



Beta diversity and specialization in plant–pollinator networks along an elevational gradient

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Abstract

Aim: To assess whether the reduced nutritional resources available for pollinators due to plant community simplification along an elevational plant-diversity gradient changes pollinator niche breadth and richness. Additionally, we evaluated how body size and proboscis length of pollinators shifted along the gradient, and whether these changes were related to pollinator niche breadth.

Location: An elevational gradient (2,350–3,520 m a.s.l.) on the oceanic high-mountain strato-volcano of El Teide (Tenerife, Canary Islands).

Taxon: Flowering plant and pollinator species.

Methods: We compared quantitative plant–pollinator networks along the plant-diversity gradient. We calculated a set of niche-based topological metrics that capture the degree of specialization, niche breadth and niche overlap. Furthermore, we obtained β -diversity measures and the proportion of replacement and richness components.

Results: There was an overall decline in species richness of pollinators with increasing elevation. This decline was mainly driven by the loss of species along the elevational gradient, which conformed a nested subset pattern. The whole network showed less specialization, greater connectance and lower modularity towards the summit. At high elevations, pollinators were more generalized and less selective in their flower choice, showing a greater trophic niche breadth compared to pollinators at lower elevations. Mean body size of pollinators increased with elevation, and species body size and proboscis length were positively associated with the number of plant species visited.

Main conclusions: Overall, results indicated that the elevational gradient filters pollinator species, probably according to their thermal tolerance and ability to exploit a wide range of trophic resources. The finding that pollinators become more generalized and opportunistic at higher elevations is a novel result, which may have implications for new research into how ecological networks vary over environmental gradients. From an applied perspective, our results highlight the importance of considering the spatial variation of species assemblages when aiming to construct functionally reliable interaction networks along environmental gradients.

KEYWORDS

Canary Islands, climate change, functional diversity, niche breadth, pollination networks, specialization



1 | INTRODUCTION

Recently, conservation management has shifted its focus from strictly preserving species diversity to also embracing the maintenance of community structure, function or ecological processes like pollination (Lois & Cowley, 2017; Tylianakis, Laliberté, Nielsen, & Bascompte, 2010). Plants and pollinating animals form complex interaction networks. For that reason, network analysis tools have become important for pollination studies, because they provide information on community structure and function and can help predict community dynamics in response to ecosystem perturbation (Fontaine, Dajoz, Meriguet, & Loreau, 2006; Kaiser-Bunbury & Blüthgen, 2015). Recently, there has been an upsurge in interest regarding how ecological networks vary through space and along environmental gradients (Pellissier et al., 2018; Poisot, Stouffer, & Gravel, 2015; Tylianakis & Morris, 2017), motivated by the need to understand how communities respond to the environment. However, we still have few insights into how plant–pollinator interaction networks vary along elevational gradients. Such gradients are associated with profound changes in abiotic conditions. Consequently, to examine the distribution of mutualistic species, and how they interact following natural gradients on mountains, is a key step towards understanding spatial variation of ecological networks (Pellissier et al., 2018; Tylianakis & Morris, 2017).

Increasing elevation is commonly related to a decline in both the species richness of plants and their pollinators, governed by the interplay between factors such as temperature, precipitation or topography, which impose significant resource limitation at higher elevations (Guo et al., 2013; Rahbek, 2005). Owing to such harsh conditions, abundance and richness of consumers are expected to decrease, leading to reduced competition (Ebeling, Klein, & Tschartke, 2011; Fründ, Linsenmair, & Blüthgen, 2010; MacArthur & Pianka, 1966). This may result in a wider pollinator diet (Hoiss, Krauss, Potts, Roberts, & Steffan-Dewenter, 2012; Miller-Struttman & Galen, 2014) and thus less structured and specialized networks with increasing elevation. Previous research has shown that specialization of pollinators can vary along productivity gradients (Fontaine, Collin, & Dajoz, 2008; Fründ et al., 2010; Lara-Romero, García, Morente-López, & Iriondo, 2016; Miller-Struttman & Galen, 2014); despite this, the variation in diet breadth along elevational gradients and its effects on a community scale remain largely unexplored (Benadi, Hovestadt, Poethke, & Blüthgen, 2014).

Beyond diet specialization, elevational gradients can also entail complex changes in community structure (i.e. elevational β -diversity), which can be partitioned into two process-related components: replacement (species turnover between elevations) and richness (species gain or loss between elevations) (Ensing & Pither, 2015). Only a few available studies assess the variation in these two components of diversity along elevational gradients. They indicate that changes in species composition are primarily caused by the replacement component, because many pollinator insects tend to appear at particular elevations rather than persisting across the entire gradient (Bishop, Robertson, Rensburg, & Parr, 2015; da Silva, Lobo, Hensen,

Vaz-de-Mello, & Hernández, 2018; González-Reyes, Corronca, & Rodríguez-Artigas, 2017; Nunes, Braga, Figueira, Siqueira Neves, & Fernandes, 2016; Perillo, Siqueira Neves, Antonini, & Martins, 2017). However, the generality of this pattern is sometimes challenged by strong context-dependency (da Silva et al., 2018; González-Reyes et al., 2017).

Variation in community structure along the elevational gradient may be associated with changes in functional diversity (Classen, Steffan-Dewenter, Kindeketa, & Peters, 2017; Hodkinson, 2005). These shifts can be characterized according to functional traits, which are measurable anatomical and morphological features of insects that reflect variation in ecological strategies (Hodkinson, 2005; Hoiss et al., 2012; Peters, Peisker, Steffan-Dewenter, & Hoiss, 2016). In the context of plant–pollinator community assembly, body size is a key trait because it is central to many life history traits and behaviours of pollinators and is sensitive to both abiotic (temperature, moisture or wind) and biotic changes (abundance, density, plant traits) (Chown & Gaston, 2010; Hodkinson, 2005). Previous research has reported less variable body-sizes at higher elevations for many pollinator species (Classen et al., 2017; Maglianesi, Blüthgen, Böhning-Gaese, & Schleuning, 2015), pointing to an environmental filtering mechanism that shapes the environmental adaptation of species with similar traits (Cornwell, Schilke, & Ackerly, 2006). Indeed, mean body size of insect species often decrease along elevational gradients (Dillon, Frazier, & Dudley, 2006; Hodkinson, 2005; Woodward et al., 2005). This trend is thought to result from the lower growth, fecundity and survival rates of large compared to small organisms in energy-limited habitats (Dillon et al., 2006; Hodkinson, 2005). Yet, some studies have reported body-size increases with elevation, which are generally explained by more efficient energy use by larger insects in cold environments (Hodkinson, 2005; Hoiss et al., 2012; Peters et al., 2016). This is actually consistent with physiology-based theories, such as those proposed to explain Bergmann's rule (Classen et al., 2017). Still, the association between body size and resource use, dispersal capacity and pollination efficiency (Chown & Gaston, 2010) might also explain the positive relationship between elevation and insect body size at the community scale, especially when trophic resources decrease with elevation (Miller-Struttman & Galen, 2014; Ramos-Jiliberto et al., 2010). Pollinator body-size is highly positively correlated with foraging distance and proboscis length in many taxa (Agosta & Janzen, 2005; Byrne, Buchmann, & Spangler, 1988; Casey, May, & Morgan, 1985; Greenleaf, Williams, Winfree, & Kremen, 2007; Levy & Nufio, 2015). Therefore, large insects are usually associated with greater floral diet spectrum, because they have more opportunities to search for and exploit potential hosts, which probably imply a functional advantage in resource-limited habitats.

In this study, we compare quantitative plant–pollinator interaction networks along an elevational gradient in the oceanic high-mountain ecosystem of El Teide strato-volcano (Tenerife, Canary Islands). This ecosystem has relatively low species richness and is characterized by a very marked elevational gradient, in which both temperature and plant richness decrease with elevation (Fernández-Palacios, 1992). We assessed whether pollinator niche

breadth and species richness change along an elevational gradient (2,350 to 3,520 m a.s.l.), how pollinator body size and proboscis length shifted along the elevational gradient, and whether this change is related to pollinator niche breadth. Pollinator richness was expected to decline with elevation, according to previous research (Guo et al., 2013; Rahbek, 2005). The rationale for this is that environmental filtering would act to limit community members to those adapted to the harsh conditions prevailing at the highest sites. These changes in species composition might be primarily driven by species replacement along the elevational gradient, because many pollinators appear at a particular elevation rather than persisting across the entire gradient. We further predicted that reduced partner availability along the gradient increases the niche breadth of pollinator species. Thus, networks at high elevations should be less specialized compared to those at low elevations. Finally, we hypothesized a general decline in the mean size of insect species with increasing elevation.

2 | MATERIALS AND METHODS

2.1 | Study site

The study was carried out along an elevational gradient on El Teide strato-volcano (3,718 m), within El Teide National Park (Canary Islands; 28°16'15"N 16°38'21"O). The area is influenced by a typical high-mountain climate with great thermal oscillations throughout the year (differences of c. 10°C between maximum and minimum monthly average temperatures). The sites receive an annual precipitation of c. 370 mm, most of which falls during winter. Four sites at different elevations were selected on the South-East faces of the strato-volcano (Table 1, Figure 1): Montaña Rajada (2,350 m), Montaña Blanca (2,730 m), Refugio de Altavista (3,300 m) and La Rambleta (3,520 m). Dry open sclerophyllous scrubland occurs above the tree line (c. 2,000 m), with vegetation cover decreasing with elevation. Eleven entomophilous plant species were found along the gradient, all of them endemic to the Canary Islands (Table S1 in Appendix S2), and some of them exclusive to the strato-volcano itself (e.g. *Viola cheiranthifolia*, *Silene nocteolens*). The number of plant species tended to decrease towards the mountain top (c. 3,520 m), where *V. cheiranthifolia* became the only entomophilous plant in the community (Table S1 in Appendix S2).

2.2 | Monitoring of plant–pollinator interactions

We established four plots of c. 1 ha distributed along an elevational gradient at the study site. Flower-visiting animals were observed on the plant species from 15 May to 15 August, for two consecutive years (2014 and 2015), coinciding with the flowering of all plant species in the different elevational communities. The censuses were carried out between 09:00 and 19:00 hr, avoiding the beginning and the end of the day, when there were usually low temperatures and little insect activity in this high mountain environment, and also avoiding windy days. All plant species were censused 7–8 hr

per locality and year, throughout the flowering phenology of each plant species, to maximize the possibility of detecting different floral visitors. Each census lasted 15 min, during which the observer remained facing the plant, recording all insects contacting the flowers as well as, whenever possible, the number of flowers contacted per individual. The individual plants to be censused of each species were arbitrarily chosen at each elevation. We recorded a plant–pollinator interaction when an insect maintained contact with the reproductive organs of a flower for more than 1 s. Thus, all flower-visiting insects (hereafter, named pollinators) that feed on flowers were recorded, regardless of the efficacy of their visit. Insects were either identified in the field or collected for later identification in the laboratory. Insect collection was not performed simultaneously with sampling of plant–pollinator interactions, to avoid affecting the data on interaction frequency. During the entire study period, a total of 868 observation hours were spent during 57 observation days. All entomophilous plant species present in the study area were sampled. Temperature was measured with a temperature data logger at 1 m height above ground at each site, during an entire year (2014–2015; Table 1).

2.3 | Measurement of morphological traits

For the main pollinators (dipterans and hymenopterans, see results), we measured both maximum body width—as a metric of body size—and proboscis length, using a binocular scope with a calibrated ocular micrometer. Body size was measured as the intertegular distance, which is the distance between the two insertion points of the wings. Proboscis length was measured as the length of the glossa in hymenopterans and the length of the labium from the base of the prementum in dipterans. Measurements were obtained for 41 and 37 species of dipterans and hymenopterans, respectively. When there were several individuals per species, we estimated the mean value for each species and elevation. Body size and proboscis length were weighted according to species abundance at each elevation, yielding a community-weighted mean value (CWM) for each pollinator species. These weighted measures were used in subsequent analysis to avoid giving rare species the same weight as abundant ones. For each elevation, pollinator abundance was estimated as the total number of visits to flowering plants by each pollinator species. Body size and proboscis length were positively correlated (linear model: intercept = -0.85 , $\beta = 0.88$; $F_{1,69} = 80.75$, $p < 0.0001$; $R^2 = 0.54$). To avoid collinearity between these variables in linear mixed models (LMM; see below), proboscis length was regressed against body size, replacing the former with the residuals from the regression in subsequent analyses (Graham, 2003).

We additionally calculated the functional dispersion of both body size and proboscis length (FDIs), using the function *fdisp* implemented in the R package “FD” (Laliberté & Legendre, 2010). This measure incorporates both functional richness and divergence within a species assemblage and can therefore be used as a multidimensional functional diversity index that can be weighted according to species



TABLE 1 Geographic and climatic characteristics, and topological network metrics at each study site on El Teide strato-volcano. Topological network metrics are displayed for each full-season and for two-season data at each elevation

	Montaña Rajada		Montaña Blanca		Refugio Altavista		La Rambleta		
Elevation (m a.s.l.)	2,350		2,730		3,300		3,520		
Coordinates	28 15.71 N/16 36.16 W		28 16.2 N/16 36.94 W		28 16.47 N/6 37.79 W		28 16.49 N/16 38.77 W		
Mean annual temperature (°C)	11.69 ^a		10.85		8.34		5.02		
Plant density (individuals per m ²)	0.017		0.021		0.007		0.005		
Network metrics	2014	2015	2014–2015	2014	2015	2014–2015	2014	2015	2014–2015
Number of plants (P)	10	10	10	9	9	4	4	4	1
Number of animals (A)	58	39	66	78	64	96	46	23	50
Number of visits (V)	633	378	1,011	781	869	1,650	332	90	422
Number of interactions (I)	125	90	163	172	142	236	75	28	82
Connectance (C)	0.22	0.23	0.25	0.28	0.25	0.27	0.40	0.41	0.41
Weighted animal linkage (wL _a)	2.98	2.51	2.95	2.3	2.27	2.64	2.06	1.22	2.05
Weighted plant linkage (wL _p)	7.03	5.55	8.07	8.37	5	8.45	9.73	12.30	11.76
Network specialization (H' ²)	0.53 ^b	0.48 ^b	0.46 ^b	0.58 ^b	0.60 ^b	0.52 ^b	0.52 ^b	0.79 ^b	0.53 ^b
H' ² Z-score	6.18	7.27	10.32	7.26	6.36	14.96	4.05	3.77	3.6
Modularity (Q)	0.51 ^b	0.42 ^b	0.46 ^b	0.49 ^b	0.36 ^b	0.39 ^b	0.45 ^b	0.36 ^b	0.45 ^b
Q Z-score	5.19	6.03	11.76	7.51	9.35	11.41	3.14	2.64	4.03

Note: Metrics were not available for the site at 3,520 m because the binary matrix only included one plant species.

^aClimatic data from the lowest site (2,350 m) are not available. Instead, we present data from a data logger placed at 2,153 m.

^bValue departs from null expectations (Z greater than 1.96 or less than -1.96, $\alpha = 0.05$).

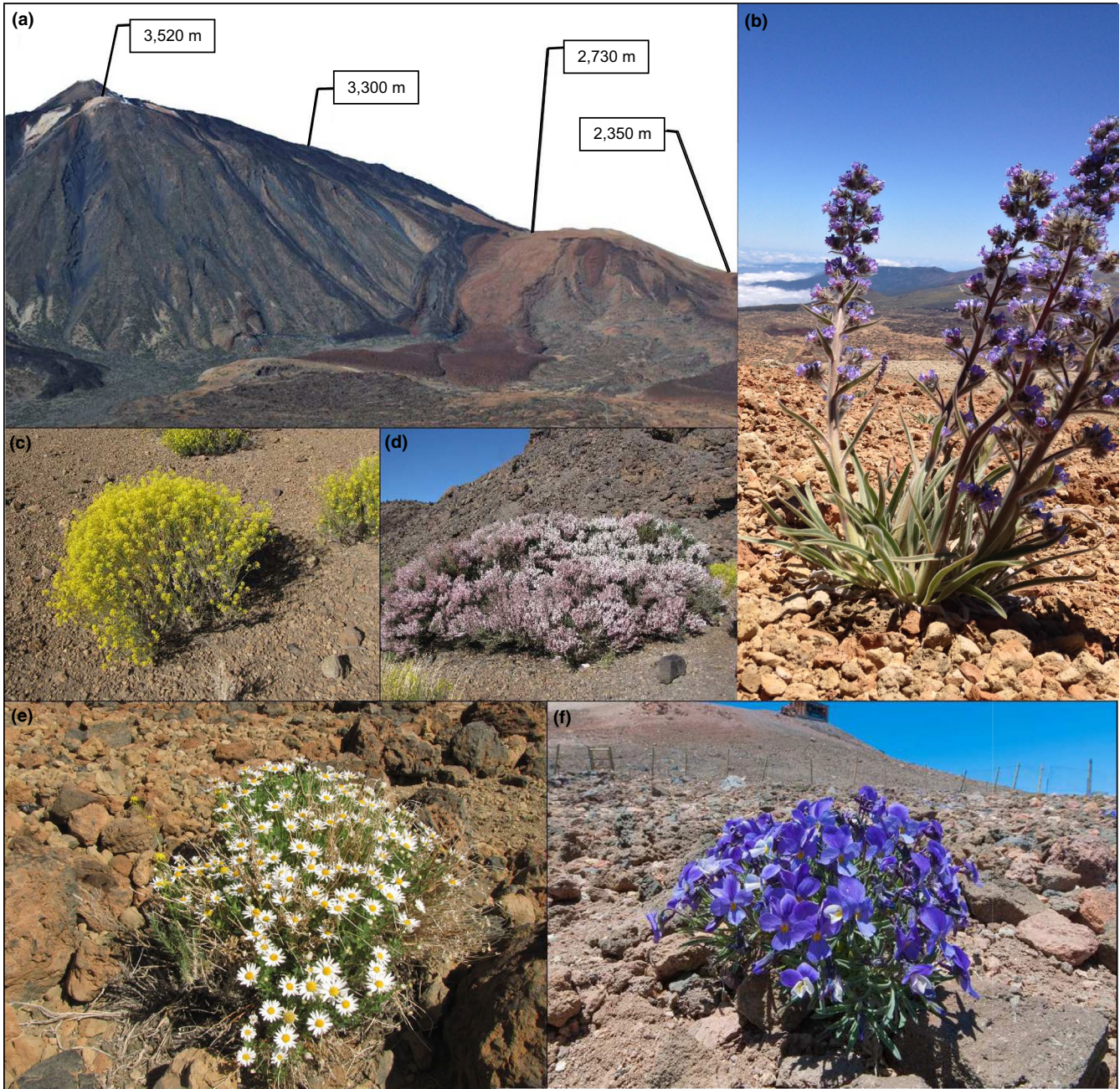


FIGURE 1 (a) Location of the study sites selected on the SE slope of El Teide stratovolcano. Common plants visited by insects: (b) *Echium auberianum*, (c) *Descurainia bourgeauana*, (d) *Spartocytisus supranubius*, (e) *Argyranthemum teneriffae*, (f) *Viola cheiranthifolia* [Colour figure can be viewed at wileyonlinelibrary.com]

abundance. The two traits were combined to obtain the multivariate index, by shifting the position of the centroid in the functional space towards the most abundant species, and then computing a weighted average distance from this new centroid, again using the relative abundances as weights (Laliberté & Legendre, 2010). The CWM trait value is a measure of the dominant trait value within a species assemblage, while FDis is a measure of the variation in trait values within a species assemblage (Laliberté & Legendre, 2010). We calculated FDis for the entire community at each elevation but could not estimate it at species level, due to lack of replication for some species.

2.4 | Data analysis

2.4.1 | Variation in the composition of species assemblages along the elevational gradient

We tested whether the total number of pollinator species decreased along the elevational gradient by using rarefaction curves. Rarefaction methods allow species richness comparison by standardizing variables by sampling effort. We used the R package “fossil” (Vavrek, 2011) to compute sample-based rarefaction curves for



each elevation, pooling data from all censuses performed in 2014 and 2015. The expected asymptotic richness of species and their 95% confidence intervals were estimated using the nonparametric Chao 2 estimator, S_{Chao2} .

Multiple-site β -diversity measures (variation of the species composition of assemblages) were applied, as proposed by Ensing and Pither (2015) (see Table 2 therein for equations), to calculate the overall β -diversity of plant and pollinator species using Jaccard dissimilarity (β_{CC}) and the proportion of replacement ($\beta_{3\text{M}}$) and richness (β_{RICH}) components. We preferred this measure over others because of its transposition into a multisite approach allows for an integrated perspective of changes in species assemblages across study sites (Ensing & Pither, 2015). The replacement component of β -diversity is determined by the substitution of species in one locality by different species in the other locality (e.g. between elevations in our study). On the other hand, the richness component of β -diversity is related to non-random species loss at a certain site, resulting in less rich biotas that are subsets of (i.e. nested in) the biotas at the species-richest site. Higher diversity of animals at the lowest elevations (the richest plant communities) was expected and therefore a higher proportion of β_{RICH} at the expense of $\beta_{3\text{M}}$. We used the R code provided by Ensing and Pither (2015) as Supporting information for calculating these measures, which is also available at GitHub (<https://github.com/CarlosLaraR/R-ecology>).

The nestedness metric based on overlap and decreasing fill (NODF) was used to further quantify the extent to which differences in species composition was due to nestedness (Almeida-Neto, Guimaraes, Guimaraes, Loyola, & Ulrich, 2008). Higher values of NODF imply more nested assemblages. NODF values were estimated with the *oecosium* function in the R package “vegan” (Oksanen et al., 2013). The function “visweb” implemented in the R package “bipartite” (Dormann & Freund, 2008) was used to obtain a nested representation of differences in species composition across study sites. A null modelling approach was used to test whether observed β -diversity values were larger or smaller than expected under a stochastic model of community assembly. This was carried out by generating 1,000 random assemblage networks and recalculating β -diversity metrics. Random assemblages were generated, preserving species richness at each site and sampling species occurrence according to their marginal probabilities (Gotelli, 2000). Observed β -diversity values were standardized to Z-scores.

$$Z_{\beta} = \frac{\beta_{\text{observed}} - \overline{\beta_{\text{expected}}}}{SD(\beta_{\text{expected}})}$$

Z-scores were then used as a measure of departure from null expectations. Values greater than 1.96 or less than -1.96 are significantly greater or less than expected, at $\alpha = 0.05$.

2.4.2 | Topological network metrics

We built quantitative bipartite networks from two-season data for each elevation and independently for each full-season dataset (i.e. 2014 and 2015), using visitation frequencies as a surrogate

of interaction strength. Visitation frequency between pollinator i and plant species j was defined as the total number of visits to j by i . Additionally, all plant individuals in each study plot were counted to estimate plant density (individuals per m^2 ; Table 1). We calculated nine niche-based topological metrics that capture the degree of specialization, niche breadth and niche overlap: (a) Number of plant species (P); (b) Number of pollinator species (A); (c) Total number of interactions, i.e. the number of pairwise interactions between a particular plant species and a particular pollinator species (I); (d) Total number of visits that each pollinator species made to each plant species (V); (e) Connectance ($C = I/AP$), i.e. the fraction of interactions occurring in the network, which increases with network generalization; (f, g) Weighted linkage for plants (lw_p) and pollinators (lw_a) as the effective mean number of partners per plant and per pollinator, respectively (Dormann et al., 2008), both indices therefore being a measure of niche breadth; (h) Index of network specialization (H'_2), which quantifies the degree of niche divergence among elements within an entire bipartite network (Blüthgen, Menzel, & Blüthgen, 2006), ranging from 0 (low specialization, high niche overlap) to 1 (high specialization, low niche overlap); and (i) Network modularity (Q), which measures the extent to which species interactions are organized into modules (subsets of species that are more linked to each other than to species in other modules). Hence, modularity increases with increasing link specificity, i.e. with higher specialization in interactions (Olesen, Bascompte, Dupont, & Jordano, 2007). Thus, a considerable decrease in Q values was expected at high elevations compared to low elevations, due to decreased specialization. Q was estimated using the *QuaBiMo* algorithm, based on a hierarchical random graph approach adapted for quantitative bipartite networks (Dormann & Strauss, 2014). As the algorithm is a stochastic process, results may vary among computations. For each network, we therefore ran the *QuaBiMo* algorithm 100 times and retained the optimal modular configuration, i.e. the iteration with highest Q value. We also estimated two species-level metrics for each plant (p) and pollinator (a) species: (a) Normalized degree (ND), i.e. the proportion of links or partners that each species had in the network; and (b) Index of species specialization (d'), which expresses the level of specialization of each species based on its discrimination from random selection of partners (Blüthgen et al., 2006) and ranges from 0 (no specialization, species that interact with their partners proportionally to their availability) to 1 (perfect specialists, species that disproportionately interact with rare partners). All network metrics were calculated using the R package “bipartite” (Dormann et al., 2008). Some network metrics were not defined for 3,520 m, since this network had only one plant. Significance levels of H'_2 and Q were assessed against a reference distribution derived from 100 random networks with the same species degree distribution as the empirical network. The values of all metrics in the randomizations were used to determine the Z-score. Networks with Z-scores equal or greater than 1.96 were considered significantly modular or specialized (Dormann & Strauss, 2014). This standardization also allowed us to compare elevations, because

H'_2 and Q can be affected by network size or sampling intensity, and to assess whether the observed trends were different from what could be expected due to chance (Blüthgen, Fründ, Vázquez, & Menzel, 2008; Dormann & Strauss, 2014). For this, we estimated pairwise differences in standardized network metrics (Z-scores) between sites and compared them to random expectations based on null model predictions. Observed differences in network metrics were standardized to Z-scores.

$$Z_{ij} = \frac{(Z_{i\text{observed}} - Z_{j\text{observed}}) - (Z_{i\text{expected}} - Z_{j\text{expected}})}{SD(Z_{i\text{expected}} - Z_{j\text{expected}})}$$

where Z_{ij} is the pairwise difference in standardized network metrics between elevation i and j , and Z_i and Z_j the standardized Z-scores of the elevation i and j , respectively. Z_{ij} was then used as a measure of departure from null expectations. Values greater than 1.96 or lower than -1.96 imply that differences are significantly greater or lower than expected at random, at $\alpha = 0.05$.

2.4.3 | Effect of elevation on network specialization, species niche breadth and morphological traits

A generalized linear mixed model was used to assess the effect of elevation on the total number of visits per insect order. This is tested for differences between insect orders in their visiting activity, and if this pattern changed across elevations. The model included elevation, insect order (Coleoptera, Diptera, Hymenoptera and Lepidoptera) and their interaction as fixed factors, and census day as a random factor to control for potential temporal non-independence (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). We assumed a negative binomial error distribution to account for overdispersion in the data. Total number of visits was ln-transformed to reach normality and homoscedasticity. Linear mixed models were used to check for differences in species-level metrics between elevations and trophic levels (i.e. plant and pollinators). Year of sampling was included as a predictor variable in models, as network metrics can vary across years and seasons (Morente-López, Lara-Romero, Ornos, & Iriando, 2018; Olesen, Stefanescu, & Traveset, 2011). We repeated these LMMs including only pollinator species common to all elevations. The models included species-level metrics as dependent variables and elevation and year of sampling as fixed factors. This approach allowed us to examine whether niche expansion of pollinator species across elevations lead to pollinator generalization. All LMMs included species as random factor to account for any effects of pseudo-replication of species across studies, such as the non-independence of multiple observations of different species (Zuur et al., 2009).

A final set of LMMs was also used to evaluate the effect of elevation, insect order (dipterans and hymenopterans), and their interaction with CWM body size and residual CWM proboscis length. Possible linear relationships between species body size, proboscis length and species niche breadth were also tested. For that, we fitted another LMM with CWM body size, residual CWM proboscis length, insect order and the interaction between CWM body size and insect order as predictor variables, and species normalized

degree as dependent variable. All models included species as random factor to control for potential non-independence (Zuur et al., 2009). We assumed Gaussian error for all LMMs, and CWM body size and normalized degree were ln-transformed to reach normality and homoscedasticity. Model residuals were checked graphically for normality and homogeneity of variances using diagnostic plots (Zuur et al., 2009). Using the ANOVA function in the R package “car”, we tested the null hypothesis that the response means are identical across elevations and trophic levels. If the overall analyses of variance indicated a significant difference ($p < 0.05$), the R package “lsmeans” (Lenth, 2016) was employed to perform a post-hoc comparison of least-square means, with a Tukey correction to further investigate differences between the elevations. Models were assessed for goodness of-fit to the data, using the marginal and conditional R^2 described by Nakagawa and Schielzeth (2013).

3 | RESULTS

3.1 | Effect of elevation on species assemblages and visitation patterns

Species richness of pollinator species were lowest at the two highest elevations (S_{Chao2} : 3,520 m = 30.50 species, 95% CI: 36.38–24.62; 3,330 m = 64.22 species, 95% CI: 68.97–59.47). Nevertheless, the highest pollinator richness was not found at the lowest elevation (S_{Chao2} : 84.05 species, 95% CI: 89.55–78.55), but at 2,730 m (S_{Chao2} : 115.2 species, 95% CI: 120.49–109.91), which harboured the most abundant plant community (Table 1). The insect pollinators belonged to six different orders: Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera and Orthoptera, with hymenopterans and dipterans representing more than 80% of total richness in all networks (Figure 2, Table S2 in Appendix S2). Insect order had a significant effect on visitation patterns (Figure 3, Table S3 in Appendix S3). This effect was mainly due to the higher number of visits by hymenopterans and dipterans, compared to the rest of the community (Figure 3, Table S3). Furthermore, the interaction elevation \times insect order was significant (Figure 3, Table S3), mainly due to the increased importance of coleopterans and lepidopterans at 3,520 m, to the detriment of dipterans (Figure 3). Most plants interacted with at least 10 insect species at all elevations, (Fig. S1 in Appendix S1, Table S1 in Appendix S2). The exceptions were *Adenocarpus viscosus* at 2,750 m, and *V. cheiranthifolia* and *Nepeta teydea* at 2,350 m. Two of the most consistently visited at all elevations were *Argyranthemum teneriffae* and *Descurainia bourgeauana*, followed by *Spartocytisus supranubius* and *Echium auberianum* (Table S1 in Appendix S2).

Regarding β -diversity, there was a wide variation in the composition of pollinator assemblages along the elevational gradient (Multi-site comparison: $\beta_{\text{CC}} = 0.76$), which was greater than expected under a random model of community assembly ($Z-\beta_{\text{CC}} = 4.62$, $p < 0.05$). Dissimilarity of pollinator assemblages was mainly driven by the loss of species along the gradient (β_{RICH}) rather than by the spatial replacement of species (β_{3M}), as shown by the multiple-site β -diversity comparison ($\beta_{\text{RICH}}/\beta_{\text{CC}} = 0.71$). However, standardized values of



β -diversity showed that β_{3M} was significantly larger ($Z-\beta_{3M} = 3.84$, $p < 0.05$), whereas β_{RICH} was significantly lower ($Z-\beta_{RICH} = -3.08$, $p < 0.05$) than expected under null expectations. NODF was significantly higher than that predicted by a random distribution model (NODF = 60.94, $p < 0.01$), indicating that pollinator assemblages in species-poor sites were a subset of the assemblages at the species-richest ones (Figure S2 in Appendix S1).

3.2 | Effect of elevation on network specialization and species niche breadth

The total number of interactions and visits were lower at the two highest elevations (3,300 and 3,520 m) than at the two lowest (2,350 and 2,730 m) (Table 1). Connectance (C) and wL_p were higher, whereas $Z-H'_2$ and $Z-Q$ were lower, at 3,300 m than at the two lowest elevations, which did not differ in any of these metrics (Table 1). All differences between elevation pairs in wL , H'_2 and Q were higher than

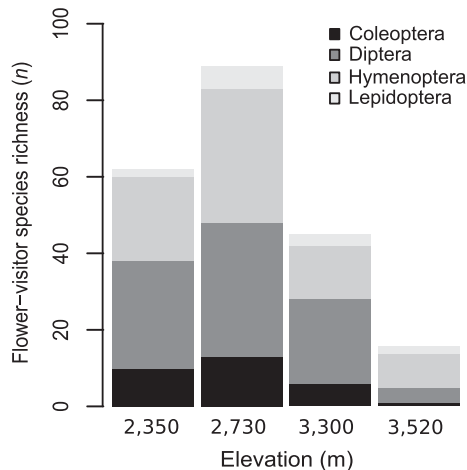
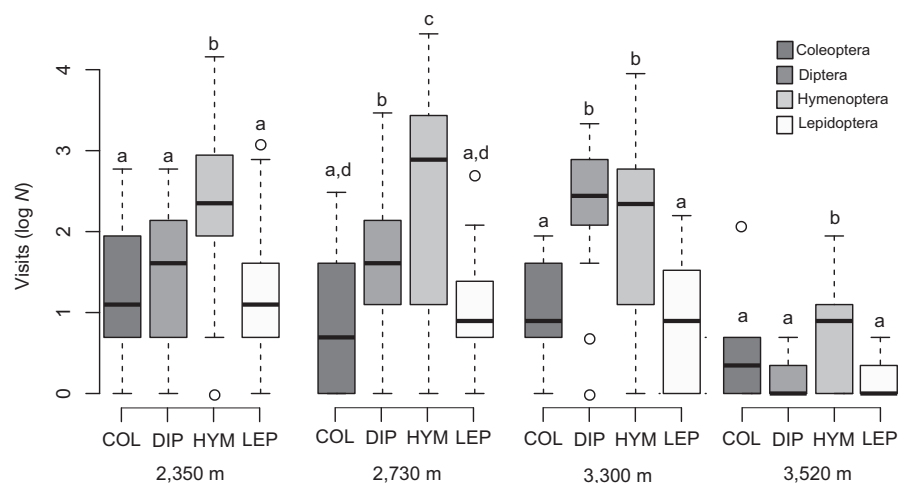


FIGURE 2 Species richness recorded on El Teide stratovolcano for the main orders of pollinators. Hemiptera and Orthoptera are not included in the figure, for clarity. See Table S2 for detailed information on each species. Each bar is divided into the four groups of insect species, and each of the four bars represents the number of pollinator species recorded

FIGURE 3 Total number of visits and interactions recorded on El Teide stratovolcano for the main orders of pollinators (COL: Coleoptera, DIP: Diptera, HYM: Hymenoptera, LEP: Lepidoptera). Each box in each graph represents the interquartile range (25%–75%) and the band inside the median. Whiskers represent the 1.5 of the lower or upper interquartile range and outliers are indicated as points. Different letters denote significant differences between elevations ($p < 0.05$) after Tukey's correction for multiple comparisons



expected at random (Z -test to test differences between elevation pairs: all $p < 0.01$), except for Q between 2,350 and 2,730 m (Z -test: $p > 0.05$) and in wL_a between 2,350 and 2,730 m (Z -test: $p > 0.05$). All networks analysed displayed a significant modular structure (Table 1, Z -test: all $p < 0.001$). Four modules were identified at 2,350 and 3,300 m and three more at 2,750 m. The number of species of each insect order was homogeneously distributed over modules at each elevation (χ^2 -tests: all $p > 0.05$), indicating that pollinators were not segregated according to taxonomic rank. The observed trends in network metrics were similar when years were considered separately (Table 1), indicating temporal consistency in the network metrics.

Plants and pollinators at 3,300 m showed significantly higher normalized degree (ND) but lower d' than at 2,350 and 2,730 m (post-hoc tests: all $p < 0.05$, Figure 4 and Table S4 in Appendix S3). This indicated higher generalization (= higher niche overlap) at 3,300 m compared to lower elevations. Moreover, plants showed higher d' values than animals, i.e. they were less selective—or more opportunistic—than them (Figure 4 and Table S4 in Appendix S3). Differences across elevations were similar in the two study years, as indicated by the lack of interaction between elevation and year. Models fitted for pollinator species occurring in all elevations also indicated higher generalization at 3,300 m, compared to lower elevations (Figure S2 in Appendix S1, Table S5 in Appendix S3).

3.3 | Effect of elevation on morphological traits

The CWM body-size of dipterans and hymenopterans varied significantly along the gradient (Figure 5a, Table S6 in Appendix S3). Overall, pollinators at the highest elevation (3,520 m) had larger body sizes than at 2,350, 2,730 and 3,300 m, and there were also significant differences in size between the 3,300 and 2,730 m elevations (Figure 5a). Neither dipterans nor hymenopterans differed in CWM body size (Table S6 in Appendix S3). Body size was also positively related to ND (Figure 5b, Table S7: $\beta = 2.27 \pm 0.41$, $p < 0.001$), meaning that larger insects had a greater niche breadth. When considering the residual CWM proboscis length, in contrast, no significant differences were found among insect orders between elevations (Table S6 in Appendix

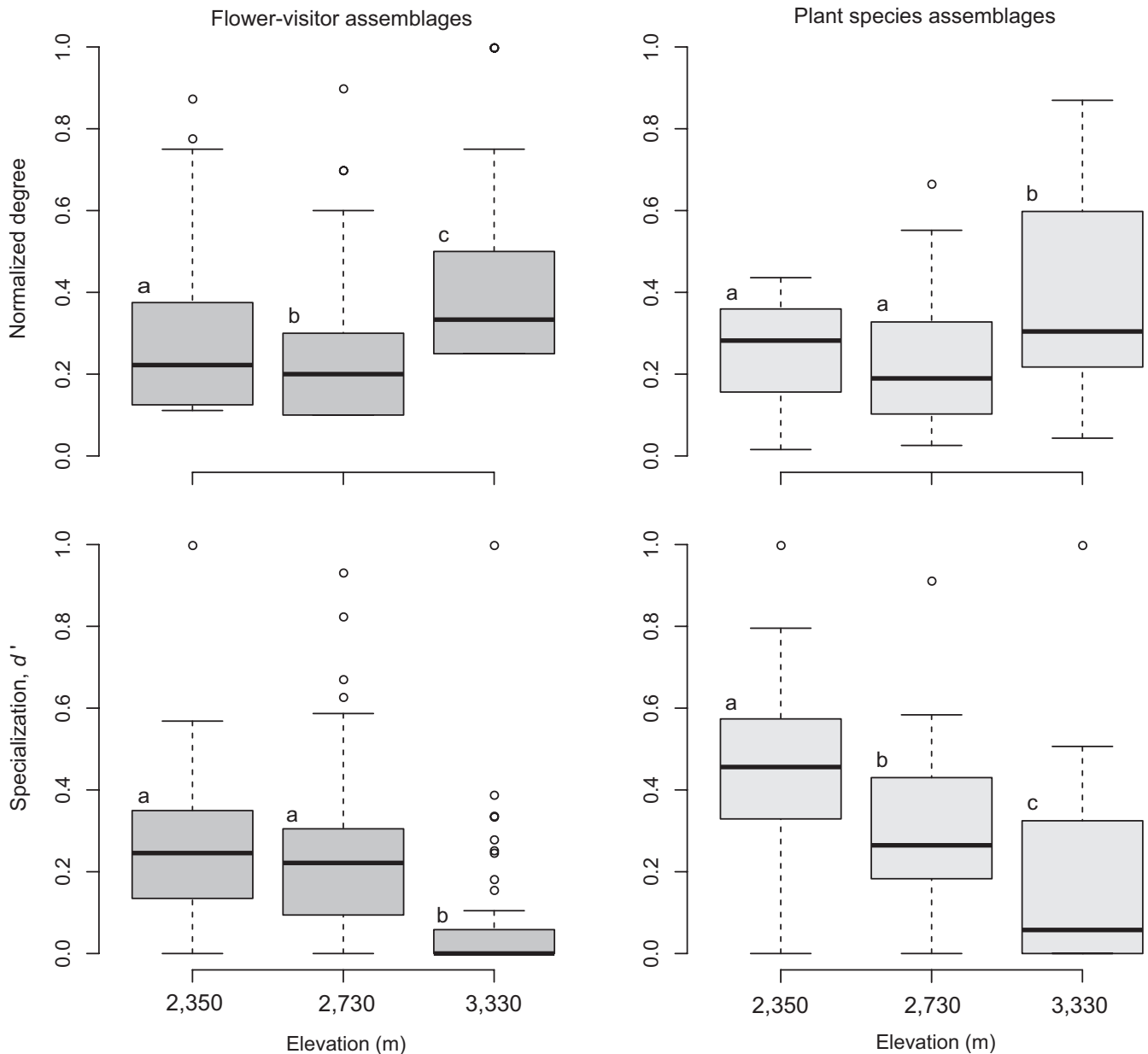


FIGURE 4 Variation of species niche-based metrics along the elevational gradient. Different letters denote significant differences between elevations ($p < 0.05$) after Tukey's correction for multiple comparisons. Each box in each graph represents the interquartile range (25%–75%) and the band inside the median. Whiskers represent the 1.5 of the lower or upper interquartile range and outliers are indicated as points. Different letters denote significant differences between elevations ($p < 0.05$) after Tukey's correction for multiple comparisons

S3), and this variable was only marginally associated with ND normalized degree. Indeed, insects with longer proboscis tended to link to more plant species (Table S7 in Appendix S3: $\beta = 14.06 \pm 7.98$, $p = 0.08$). The functional dispersion (FD_s) decreased with elevation (2,350 m: 0.16; 2,730 m: 0.15; 3,350 m: 0.13; 3,520 m: 0.08).

4 | DISCUSSION

Our study confirmed that the structure of the quantitative plant-pollinator visitation network varied along an elevational plant-diversity gradient in El Teide National Park. Variation at the species

level was wide in the composition of pollinator assemblages and mainly driven by the richness component of β -diversity. At high elevations, pollinators were more generalized and more opportunistic (less selective in their flower choice); they thus had greater trophic niche breadth compared to pollinators at lower elevations. This pattern of higher generalization with elevation remained when only common pollinator species were considered, which pointed to niche shift in response to elevation. At the community level, plants were visited by a wider array of insect species, and the whole network showed lower specialization, greater connectance and lower modularity towards the summit. These findings are consistent with previous research showing that network topology is affected

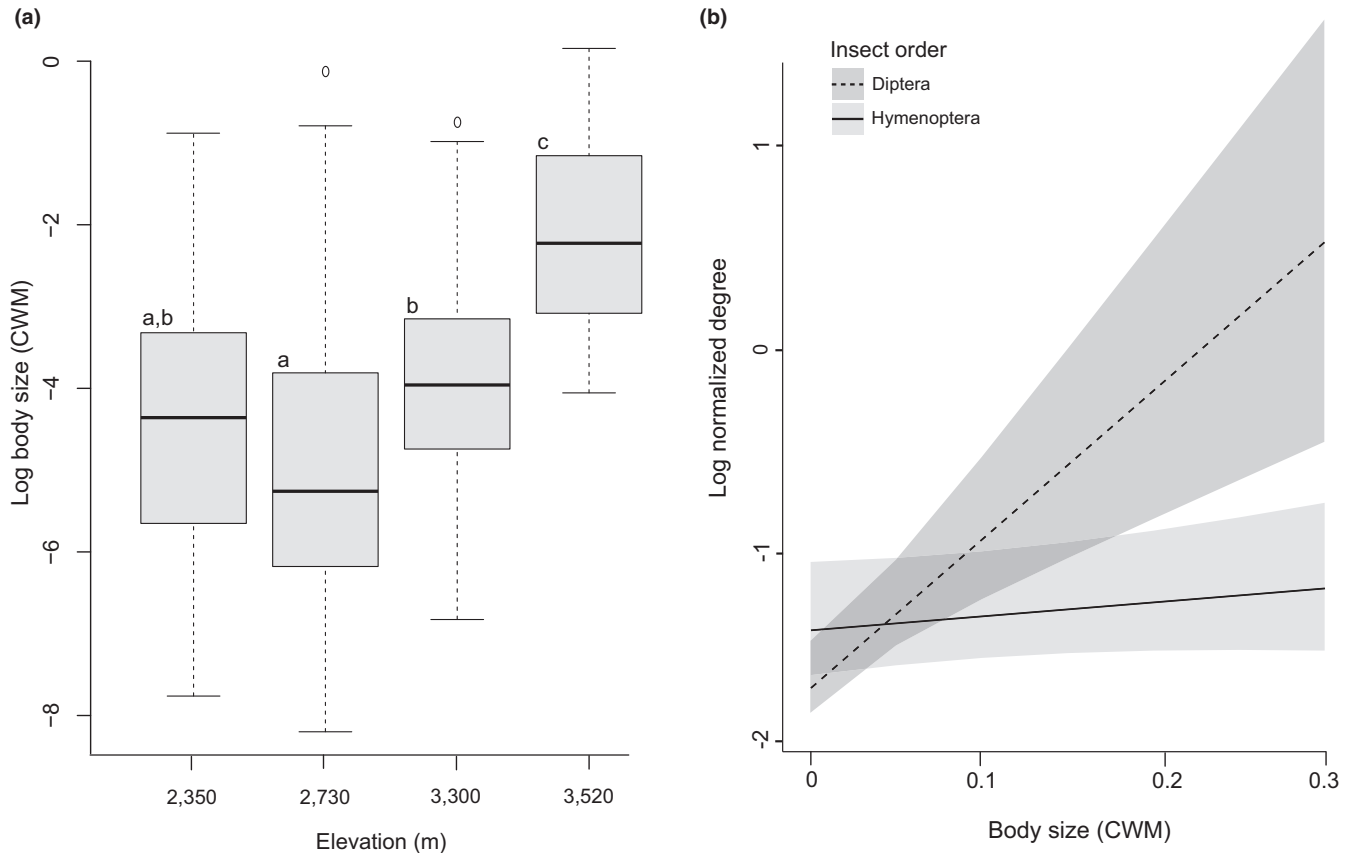


FIGURE 5 (a) Variation of community-weighted body size for dipterans and hymenopterans along the elevational gradient. Different letters denote significant differences between elevations ($p < 0.05$) after Tukey's correction for multiple comparisons. (b) LMM predictions (i.e. fitted model) for effects of weighted body size on normalized degree of dipterans and hymenopterans. Body size was weighted by the abundance of each species at each elevation

by elevation (Hoiss, Krauss, & Steffan-Dewenter, 2015; Ramos-Jiliberto et al., 2010). However, as far as we know, the finding that pollinator insects become more opportunistic at higher elevations and thus have greater trophic niche breadth has not been reported in prior studies. This result is consistent with the expected reduction in interspecific competition in unproductive environments at high elevations (Ebeling et al., 2011; Fründ et al., 2010; MacArthur & Pianka, 1966), which may lead to niche expansion of pollinator species (Hoiss et al., 2012; Miller-Struttmann & Galen, 2014). The findings are also congruent with previous research in other pollinator taxa, such as hummingbirds, which have been found to be more generalist at high elevations because of both food niche expansion and environmental filtering (Maglianesi et al., 2015; but see Dalsgaard et al., 2018 for contrasting results). Still, another key result was that the most common pollinators groups, dipterans and hymenopterans, showed a larger body size but also trait clustering (lower FDis) at higher elevation, and trait overdispersion (larger FDis) at lower elevation. This reduction in functional diversity with increased elevation can be ascribed to an environmental filtering mechanism, where stressful environmental conditions lead to the coexistence of species with similar traits adapted to the local environment, resulting in a pattern of functional clustering (Classen et al., 2017; Cornwell et al., 2006; Maglianesi et al., 2015).

As predicted, there was an overall decline in species richness of pollinators with increasing elevation. We found that this decline was mainly driven by the loss of species along the elevational gradient rather than by spatial replacement of species. This indicated that high-elevation assemblages were nested within (were subsets of) low-elevation assemblages. Species β -diversity was expected to be driven largely by replacement, because many pollinator insects tend to occur at particular elevations rather than persisting across the entire gradient (Bishop et al., 2015; da Silva et al., 2018; González-Reyes et al., 2017; Nunes et al., 2016; Perillo et al., 2017). Many of the insect species were, however, found in broad gradients covering several vegetation belts. This could promote turnover because few species can prevail throughout many different habitats along such gradients (Guo et al., 2013; Rahbek, 2005). In contrast, our study was situated above the tree line, encompassing a relatively homogenous habitat, which allowed many species to colonize both low and high elevations. Yet, this pattern of a nested sequence of extinction along the gradient has been reported elsewhere (Bernadou, Espadaler, Goff, & Fourcassié, 2015; Lessard, Dunn, Parker, & Sanders, 2007). A nested pattern of β -diversity emerges when the environment filters only a subset of an assemblage along a gradient in a non-random, directional way (Soininen, Heino, & Wang, 2018). In our system, the elevational gradient may have filtered pollinators due to their ability

to exploit a wide range of trophic resources. This is consistent with the increase in trophic niche breadth, generalization and body size towards higher elevations, which could be reflecting the response of pollinators to drastic reduction in abundance and density of all plant species towards the mountain-top. This limitation of trophic resources may increase trophic generalization in both plants and pollinators. Previous research has indeed shown that pollinator specialization can vary along productivity gradients (Fontaine et al., 2008; Fründ et al., 2010; Miller-Struttman & Galen, 2014), and that elevation-induced environmental stress affects the topology of plant-pollinator networks (Miller-Struttman & Galen, 2014).

In this context of increased resource limitation with elevation, insects with large body size had a competitive advantage, as seen in the positive relationship between body size, proboscis length and diet breadth found for dipterans and hymenopterans (Byrne et al., 1988; Casey et al., 1985; Greenleaf et al., 2007). Furthermore, large-bodied insects might be better buffered against environmentally induced physiological stress at high elevations, owing to more efficient energy use by larger insects in cold environments (Addo-Bediako, Chown, & Gaston, 2002; Hodkinson, 2005; Peters et al., 2016). However, there are serious doubts as to whether physiology-based theories that predict generally larger body sizes in colder climates can be applied to ectothermic species, since previous studies have revealed no consistent overall trends in many of the taxa concerned, including Dipterans and Hymenopterans (Brehm & Fiedler, 2004; Dillon et al., 2006); but see Classen et al. (2017) for a harmonization of several theories. In any case, the physiology- and niche-based interpretations proposed here are not mutually exclusive. They may operate simultaneously, allowing large-bodied insects to reduce energy losses as well as to increase trophic-niche breadth in resource-limited habitats at high elevations (Addo-Bediako et al., 2002; Greenleaf et al., 2007; Peters et al., 2016; Waddington & Herbst, 1987).

4.1 | Concluding remarks and caveats

The replication of the study in other elevational gradients would provide insight about the spatial replicability of our results. However, the elevational gradient of the Teide stratovolcano cannot be accurately replicated because there is no other gradient with the same characteristics in the Canary Islands. Despite the limitations (number of replicates at island level), our finding that pollinators at higher elevations have wider trophic niche breadth compared to those at lower elevations support previous studies underlining the importance of new research into how ecological networks vary over environmental gradients. The two main causes of a higher pollinator generalization at higher elevations appear to be (a) the loss of specialized pollinator species and (b) the pollinator niche expansion given the lower interspecific competition. The extent to which this pattern can be generalized elsewhere must be thoroughly investigated in order to assess its prevalence and magnitude in a wide array of mountain ecosystems. From an applied perspective, our results highlight the importance of

considering the spatial variation of species interactions when trying to construct functionally consistent interaction networks over environmental gradients. Physiological studies aimed at estimating thermal tolerance of species can help clarify the effects of global warming on pollinator assemblages and their capacity to generate upward shifts and new interactions.

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DATA AVAILABILITY STATEMENT

Plant-pollinator interaction data are deposited in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.b23v8nn> (Lara-Romero, Segí, Pérez-Delgado, Nogales, & Traveset, 2019).

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SUPPORTING INFORMATION

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

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