of different pollinator guilds.

4.1 | Impact of altitude on local (α-) diversity

Although it occupies less than 0.4% of the Greek territory, Mt. Olympus harbours ca. 25% of the Greek flora (Strid, 1980; Strid & Tan, 1986, 1991) and constitutes a biodiversity hotspot and centre of endemism for plant diversity (Kougioumoutzis et al., 2021). As shown recently, the pollinating fauna corresponds well to this hyperdiverse flora; for example, Mt. Olympus hosts the majority of bumblebee species of Greece, that is, 22 species (plus one species complex comprising three species) of 33 species occurring in the country (Minachilis et al., 2020). This is corroborated by our results: stemming from only 10 sites, we recorded 205 bee species, corresponding to 17% of the entire bee fauna of Greece (Petanidou et al. unpublished data) and is higher than the diversity of the entire island of Limnos (occupying almost the same area as Mt. Olympus), in which a comparable sampling effort (# of sites) and methods were employed (178 species: Kaloveloni et al., 2018). Furthermore, the mountain hosts a high diversity of hoverflies [a total of 123 species of 418 species occurring in Greece (Vujić et al., 2020); 53 found in this study] and butterflies [a total of 155 species of 234 species occurring in Greece (Pamperis, 1997); 55 found in this study]. Finally,

this study unveiled a high diversity of plant–pollinator interactions along the altitudinal gradient, as well as high uniqueness of interactions among the communities. Comparing to other studies on mountains all over the world, Mt. Olympus presents equal or even higher pollinator diversity, taking into account all pollinators (Table 1, lines 1–7) or pollinator groups (Table 1, lines 8–19). In epitome, Mt. Olympus can be considered as a hyperdiverse system solely owing to its pollination system.

On Mt. Olympus, the α-diversities of pollinators, plants and their interactions were all related to altitude; however, only the α-diversity of all pollinators showed a significant linear decline along the altitudinal gradient [yet, we found a unimodal pattern for plants, when plant species richness was considered instead of Shannon–Wiener index: Minachilis et al., 2020]. The drivers of α-diversity patterns along altitudinal clines are debated among ecologists [see Lomolino, 2001, for a review]. Depending on the study organism and the local climatic conditions, monotonic decline or unimodal patterns usually occur [Grytnes & McCain, 2013; see Table 1 for a literature review]. Regarding insect pollinators, their total α-diversity pattern is driven mainly by the altitudinal temperature decline and is in turn connected to the participation of pollinator guilds that are resilient to low temperatures. Indeed, on Mt. Olympus pollinators comprise mainly small bees (186 non-bumblebee species) which, contrary to bumblebees (18 species and one complex of three species found in this study) and hoverflies (53 species), show less tolerance to low temperatures (McCabe & Cobb, 2021; Peters et al., 2016), and thus driving the observed α-diversity of pollinators to linearly decline along the altitudinal gradient.

Altitudinal patterns of α-diversity of the different pollinator groups were dissimilar: bees, non-bumblebee bees, bee flies and butterflies followed a linear decline, while hoverflies and bumblebees showed a unimodal pattern. Findings among other studies considering α-diversity of all pollinators (Table 1, lines 1–7) or pollinator groups (Table 1, lines 8–19) along altitudinal gradients vary highly. Like in our study, in most cases, bees (Table 1, lines 8, 9, 19) and butterflies (Table 1, lines 15, 16 but see line 17) tended to decrease with altitude, whereas bumblebees and hoverflies always showed a unimodal pattern (Table 1, lines 10–14 and 18–19 respectively) reflecting their differences in temperature change compared to other pollinator groups.

At high altitudes, hoverflies replace small solitary bees due to their better adaptation to harsh alpine conditions (McCabe & Cobb, 2021; McCabe, Colella, et al., 2019; Sommaggio et al., 2022). A recent review, indicated temperature as the main driver of this bee-to-fly transition, showing that below 4.9°C, the pollinator communities were fly dominated, while above 5.7°C were bee dominated (McCabe & Cobb, 2021); yet, other factors like the tree
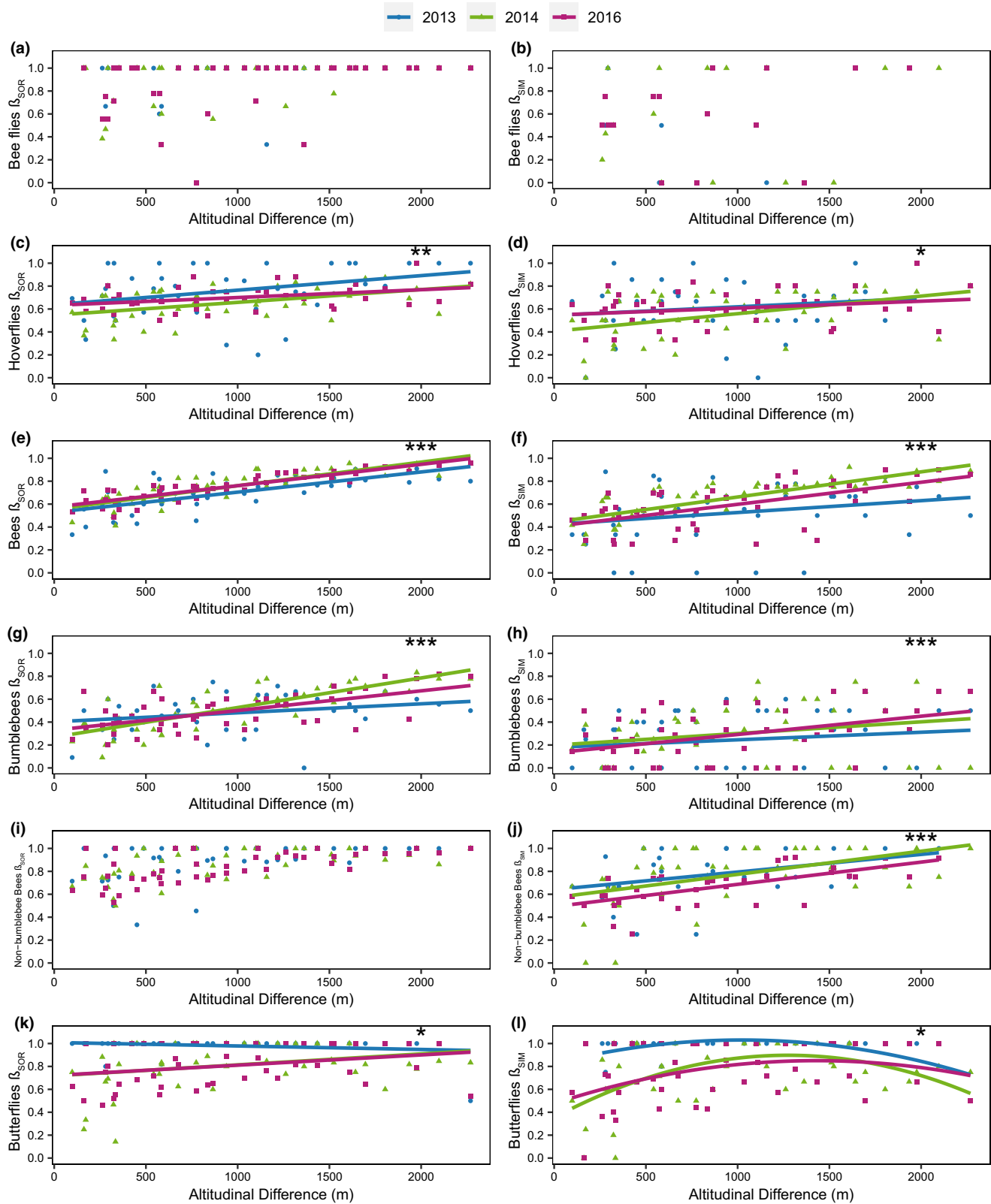
FIGURE 4 Pairwise altitudinal difference as predictor of β-diversity of pollinator groups on Mt. Olympus, described with pollinators β_{SOR} index and the component β_{SIM} for bee flies (a, b), hoverflies (c, d), bees (e, f), bumblebees (g, h), non-bumblebee bees (i, j) and butterflies (k, l). The colours correspond to different sampling years, representing random effect factors in the fitted models, while fitted lines are shown only for the statistically significant relationships (*$p \leq 0.05$; **$p \leq 0.010$; ***$p \leq 0.001$).

canopy cover or precipitation may also play a role (McCabe, Cobb, et al., 2019; McCabe, Colella, et al., 2019). In addition to hoverflies, the cold-adapted bumblebee species remain active at high altitudes (Bingham & Orthner, 1998; Heinrich, 1979). Indeed, contrary to small bees, bumblebees can regulate their internal temperature with hair insulation and metabolic heat production (endothermy), and so being able to cope with low temperatures (Heinrich, 1974, 1975; Hodkinson, 2005; Peters et al., 2016). We conclude that the unimodal α-diversity pattern of hoverflies and bumblebees alike is due to eco-physiological traits enabling them to thrive in harsh high-altitude environmental conditions.

4.2 | Impact of altitude on dissimilarity (β-diversity)

Beta diversity of both pollinators and plants (β_{SOR}) was high, mainly due to the turnover component (β_{SIM}). This implies that the high dissimilarity between the Mt. Olympus communities is attributed to the between-site replacement of species by new ones (Baselga, 2010; Legendre, 2014). As expected, the dissimilarity increased with pairwise altitudinal difference between sites, implying that the higher the altitudinal difference between two communities, the higher dissimilarity between these communities. The latter agrees with the diversity distance–decay similarity relationship (in vertical order in our study), that is, the longer the distance between two communities, the higher their dissimilarity and their β-diversity (Carstensen et al., 2014; Nekola & White, 1999). Interestingly, in a recent meta-analysis considering different organisms and ecosystems, although without including any pollination system, Soininen et al. (2018) found high turnover component in latitudes lower than 41°N, an area which includes the Eastern Mediterranean Basin; this breakpoint for turnover component was attributed to the glacial history of this area (see Section 4.3).

Studies on pollination systems along altitudinal gradients report increased species β-diversity (β_{SOR}) with altitudinal difference between sites, determined either as species turnover (β_{SIM}; i.e. replacement of species by new ones from site to site) or as nestedness (β_{SNE}; i.e. species in a site constituting a subset of the species occurring in another) (see Table 1, lines 2, 4, 6, 8 and 13). This clear positive correlation of pollinator species β-diversity with altitude may be attributed to environmental filtering and dispersion limitations between low and high altitudes (Perillo et al., 2017), and/or to high dissimilarity between communities due to unique community compositions along the altitude (Cuartas-Hernández & Gómez-Murillo, 2015). Increasing dissimilarity with altitudinal difference was found also when we considered specific pollinator groups alone, except for bee flies that showed no trend. The latter is probably owed to their very low number (only 20 species found in this study) and their known affiliation to low altitudes. Bee flies are generally associated with arid and warm Mediterranean environments (Ávalos-Hernández et al., 2016; Petanidou & Ellis, 1993; Robertson et al., 2020); no bee fly was observed on Mt. Olympus above 1500m.

In contrast to plant–pollinator interactions β-diversity (β_{WN}) and its turnover component (β_{ST}), the rewiring component (β_{OS}) exhibited low values, implying that pollination interactions on Mt. Olympus were not driven by rewiring between already existing species (Poisot et al., 2012). It should be highlighted that an increasing trend of the interaction dissimilarity with altitudinal difference was found only below 1000m (Figure 3g–i). A similar, although minimal dissimilarity in plant–pollinator interactions β-diversity along an altitudinal gradient (however, limited to only a 335-m altitudinal zone of the gradient 2975–3310m), was reported only once (Simanonok & Burkle, 2014). In contrast, a recent study on the German Alps (641–2032m) showed a sigmoidal pattern of interaction β-diversity considering though only bumblebees (Sponsler et al., 2022). Finally, there was one study that, even though with high turnover component, it reported no trend as to interaction dissimilarity with altitudinal difference (Encinas-Viso et al., 2022; study limited to only a 146-m altitudinal gradient: 1800–1946m). We believe that the lack of trend on Mt. Olympus is due to the consistently high β-diversity of plant–pollinator interactions (β_{WN}) across the entire altitudinal gradient, as a result of unique interactions enrolled within each one of the pollination networks. In support to this argument, uniqueness of interactions (LNU) was always high, and commonness (SIF) low; none of these metrics was related to altitude, implying that every site along the altitudinal gradient is characterized by relatively unique interactions between pollinators and host plants in comparison to the rest of the sites (Luna et al., 2020).

As indicated by all biodiversity metrics, our findings on plant–pollinator interactions highlight the hyperdiversity of Mt. Olympus, as it happens with its bumblebee diversity (Minachilis et al., 2020), vis-à-vis its high endemism (Strid, 1980). Mountain pollinator and flowering plant communities showed a high turnover of species along the altitudinal gradient. Additionally, plant–pollinator networks were characterized by high turnover of interactions, hence endowed with new links between new species and unique interactions among sites, resulting in a high interaction dissimilarity and diversity. These findings convey implications regarding conservation: given that pollinator fauna, flowering flora and plant–pollinator interactions are rare and unique elements of the study communities, for conservation measures to be efficient, these measures must encompass the entire altitudinal gradient (Cuartas-Hernández & Gómez-Murillo, 2015). Furthermore, our results stress the need of including interaction networks into protection measures of mountain ecosystems and particularly into their regular conservation monitoring schemes (Kaiser-Bunbury & Blüthgen, 2015; Tylianakis et al., 2010).

4.3 | The past of Mt. Olympus—Glacial history

As already mentioned, the turnover component (β_{SIM}) of pollinators and plants on Mt. Olympus was higher than the nestedness component (β_{SNE}). In southern-European (Mediterranean) regions, the high species turnover is usually attributed to high species diversity and endemism (Baselga, 2008, 2010), and the role these regions played during the glacial periods as refugia and speciation centres

(Médail & Diadema, 2009). Indeed, Mt. Olympus constituted a species refugium and speciation centre during the recent geological past (Kougioumoutzis et al., 2021; Médail & Diadema, 2009); it is thus highly plausible that the mountain's glacial history drove the observed high levels of diversity and endemism which in turn explain the high turnover of pollinators and plants among the communities (Soininen et al., 2018).

Interestingly, the nestedness component (β_{OS}) of pollinators and plants was higher than the turnover component (β_{SIM}) only among the alpine sites of Mt. Olympus (yet, only in 2014). As showed in earlier studies, the nestedness component prevails as a result of recolonization in areas covered by ice in the last glaciation period, as was the case in northern Europe and northern America (Baselga, 2008, 2010; Dobrovolski et al., 2012) and it is higher in the most recent deglaciations of a region in northern America (Dobrovolski et al., 2012). This could also be the case on Mt. Olympus, as the mountain retained a certain level of glaciation at high altitudes in the Pleistocene interglacial periods and even up to the Holocene (Smith et al., 1997; Styllas et al., 2018). Therefore, we suggest that the alpine sites may be relatively recently recolonized, resulting in the observed pronounced nestedness component in species β-diversity. To this effect, climate change may also add further.

4.4 | Climate change and the future of Mt. Olympus

The climate change of the Anthropocene has already started to affect vegetation on Mt. Olympus, as indicated by the tree line that has shifted ca. 400m upwards the last 60 years, and the mountain lost more than one quarter of its forest-bare area (Zindros et al., 2020). An often-overlooked effect of climate change on ecosystems is the homogenization of community assemblages resulting in β-diversity decrease and lower levels of resilience against future environmental stochasticity (Fourcade et al., 2021; Vasiliev & Greenwood, 2021). Homogenization is a consequence of the species extinction and/or range shift towards higher altitudes (Olden et al., 2004; Vasiliev & Greenwood, 2021). There are no historical data to compare our results with and provide solid evidence on homogenization. At present, we consider that the assemblages of pollinators and flowering plants, as well as their interaction networks, are highly dissimilar along the altitudinal gradient of Mt. Olympus; yet, as it has been documented elsewhere, based on present versus historical data (Fourcade et al., 2021; Ploquin et al., 2013) or versus predicted future data (Pradervand et al., 2014), it is highly probable that some level of homogenization of the biodiversity on Mt. Olympus is inevitable. Besides, a recent study of some of us, employing species distribution models, showed that there is a high probability that the pollinator assemblages will move uphill by the end of the 21st century, because of loss of suitable habitat (Minachilis et al., 2021), which may indeed lead towards more homogenized interacting communities. In this light, a regular and systematic monitoring of pollination networks will be of pivotal importance to alert for dramatic climate change impacts on the mountain.

5 | CONCLUSIONS

Here we unveiled the drivers of hyperdiversity along the altitudinal cline on Mt. Olympus, a Mediterranean mountain representing a biodiversity hotspot. We considered the α- and β-diversity of pollinators, flowering plants and plant–pollinator interaction networks along the entire altitudinal gradient. We found high biodiversity levels accompanied by high dissimilarity and uniqueness of pollination networks along the altitude, which is driven by species turnover and the formation of new interactions between new species enrolled into the networks.

Our approach and conclusions are extendable to other mountain ecosystems of the world, especially those constituting biodiversity hotspots. For example, high dissimilarity of pollinator and plant communities along an altitudinal gradient were also drawn for a tropical mountain forest in the Colombian Andes by Cuartas-Hernández and Gómez-Murillo (2015), who indicated the need for conservation and protection measures over wider altitudinal gradients. Based on our data from Mt. Olympus, we stress the need these measures do include the entire mountain area and should comprise pollinators. Moreover, given the pivotal importance of pollination for the sustainability of natural ecosystems, conservation must incorporate monitoring of flowering plants and pollinators alike, as well as the structure and dynamics of pollination networks, especially considering the α and β components of diversity.

AUTHOR CONTRIBUTIONS

Konstantinos Minachilis and Theodora Petanidou conceived the ideas and designed the methodology; Konstantinos Minachilis collected the data; Alain Pauly, Ante Vujic and Jelle Devalez identified the pollinator data; Aphrodite Kantsa and Konstantinos Minachilis analysed the data; Konstantinos Minachilis wrote the first draft of the manuscript; Aphrodite Kantsa, Konstantinos Minachilis and Theodora Petanidou led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data used for this publication are available on Dryad Digital Repository https://doi.org/10.5061/dryad.8pk0p2nq9 (Minachilis et al., 2023).

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SUPPORTING INFORMATION

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

Table S1: Pollinator taxa recorded on Mt. Olympus and used in pollination networks.

Table S2: Plant taxa recorded (plants in flower measured for flower cover and plants visited by pollinators) during the research on Mt. Olympus.

Table S3: Alpha diversity of pollinators, plants in flower and plant–pollinator interactions calculated for each study site and year.

Table S4: Beta diversity of pollinators, plants in flower and plant–pollinator interactions calculated for each study site and year.

Table S5: Uniqueness (LNU) and commonness (SIF) of the pollination network interactions along the altitudinal gradient of Mt. Olympus for each study site and year.

Table S6: Relation of α-diversity to altitude, as defined by the best model characteristics. The significant values ($p < 0.05$) appear in bold.

Table S7: Relation of β-diversity to pairwise altitudinal difference, as defined by the best model characteristics. The significant values ($p < 0.05$) appear in bold.