

Alien honeybees increase pollination risks for range-restricted plants

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Abstract

Aim: Range-restricted species are of high conservation concern, and the way in which they interact with more widespread species has implications for their persistence. Here, we determine how the specialization of mutualistic interactions varies with respect to the geographic range size of plants and pollinators and assess how they respond to the introduction of the alien honeybee. We also compare network characteristics (connectance, specialization and nestedness) between an invaded low mountain and non-invaded high mountain network.

Location: St Katherine Protectorate, South Sinai, Egypt.

Methods: We quantified bee–plant interactions in 42 plots between April and July 2013 and created visitation networks for the low mountains (beehives present) and the high mountains (beehives absent). We then compared visitation network metrics between range-restricted, regionally distributed and widespread plants and pollinators and assessed topological differences between the low and high mountain networks.

Results: Range-restricted bees were involved in a significantly higher number of total interactions than regional and widespread native bees, but showed no evidence of increased generalization. In contrast, range-restricted plants were involved in fewer interactions and exhibited significantly higher specialization and a high dependency on range-restricted pollinators. The introduced honeybee acted as a super-generalist and was associated with an increase in network-level generalization and nestedness. Honeybees exhibited high levels of resource overlap with range-restricted bees and made few visits to range-restricted plant species.

Main conclusions: Range-restricted plants are more specialized in their interactions than range-restricted pollinators, suggesting that the forces shaping the structure of interaction network can vary between partners. Alien honeybees made few visits to range-restricted plants, but exhibited disproportionately high levels of floral competition with range-restricted bees. If high levels of competition lead to population declines then specialized range-restricted plants will be at higher risk of pollen deficits than more widespread species.

KEYWORDS

endemism, honeybee, invasive, mutualism, pollination, range size

1 | INTRODUCTION

Endemic species are highly valued from a conservation perspective, but their restricted distributions leave them particularly threatened by habitat destruction and vulnerable to extinction (Dirzo & Raven, 2003). Previous studies have established which habitat characteristics are associated with endemism (Boulangeat, Lavergne, Van Es, Garraud, & Thuiller, 2012; Markham, 2014), quantified genetic differences between endemic and non-endemic species (Cole, 2003) and demonstrated that endemic species exhibit distinct ecological traits (Kunin & Gaston, 1997). There have been fewer studies investigating the functional consequences of endemism (Gorman, Potts, Schweitzer, & Bailey, 2014; Lavergne, Thompson, Garnier, & Debussche, 2004), and less is known about how ecological interactions differ between range-restricted and widespread species. As the preservation of mutualistic interactions is essential for the long-term persistence of both plant and animal communities (Bascompte & Jordano, 2007; Kearns, Inouye, & Waser, 1998; Memmott, Waser, & Price, 2004), it is useful to consider the manner in which range-restricted species interact with their more widespread counterparts.

Recent studies addressing geographic range in the context of plant–pollinator interactions have tended to focus on the impacts that exotic plant species have on visitation networks outside their native range. Exotic plants easily integrate into novel visitation networks and tend to form species hubs, interacting with a higher abundance and diversity of pollinators than native plants (Bartomeus, Vilà, & Santamaría, 2008; Russo, Memmott, Montoya, Shea, & Buckley, 2014; Stouffer, Cirtwill, & Bascompte, 2014; Vilà et al., 2009). Network roles vary consistently between plant species across both their native and alien ranges (Emer, Memmott, Vaughan, Montoya, & Tylianakis, 2016), suggesting that the tendency to be a generalist or specialist is intrinsic to each species. Although super-generalism has been established as a trait associated with range expansion in exotic plants, it has not been established whether network roles vary consistently between native plants of varying geographic extents.

The invasion of pollination networks has also been well studied in oceanic islands where species are easily categorized as endemic, non-endemic native or introduced. In these systems, endemic plants and pollinators consistently exhibit higher levels of generalization than non-endemic and introduced species, with endemic super-generalists incorporating new invaders into their pollination niche (Olesen, Eskildsen, & Venkatasamy, 2002; Traveset et al., 2013). This phenomenon of island super-generalists is thought to be a consequence of the lower species densities on islands, which allows ecological release and an expansion of endemic niche breadth (Olesen et al., 2002). Less is known about how range size influences plant–pollinator dynamics in mainland systems, but comparative studies have found that range-restricted species of both *Astragalus* and *Ipomoea* receive lower levels of visitation than those with wider ranges (Astegiano, Funes, & Galetto, 2010; Karron, 1987), suggesting that wide-ranging plants are more able to attract pollinators. Being able to interact with a range of partners has clear advantages in terms of range expansion, so in

mainland systems, we may expect widespread species to have higher generalization than range-restricted species.

We investigated how geographic range size influences the network dynamics of a mountain visitation network in South Sinai, Egypt. Like islands, mountain ecosystems are characterized by high levels of endemism and exhibit an equivalent reduction in species richness at high altitudes (McCain & Grytnes, 2010). Mountains generally have low rates of ecological invasion, but invasion rates are increasing in response to climate change (McDougall et al., 2011; Pauchard et al., 2009), leading to growing concerns about future impacts of invasive species on isolated mountain ecosystems (Kueffer et al., 2014). Our study site is characterized by high levels of endemism with over half of Egypt's endemic flora restricted to the mountains of South Sinai (Ayyad, Fakhry, & Moustafa, 2000; Moustafa, Zaghoul, El-Wahab, & Shaker, 2001). Honeybees (*Apis mellifera*) were introduced to the region approximately 20 years ago and are now widely managed in the town and lower mountains, but hives are absent in the less accessible high mountains. Initial research in the region suggests that honeybees can displace native bees from shared floral resources (Semida & El Banna, 2006), but it is not clear how their introduction has affected visitation network structure.

Here, we characterize the bee–plant interactions within the low and high mountains of St Katherine to address whether species roles vary consistently in accordance with the geographic range size of plants and pollinators. Specifically, we assess (1) whether there is evidence of super-generalism in range-restricted species (akin to the island phenomenon) or (2) whether range-restricted species exhibit higher specialization than their widespread counterparts. We also investigate the network role of the introduced honeybee and compare network topology (connectance, nestedness and specialization) between the low mountain and the high mountain networks. The study provides insight into how mountain visitation networks respond to introduced species, and the relative vulnerability of range-restricted species in comparison with those with wider ranges.

2 | METHODS

2.1 | Study site

The St Katherine Protectorate (28°33'N, 33°56'E) encompasses the South Sinai massif, an isolated mountain range where altitudes range from 1,200 to 2,624 m. The region is hyperarid and characterized by a Saharan-Mediterranean climate from an average monthly maximum of 36°C (August) to an average monthly minimum of –7°C (February; Grainger & Gilbert, 2008). The Sinai Peninsula forms a land bridge between Africa and Asia, and as such, the region supports a mixture of plants with distributions extending into North Africa, the Mediterranean and Asia (Grainger & Gilbert, 2008). The mountain range has been recognized as a centre of Middle Eastern plant diversity, with over half of Egypt's endemic flora occurring within the St Katherine Protectorate (35 species; Ayyad et al., 2000, Moustafa et al., 2001). The region is also extremely important for insect life with over two-thirds of Egyptian butterflies occurring in the Protectorate,

including two endemics (Larsen, 1990) and high levels of endemism documented within the Bombyliidae (El-Hawagry & Gilbert, 2014) and the Apoidea (Norfolk, Dathe, O'Toole, & Gilbert, 2017).

The mountains are characterized by the presence of distinctive Bedouin orchard gardens which line the bases of the valleys and have been shown to act as hotspots for pollinators in the region (Norfolk, Eichhorn, & Gilbert, 2014). These agricultural gardens form the basis of traditional Bedouin livelihoods, but recently managed honeybee hives have been introduced to supplement Bedouin income. Hives are now common in the low mountains near to human settlements, but remain absent in the high mountains. The high mountains have a cooler and wetter climate associated with high natural floral diversity, but their accessibility means that hives are yet to be introduced at high altitudes (Norfolk et al., 2014). Here, we quantify the visitation networks both in the low mountains where hives are present and in the less accessible high mountains where hives remain absent.

2.2 | Plant-pollinator surveys

Plant-pollinator interactions were surveyed in total of 42 plots between April and July 2013. The total survey area spanned an area of 25 km² with half of the plots in the low mountains (1,300–1,550 m a.s.l.) in St Katherine Town and Wadi Itlah (12 in gardens, nine in natural habitat) and half in the high mountains (1,800–1,850 m a.s.l.) in Wadi Gebel and Wadi Tinya (12 in gardens, nine in natural habitat). See Fig. S1 for a map of plot locations. The density of orchard gardens was constant between the high and low mountain sites (7 gardens/km²) but external conditions did vary, with low mountains experiencing higher levels of urbanization and associated disturbance. For each plot, five 10 × 10-m quadrats were measured out for repeated surveys (one per month) across the four-month field season, giving a total survey area of 1,050 m² in the low mountains and high mountains, respectively.

Surveys were carried out during sunny, non-windy days between 9 a.m. and 4 p.m. A single collector walked at a steady pace around each 10 × 10-m quadrat, searching each flowering plant in turn and recording all bees observed feeding on a flower. If there were no bees visiting flowers, the surveyor moved on to the next plant. All observed bees were net-collected directly from the plants, apart from honeybees which could confidently be identified in the field. A visit was determined if contact with the stamen or stigma of a flower was observed; resting upon the petal was not sufficient. The identity of each visited plant species was also recorded to establish the plant-pollinator interaction. When multiple bees were observed simultaneously on one plant, no more than 5 min (excluding handling time) was spent catching bees from that particular plant.

Plants were identified in the field where possible or collected for identification using Boulos (2002). Floral trait data were collated for each plant species based on measurements taken in the field (average from three specimens). These included corolla depth (mm), floral radius (mm), symmetry (actinomorphic or zygomorphic) and shape (Bilabiate, Campanulate, Carinate, Connate, Cruciform, Ligulate, Papilionaceous, Rotate, Salverform and Tubular). All captured insects were pinned and identified to species level by taxonomists (see Acknowledgements).

The global distribution of each bee species was assessed using the Atlas Hymenoptera database (Rasmont et al., 2016) and the Discover Life database (Schuh, Hewson-Smith, & Ascher, 2010). Plant distributions were assessed using Boulos (2002) and the Euro+Med PlantBase (Euro+Med 2006). Species geographic range sizes were classified as follows: (1) *Restricted*: known only from the Middle East, (2) *Regional*: also known from Northern Africa or the Mediterranean, (3) *Widespread*: known from other areas (Europe, Africa and Asia). We did not distinguish between naturally occurring and historically introduced plant species, so crop species such as *Allium*, *Cucurbita*, *Eruca*, *Solanum* and *Nicotiana* were classified as widespread.

2.3 | Network analysis

We pooled data from the repeated surveys to build three quantitative plant-pollinator interaction matrices, for the low and high mountains and a combined network of all sampled plots. Network topology descriptors were calculated using R package *bipartite* (Dormann, Frund, Blüthgen, & Gruber, 2009). We calculated three species-level metrics: (1) *interaction number* (I), the number of interactions each species has within the network; (2) *linkage level* (L), the number of partner species (links) for each species within the network; (3) *species specialization* (d'), measures how strongly a species deviates from a random sampling of interacting partners, ranging from 0 (no specialization) to 1 (perfect specialization) (Blüthgen, Menzel, & Blüthgen, 2006), and four network-level metrics: (4) *connectance* (C): the proportion of realized interactions out of those possible in the network; (5) *interaction evenness* (IE); Shannon's evenness of interactions within the network, measures the uniformity of species; (6) *network specialization* (H'_2), measures the extent to which observed interactions deviate from those that would be expected given the species marginal totals, ranges from 0 (no specialization) and 1 (complete specialization); (7) *weighted-interaction nestedness estimator* (WINE), ranges from 0 (no nestedness) to 1 (maximal nestedness), to test whether the matrix differed significantly from random, we compared WINE to those calculated from 1,000 randomly simulated matrices with equal dimensions (Ulrich & Gotelli, 2007). Species were defined as a super-generalist if they interacted with more than 20% of the available partner species within the matrix.

Generalized linear models were used to compare species-level metrics (1) between species with varying geographic range sizes (for the combined network) and (2) between the low mountain network (full), low mountain network (excluding honeybees) and high mountain networks. Models of interaction number and linkage level were fitted with Poisson error distribution and models of specialization (d') with a normal effort distribution. Tukey's post hoc tests were used to test for variation between categories.

The overlap of species in the high and low mountain networks was assessed using the Sørensen similarity index, which ranges from 0 (no species shared) through to 1 (all species shared). Detrended correspondence analysis was used to assess whether floral morphology (corolla depth, floral radius, symmetry and shape) differed in accordance with plant species geographic range size. Categorical traits were

converted into binary and numerical data for analysis. Analyses were all performed in R version 3.3.1 (R Core Team 2017) using the *vegan* package (Oksanen et al., 2016).

3 | RESULTS

The combined mountain network consisted of 190 links between 44 bee species and 60 plant species, resulting in a network connectance of 7.92%. A higher number of links were realized in the low mountain network (140 links between 84 species) as compared to the high mountain network (78 links between 63 species). Just under half of all plant species were shared between the high and low mountain networks (Sørensen similarity = 0.46), while the pollinator showed slightly higher levels of overlap (Sørensen similarity = 0.67). Full visualization of the combined mountain network is shown in Figure S2.

3.1 | Range-size and generalization

Approximately 30% of species within the combined network were restricted to the Middle East, with eight species endemic to Egypt and Israel (four plant and four bee species; Tables S1 and S2). Twenty-nine per cent of species had regional distributions, but the majority were widespread (40%; Table 1). Range-restricted and widespread bee species were involved in a significantly higher number of interactions than regionally distributed species (glm: Δ AIC = 67.44, $\chi^2 = 71.44$, $df = 2$, $p < .001$), but when the introduced honeybee (*A. mellifera*) was excluded, range-restricted bees exhibited the highest mean number of interactions per species (Table 1). The honeybee stood out as a super-generalist within the network, accounting for 20% of observed interactions in the combined network and visiting a total of 33 plant species. On average, widespread pollinators visited the highest number of plant species (Δ AIC = 14.34, $\chi^2 = 18.34$, $df = 2$, $p = .001$), although when the honeybee was excluded mean linkage levels did not differ by pollinator range (Table 1). Despite being involved in the highest number of interactions, range-restricted pollinators showed the highest levels

of specialization (d' ; Table 1), although the effect was marginally non-significant (Δ AIC = 1.72, $\chi^2 = 0.40$, $df = 2$, $p = .058$).

Regionally distributed plants received twice as many visits, from twice as many pollinator species, than restricted and widespread plants (Ints: Δ AIC = 131.67, $\chi^2 = 135.67$, $df = 2$, $p < .001$, links: Δ AIC = 3.27, $\chi^2 = 7.24$, $df = 2$, $p = .027$). Mean plant specialization d' did not differ between regional and widespread plants, but was significantly higher for range-restricted plants (d' : Δ AIC = 5.02, $\chi^2 = 0.50$, $df = 2$, $p = .010$; Table 1). Despite these differences in specialization, the ordination analysis of floral traits revealed no significant difference between the floral morphology of range-restricted, regional and widespread plants ($R^2 = .08$, $p = .125$; Fig. S3). Three plant species stood out as super-generalists within the network: the regionally distributed *Achillea santolina*, involved in 16% of all interactions and visited by 18 bee species; the regionally distributed *Caylusea hexagyna*, involved in 9% of interactions and visited by 15 species; and the widespread cultivated *Foeniculum vulgare*, involved in 7% of interactions and visited by 12 species.

3.2 | Nestedness

The combined network had a WINE value of 0.65 and was characterized by a significantly nested structure (mean of 1,000 random simulations = 0.33, max = 0.53; $Z = 15.72$, $p < .001$). The nested structure meant that a subset of rarer pollinators tended to interact with common super-generalist plants such as *A. santolina*, *F. vulgare* and *C. hexagyna* (Figure 1; bottom left of network) and that common, generalist pollinators such as *A. mellifera* and *Halictus gemmellus* tended to visit a subset of rarer, specialist plants, many of which had restricted distributions (Figure 1: top right of network).

3.3 | Impact of honeybees on network structure

Honeybees were largely absent from the high mountain network (<5% of all interactions) but accounted for 27% of all interactions within the low mountain network where hives are widely managed (Figure 2a). Although honeybees visited over half of the available plant species within the low mountain network, they almost exclusively interacted

	N	I (X ± SE)	L (X ± SE)	L _{max}	d' (X ± SE)
Pollinators					
Restricted	14	18.07 (± 5.11) ^a	3.86 (± 0.84) ^a	9	0.60 (± 0.05) ^a
Regional	15	8.73 (± 3.23) ^b	2.93 (± 0.61) ^a	9	0.38 (± 0.09) ^a
Widespread (excluding honeybee)	14	11.36 (± 5.19) ^c	4.29 (± 1.12) ^a	14	0.42 (± 0.06) ^a
Widespread (all)	15	19.33 (± 9.33) ^a	6.13 (± 2.12) ^b	32	0.43 (± 0.06) ^a
Plants					
Restricted	18	8.5 (± 2.68) ^a	2.89 (± 0.55) ^a	8	0.62 (± 0.05) ^a
Regional	15	20.53 (± 7.73) ^b	4.27 (± 1.33) ^b	18	0.40 (± 0.06) ^b
Widespread	27	7.89 (± 2.63) ^a	2.74 (± 0.59) ^a	12	0.44 (± 0.04) ^b

TABLE 1 The impact of plant and pollinator geographic range size on species-level network metrics

N = number of species; I = number of realized interactions; L = linkage level and d' = specialization. In all cases, X represents the mean across all species (±SE). Significant differences between range size categories are indicated by different letters ($p < .05$).

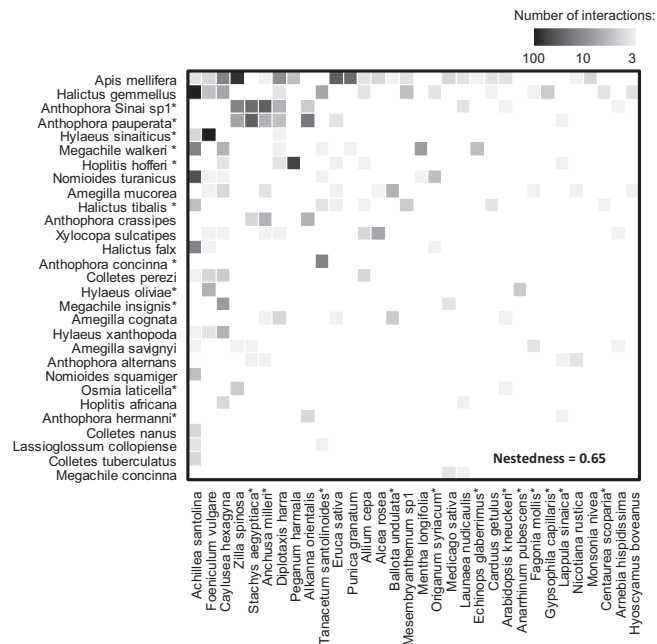


FIGURE 1 The maximally packed plant–pollinator visitor matrix. Bee species are shown on the vertical axis and plants on the horizontal. Species are ranked according to linkage level, with the strength of interactions represented by the level of shading (darker = more interactions). Range-restricted species are highlighted with an asterisk. For simplicity, this figure excludes rare interactions that were observed fewer than three times

with regional and widespread plants, with just 7% of interactions involving range-restricted plants (Figure 2b). Range-restricted bees showed the highest dependency on plants utilized by honeybees in the low mountain network (*Restricted*, 13 shared plant species, 47% visits overlapping; *regional*, eight plant species, 15% visits; *widespread*, 19 plant species, 37% visits).

The low mountain network was larger than the high mountain network, but an equal number of pollinator species had equal connectance (Table 2). Network specialization was higher in the high mountain network (Table 2), with pollinators showing significantly lower linkage levels (links: Δ AIC = 17.59, $\chi^2 = 21.59$, $df = 2$, $p < .001$) and plants showing significantly higher specialization (d' : Δ AIC = 25.20, $\chi^2 = 1.90$, $df = 2$, $p < .001$). Simulated removal of the honeybee from the low mountain network also led to a decrease in pollinator generalization and increase in plant specialization (Table 2). The low mountain network had significantly higher nestedness than the high mountain network (comparison of maximal nestedness matrices: $p = .031$), and removal of the honeybee from the low mountain network led to a significant decrease in nestedness ($p = .014$).

4 | DISCUSSION

The introduced honeybee acted as a super-generalist increasing overall network generalization, but made very few visits to range-restricted plants and exhibited disproportionately high levels of resource overlap

range-restricted bees. This suggests that introduction of honeybees can have differential impacts on native species in accordance with their geographic range size and that range-restricted species may be more vulnerable to visitation deficits or increased floral competition. Range-restricted plants show a greater degree of specialization in this system than pollinators with comparably limited ranges. In the case of plants, this may reflect both cause and consequence; plants with few pollinators may struggle to expand their ranges due to pollen limitation, while widespread pollinators might favour commonly encountered plants. Range-restricted pollinators, in contrast, might be less discriminatory in their interactions out of necessity, although this implies that some other factor(s) prevents them from expanding their range. Each side of the interaction must therefore be responding to a different balance of forces shaping their overall degree of specialization.

Previous studies investigating the relationship between pollinator range size and generalization have tended to focus on oceanic islands, where endemic bees have been shown to visit a higher diversity of plants than non-endemic and exotic bees (Olesen et al., 2002; Traveset et al., 2013). In this mountain system, range-restricted bees were abundant and involved in a large proportion of interactions, but showed no evidence of the super-generalism associated with oceanic islands. Islands and mainland systems inevitably differ in the causal forces leading to range restriction, and these shaping forces may exert contrasting pressures on how species form their interactions. On islands, endemic species are forced to become generalized because they have limited partner choice and nowhere else to go. This extreme isolation rarely occurs in mainland systems (other than for strict habitat specialists), so species are able to move and seek preferred interactions rather than being forced into super-generalism.

4.1 | Geographic range size and species roles

Range-restricted bees may not have exhibited island-like super-generalism, but they were involved in significantly more interactions than more widely distributed natives and visited a range of plants with restricted, regional and widespread distributions. Trends were very different for range-restricted plants that received significantly fewer interactions than regionally distributed plants. Not only were range-restricted plants significantly more specialized than wider-ranged counterparts, they also showed a much higher dependence on range-restricted pollinators and received very few visits from the introduced honeybee. We found no evidence of range-restricted plants being more morphologically specialized than their widespread counterparts in terms of floral traits, suggesting that it is not simply a morphological constraint (such as corolla tube length) that is limiting the diversity of their floral visitors. Other studies have shown that endemic plants are at greater risk of pollination failure than non-endemic plants (e.g., Alonso, Vamosi, Knight, Steets, & Ashman, 2010), suggesting that endemic specialization is not simply a coevolutionary artefact, but that competition for pollinators may actively impose constraints on plant range expansion.

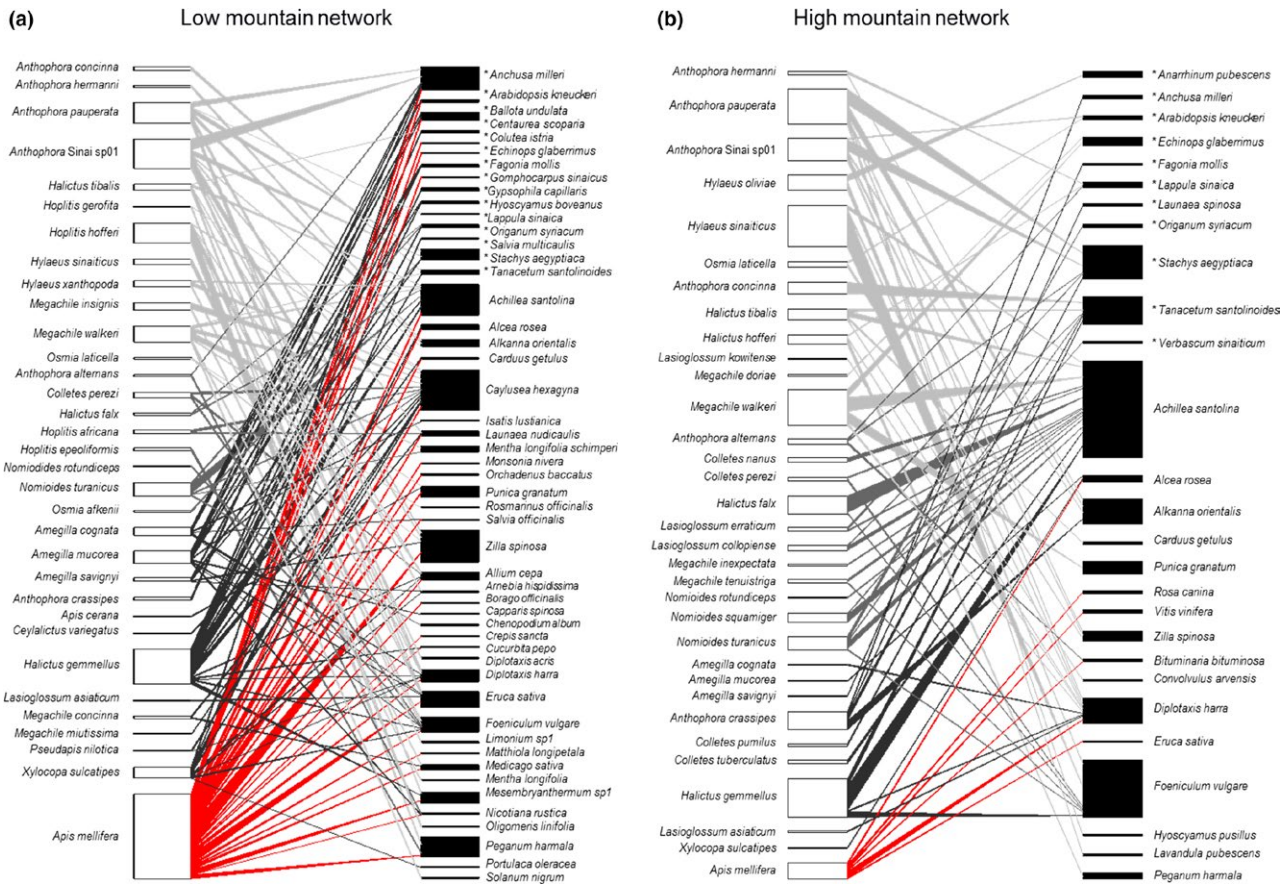


FIGURE 2 Comparison of the (a) low and (b) high mountain visitation networks in St Katherine, with the integration of the introduced honeybee shown in red. White nodes (left) represent pollinators, black nodes (right) represent plants, and the width of the linking lines represents the number of pollinator–plant interactions. Colour of interaction describes geographic range of pollinators: Light grey = restricted, Medium grey = regional, Dark grey = widespread, Red = honeybee. [Colour figure can be viewed at wileyonlinelibrary.com]

Evidence of whether pollination can actively limit range expansion is mixed. Although some research has shown pollen limitation towards the edge of the range (Moeller, Geber, Eckhart, & Tiffin, 2012), other studies have shown no change in visitation rate (Hargreaves, Weiner, & Eckert, 2015) and no consistent decrease in pollen limitation towards the (altitudinal) range limits (Theobald et al. 2016). Our study does not assess whether plant generalization is cause or a response to range size, but the results do provide novel insight into the potential vulnerability of specialized range-restricted plants within visitation networks.

Despite being the most species-rich group, widespread plants received fewer visits and exhibited lower linkage levels than those with regional distributions. Some of these widespread plants are historically introduced crop species (*Allium*, *Cucurbita*, *Eruca*, *Solanum* and *Nicotiana*), which are maintained by active management and irrigation. Introduced plants often exhibit high levels of generalization and frequently act as species hubs in their non-native range (Bartomeus et al., 2008; Traveset et al., 2013; Vilà et al., 2009), but super-generalism in plants is associated with a tendency to become invasive (Emer et al., 2016) and community-level studies have shown that alien plants have lower linkage levels than native plants (Memmott & Waser, 2002).

The fact that many widespread plants in this study are cultivated, rather than invasive, may contribute towards the lower linkage levels observed.

4.2 | Impact of the introduced honeybee on network structure

Unlike widespread plants, the honeybee stood out as a super-generalist interacting with half of all available plant species. The low mountain network was dominated by honeybee interactions (27% of all interactions) and exhibited significantly lower specialization and higher nestedness than the high mountain network. The observed difference in network-level specialization is likely to be influenced by the presence–absence of the super-generalist honeybee, but may also reflect underlying variation in the environmental conditions of the low and high mountains. The characteristics of visitation networks are known to be influenced by altitudinal and environmental variation, with higher altitude networks typically containing fewer interactions and partners (Olesen et al., 2002), so the higher specialization of the high mountain network may simply be a consequence of altitudinal isolation. However, the simulated removal of honeybees from the

TABLE 2 Topology descriptors of the visitation networks in the low and high mountains of the St Katherine region

	P	A	I	C	L _p (X ± SD)	L _a (X ± SD)	G _p	G _a	IE	H ₂	d _p (X ± SD)	d _a (X ± SD)	WINE
Whole network	60	44	190	7.92	3.17 ± 3.53 ^a	4.36 ± 5.60 ^a	5.08	7.06	0.58	0.47	0.34 ± 0.20 ^a	0.38 ± 0.20 ^a	0.65
Low mountain(full)	51	33	145	8.62	2.84 ± 2.71 ^a	4.39 ± 0.95 ^a	4.22	7.70	0.60	0.47	0.33 ± 0.03 ^a	0.43 ± 0.03 ^a	0.60
Low mountain (excluding honeybee)	42	32	116	8.63	2.76 ± 0.40 ^a	3.63 ± 0.58 ^{ab}	4.14	4.81	0.59	0.51	0.40 ± 0.03 ^{ab}	0.47 ± 0.04 ^a	0.47
High mountain	27	33	77	8.33	2.85 ± 3.31 ^a	2.33 ± 0.26 ^c	5.21	2.71	0.57	0.59	0.51 ± 0.03 ^b	0.42 ± 0.05 ^a	0.49

P and A, the number of plant and animal species, respectively; I, the number of realized interactions; C, connectance (I/AP*100); L, linkage level, IE, interaction evenness; H₂, index of network specialization; WINE, weighted-integrated nested estimator value (0 random, 1 perfectly nested). For plants (p) and animals (a), the number of links (L), generality (G) and index of species specialization (d') are also given. In the L and d columns, significant differences between networks are indicated by different letters (p < .05).

network led to equivalent changes in network structure, suggesting that the higher nestedness observed in the low mountain network is at least partially attributable to the introduction of the super-generalist honeybee.

Similar trends have been observed in Spain, where competition with managed honeybees has been shown to decrease wild pollinator niche breadth and increase overall network specialization (Magrach, González-Varo, Boiffier, Vilà, & Bartomeus, 2017), and in Brazil where the presence of the Africanized honeybee has been linked to increased nestedness (Santos et al., 2012). Comparative studies in Brazil have shown that native super-generalist bees are not associated with the same increases in nestedness, suggesting that exotic generalists do not integrate into networks in the same way as native generalists (Giannini et al., 2015). Increased nestedness could be considered positive, because nestedness is associated with higher levels of robustness in scenarios when the least-linked species go extinct first (Burgos et al., 2007). However, as honeybees tended to link with regional and widespread plants, the least-connected endemic plants become those with the highest extinction risk and so do not benefit from any increase in nestedness in this system.

There was strong evidence of resource overlap between honeybees and native bees, with range-restricted bees showing the highest dependency on the plants utilized by honeybees. In California, high numbers of feral honeybees have been shown actively to reduce bumblebee populations through intensified competition over floral resources (Thomson, 2016), and earlier research in St Katherine has suggested that honeybees are able to displace native bees from shared floral resources (Semida & El Banna, 2006). In this arid resource-limited environment, the presence of such high numbers of the super-generalist honeybee may pose a competitive threat to native bees, particularly in the dry season or in periods of prolonged drought.

Plants could also suffer as a result of such floral competition, if honeybees out-compete more efficient native pollinators. This has been documented following the introduction of beehives in Tenerife, where plants that received high honeybee visitation exhibited a drop in native bee visitation and a subsequent decrease in their reproductive success (Valido, Rodríguez-Rodríguez, & Jordano, 2014), and in Spain where high rates of honeybee visitation have been shown to limit pollen tube growth in a common wild plant following spillover from an adjacent mass-flowering crops (Magrach et al., 2017).

4.3 | Conservation implications

In this mountain network, range-restricted plants exhibit much higher levels of specialization than their pollinators, suggesting that they may be more vulnerable to extinction. Range-restricted pollinators were abundant and visited a variety of plant species with wider distributions; however, they exhibited high resource overlap with the superabundant honeybee, which could lead to resource competition. Even a small reduction in the population size

of range-restricted bees could be detrimental for the reproductive success of range-restricted plants, which depend on low numbers of specialized interactions. At a local level, this study highlights the potential vulnerability of local range-restricted species in response to an introduced super-generalist. More generally, this system provides evidence that range-restricted plants are more specialized in their interactions than range-restricted pollinators and that the forces shaping the structure of interaction networks vary between partners.

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DATA ACCESSIBILITY

Data to be deposited in the Dryad Repository following manuscript acceptance.

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Author contributions: O.N., F.G. and M.P.E. conceived the ideas; O.N. gathered data, ran the analyses and led the writing of the manuscript; all authors contributed to revision of the text.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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