

1 **Alien honeybees increase pollination risks for range-**
2 **restricted plants**

3 Running heading: Range size and pollinator specialisation

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1 **ABSTRACT**

2 **Aim**

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

10 **Location**

11 St Katherine Protectorate, South Sinai, Egypt.

12 **Methods**

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

18 **Results**

19 Range-restricted bees were involved in a significantly higher number of total interactions
20 than regional and widespread native bees, but showed no evidence of increased
21 generalisation. In contrast, range-restricted plants were involved in fewer interactions and
22 exhibited significantly higher specialisation and a high dependency on range-restricted
23 pollinators. The introduced honeybee acted as a super-generalist and was associated with
24 an increase in network-level generalisation and nestedness. Honeybees exhibited high

1 levels of resource overlap with range-restricted bees and made few visits to range-restricted
2 plant species.

3 **Main conclusions**

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

10 Key words: pollination; mutualism; endemism; range size; honeybee; invasive

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12 **1. INTRODUCTION**

13 Endemic species are highly valued from a conservation perspective, but their restricted
14 distributions leave them particularly threatened by habitat destruction and vulnerable to
15 extinction (Dirzo and Raven 2003). Previous studies have established which habitat
16 characteristics are associated with endemism (Boulangeat et al. 2012; Markham 2014),
17 quantified genetic differences between endemic and non-endemic species (Cole 2003) and
18 demonstrated that endemic species exhibit distinct ecological traits (Kunin and Gaston
19 1997). There have been fewer studies investigating the functional consequences of
20 endemism (Gorman et al. 2014; Lavergne et al. 2004) and less is known about how
21 ecological interactions differ between range-restricted and widespread species. Since the
22 preservation of mutualistic interactions is essential for the long-term persistence of both plant
23 and animal communities (Bascompte and Jordano 2007; Kearns et al. 1998; Memmott et al.
24 2004), it is useful to consider the manner in which range-restricted species interact with their
25 more widespread counterparts.

1 Recent studies addressing geographical range in the context of plant-pollinator
2 interactions have tended to focus on the impacts that exotic plant species have on visitation
3 networks outside their native range. Exotic plants easily integrate into novel visitation
4 networks and tend to form species-hubs, interacting with a higher abundance and diversity
5 of pollinators than native plants (Bartomeus et al. 2008; Vilà et al. 2009, Russo et al. 2014,
6 Stouffer et al. 2014). Network roles vary consistently between plant species across both their
7 native and alien ranges (Emer et al. 2016), suggesting that the tendency to be a generalist
8 or specialist is intrinsic to each species. Though super-generalism has been established as a
9 trait associated with range expansion in exotic plants, it has not been established whether
10 network roles vary consistently between native plants of varying geographic extents.

11 The invasion of pollination networks has also been well studied in oceanic islands
12 where species are easily categorised as endemic, non-endemic native or introduced. In
13 these systems, endemic plants and pollinators consistently exhibit higher levels of
14 generalisation than non-endemic and introduced species, with endemic super-generalists
15 incorporating new invaders into their pollination niche (Olesen et al. 2002; Travaset et al.
16 2013). This phenomenon of island super-generalists is thought to be a consequence of the
17 lower species densities on islands, which allows ecological release and an expansion of
18 endemic niche breadth (Olesen et al. 2002). Less is known about how range size influences
19 plant-pollinator dynamics in mainland systems, but comparative studies have found that
20 range-restricted species of both *Astragalus* and *Ipomoea* receive lower levels of visitation
21 than those with wider ranges (Karon 1987; Astegiano et al. 2010), suggesting that wide-
22 ranging plants are more able to attract pollinators. Being able to interact with a range of
23 partners has clear advantages in terms of range expansion, so in mainland systems we may
24 expect widespread species to have higher generalisation than range-restricted species.

25 We investigated how geographic range size influences the network dynamics of a
26 mountain visitation network in South Sinai, Egypt. Like islands, mountain ecosystems are
27 characterised by high levels of endemism and exhibit an equivalent reduction in species

1 richness at high altitudes (McCain and Grytnes 2010). Mountains generally have low rates of
2 ecological invasion, but invasion rates are increasing in response to climate change
3 (Pauchard et al. 2009; McDougall et al. 2011), leading to growing concerns about future
4 impacts of invasive species on isolated mountain ecosystems (Kueffer et al. 2014). Our
5 study site is characterised by high levels of endemism with over half of Egypt's endemic flora
6 restricted to the mountains of South Sinai (Ayyad et al. 2000; Moustafa et al. 2001).
7 Honeybees (*Apis mellifera*) were introduced to the region approximately 20 years ago, and
8 are now widely managed in the town and lower mountains, but hives are absent in the less
9 accessible high mountains. Initial research in the region suggests that honeybees can
10 displace native bees from shared floral resources (Semida and El Banna 2006), but it is not
11 clear how their introduction has affected visitation network structure.

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

22 **2. METHODS**

23 2.1 Study Site

24 The St Katherine Protectorate (28°33'N, 33°56'E) encompasses the South Sinai massif, an
25 isolated mountain range where altitudes range from 1200--2624 m. The region is hyper-arid
26 and characterised by a Saharan-Mediterranean climate from an average monthly maximum

1 of 36°C (August) to an average monthly minimum of -7°C (February; Grainger and Gilbert
2 2008). The Sinai Peninsula forms a land-bridge between Africa and Asia and as such the
3 region supports a mixture of plants with distributions extending into North Africa, the
4 Mediterranean and Asia (Grainger and Gilbert 2008). The mountain range has been
5 recognised as a centre of Middle Eastern plant diversity, with over half of Egypt's endemic
6 flora occurring within the St Katherine Protectorate (35 species; Avyad et al., 1999, Moustafa
7 et al., 2001). The region is also extremely important for insect life with over two-thirds of
8 Egyptian butterflies occurring in the Protectorate, including two endemics (Larsen, 1990) and
9 high levels of endemism documented within the Bombylidae (El-Hawagry and Gilbert 2014)
10 and the Apoidea (Norfolk et al, 2017).

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

21 2.2 Plant-pollinator surveys

22 Plant-pollinator interactions were surveyed in total of 42 plots between April and July 2013.
23 The total survey area spanned an area of 25 km² with half of the plots in the low mountains
24 (1300–1550 m a.s.l.) in St Katherine Town and Wadi Itlah (12 in gardens, 9 in natural
25 habitat) and half in the high mountains (1800–1850 m a.s.l) in Wadi Gebel and Wadi Tinya
26 (12 in gardens, 9 in natural habitat). See Fig S1 for a map of plot locations. The density of

1 orchard gardens was constant between the high and low mountain sites (7 gardens/ km²)
2 but external conditions did vary, with low mountains experiencing higher levels of
3 urbanisation and associated disturbance. For each plot, five 10 x 10-m quadrats were
4 measured out for repeated surveys (one per month) across the four-month field season,
5 giving a total survey area of 1050 m² in the low mountains and high mountains respectively.

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

16 Plants were identified in the field where possible, or collected for identification using
17 Boulos (2002). Floral trait data were collated for each plant species based on measurements
18 taken in the field (average from 3 specimens). These included Corolla depth (mm), Floral
19 radius (mm), Symmetry (actinomorphic or zygomorphic) and Shape (Bilabiate, Campanulate,
20 Carinate, Connate, Cruciform, Ligulate, Papilionaceous, Rotate, Salverform, Tubular). All
21 captured insects were pinned and identified to species level by taxonomists (see
22 Acknowledgements).

23 The global distribution of each bee species was assessed using the Atlas
24 Hymenoptera database (Rasmont et al. 2016) and the Discover Life database (Schuh et al.
25 2010). Plant distributions were assessed using Boulos (2002) and the Euro+Med PlantBase
26 (Euro+Med 2006). Species geographic range sizes were classified as: 1) Restricted: known

1 only from the Middle East, 2) Regional: also known from Northern Africa or the
2 Mediterranean, 3) Widespread: known from other areas (Europe, Africa and Asia). We did
3 not distinguish between naturally occurring and historically introduced plant species, so crop
4 species such as *Allium*, *Curcubita*, *Eruca*, *Solanum*, *Nicotiana* were classified as
5 widespread.

6 2.3 Network analysis

7 We pooled data from the repeated surveys to build three quantitative plant-pollinator
8 interaction matrices, for the low and high mountains and a combined network of all sampled
9 plots. Network topology descriptors were calculated using R package *bipartite* (Dormann et
10 al. 2009). We calculated three species-level metrics: (1) *Interaction number (I)*, the number
11 of interactions each species has within the network; (2) *Linkage level (L)*, the number of
12 partner species (links) for each species within the network; (3) *Species specialisation (d')*,
13 measures how strongly a species deviates from a random sampling of interacting partners,
14 ranging from 0 (no specialisation) to 1 (perfect specialisation) (Blüthgen et al, 2006). And
15 four network-level metrics: (4) *Connectance (C)*: the proportion of realised interactions out of
16 those possible in the network; (5) *Interaction Evenness (IE)*; Shannon's evenness of
17 interactions within the network, measures the uniformity of species; (6) *Network*
18 *Specialisation (H'₂)*, measures the extent to which observed interactions deviate from those
19 that would be expected given the species marginal totals, ranges from 0 (no specialisation)
20 and 1 (complete specialisation); (7) *Weighted-Interaction Nestedness Estimator (WINE)*,
21 ranges from 0 (no nestedness) to 1 (maximal nestedness), to test whether the matrix differed
22 significantly from random we compared WINE to those calculated from 1000 randomly
23 simulated matrices with equal dimensions (Ulrich and Gotelli 2007). Species were defined as
24 a super-generalist if they interacted with more than 20% of the available partner species
25 within the matrix.

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

7 The overlap of species in the high and low mountain networks was assessed using the
8 Sørensen similarity index, which ranges from 0 (no species shared) through to 1 (all species
9 shared). Detrended correspondence analysis was used to assess whether floral morphology
10 (corolla depth, floral radius, symmetry and shape) differed in accordance to plant species
11 geographic range size. Categorical traits were converted into binary and numerical data for
12 analysis. Analyses were all performed in R version 3.3.1 (R Core Team 2017) using the
13 *vegan* package (Oksanen et al. 2016).

14

15 **3. RESULTS**

16 The combined mountain network consisted of 190 links between 44 bee species and 60
17 plant species, resulting in a network connectance of 7.92 per cent. A higher number of links
18 were realised in the low mountain network (140 between 84 species) as compared to the
19 high mountain network (78 links between 63 species). Just under half of all plant species
20 were shared between the high and low mountain networks (Sørensen similarity = 0.46),
21 whilst the pollinator showed slightly higher levels of overlap (Sørensen similarity= 0.67). Full
22 visualisation of the combined mountain network is shown in Figure S2.

23 **3.1 Range-size and generalisation**

24 Approximately thirty percent of species within the combined network were restricted to the
25 Middle East, with eight species endemic to Egypt and Israel (4 plant and 4 bee species;

1 Tables S1 and S2). Twenty-nine percent of species had regional distributions but the
2 majority were widespread (40%; Table 1). Range-restricted and widespread bee species
3 were involved in a significantly higher number of interactions than regionally distributed
4 species (glm: $\Delta AIC=67.44$, $\chi^2=71.44$, $df=2$, $P<0.001$), but when the introduced honeybee
5 (*A. mellifera*) was excluded, range-restricted bees exhibited the highest mean number of
6 interactions per species (Table 1). The honeybee stood out as a super-generalist within the
7 network, accounting for 20% of observed interactions in the combined network and visiting a
8 total of 33 plant species. On average, widespread pollinators visited the highest number of
9 plant species ($\Delta AIC=14.34$, $\chi^2=18.34$, $df=2$, $P=0.001$), although when the honeybee was
10 excluded mean linkage levels did not differ by pollinator range (Table 1). Despite being
11 involved in the highest number of interactions, range-restricted pollinators showed the
12 highest levels of specialisation (d' ; Table 1), although the effect was marginally non-
13 significant ($\Delta AIC=1.72$, $\chi^2=0.40$, $df=2$, $P=0.058$).

14 Regionally distributed plants received twice as many visits, from twice as many
15 pollinator species, than restricted and widespread plants (*Ints*: $\Delta AIC=131.67$, $\chi^2=135.67$,
16 $df=2$, $P<0.001$, *links*: $\Delta AIC=3.27$, $\chi^2=7.24$, $df=2$, $P=0.027$). Mean plant specialisation d' did
17 not differ between regional and widespread plants, but was significantly higher for range-
18 restricted plants (d' : $\Delta AIC=5.02$, $\chi^2=0.50$, $df=2$, $P=0.010$; Table 1). Despite these differences
19 in specialisation, the ordination analysis of floral traits revealed no significant difference
20 between the floral morphology of range-restricted, regional and widespread plants ($R^2=0.08$,
21 $P=0.125$; Fig S3). Three plant species stood out as super-generalists within the network: the
22 regionally distributed *Achillea santolina*, involved in 16% of all interactions and visited by 18
23 bee species; the regionally distributed *Caylusea hexagyna*, involved in 9% of interactions
24 and visited by 15 species; and the widespread cultivated *Foeniculum vulgare*, involved in 7%
25 of interactions and visited by 12 species.

26 3.2 Nestedness

1 The combined network had a WINE value of 0.65 and was characterised by a significantly
2 nested structure (mean of 1000 random simulations = 0.33, max=0.53; $Z=15.72$, $P<0.001$).
3 The nested structure meant that a subset of rarer pollinators tended to interact with common
4 super-generalist plants such as *A. santolina*, *F. vulgare* and *C. hexagyna* (Fig. 1; bottom left
5 of network) and that common, generalist pollinators such as *A. mellifera* and *Haltictus*
6 *gemmaellus* tended to visit a subset of rarer, specialist plants, many of which had restricted
7 distributions (Fig. 1: top right of network).

8 3.3 Impact of honeybees on network structure

9 Honeybees were largely absent from the high mountain network (<5% of all interactions) but
10 accounted for 27% of all interactions within the low mountain network where hives are widely
11 managed (Fig 2a). Although honeybees visited over half of the available plant species within
12 the low mountain network, they almost exclusively interacted with regional and widespread
13 plants, with just 7% of interactions involving range-restricted plants (Fig 2b). Range-
14 restricted bees showed the highest dependency on plants utilised by honeybees in the low
15 mountain network (*Restricted*, 13 shared plant species, 47% visits overlapping; *regional*, 8
16 plant species, 15% visits; *widespread*, 19 plant species, 37% visits).

17 The low-mountain network was larger than the high-mountain network, but supported
18 an equal number of pollinator species and had equal connectance (Table 2). Network
19 specialisation was higher in the high-mountain network (Table 2), with pollinators showing
20 significantly lower linkage levels (links: $\Delta AIC=17.59$, $\chi^2=21.59$, $df=2$, $P<0.001$) and plants
21 showing significantly higher specialisation (d' : $\Delta AIC=25.20$, $\chi^2=1.90$, $df=2$, $P<0.001$).
22 Simulated removal of the honeybee from the low-mountain network also led to a decrease in
23 pollinator generalisation and increase in plant specialisation (Table 2). The low-mountain
24 network had significantly higher nestedness than the high-mountain network (comparison of
25 maximal nestedness matrices: $P=0.031$), and removal of the honeybee from the low-
26 mountain network led to a significant decrease in nestedness ($P=0.014$).

1 **4. DISCUSSION**

2 The introduced honeybee acted as a super-generalist increasing overall network
3 generalisation, but made very few visits to range-restricted plants and exhibited
4 disproportionately high levels of resource overlap range-restricted bees. This suggests that
5 introduction of honeybees can have differential impacts on native species in accordance to
6 their geographic range size and that range-restricted species may be more vulnerable to
7 visitation deficits or increased floral competition. Range-restricted plants show a greater
8 degree of specialisation in this system than pollinators with comparably limited ranges. In the
9 case of plants, this may reflect both cause and consequence; plants with few pollinators may
10 struggle to expand their ranges due to pollen limitation, while widespread pollinators might
11 favour commonly-encountered plants. Range-restricted pollinators, in contrast, might be less
12 discriminatory in their interactions out of necessity, though this implies that some other
13 factor(s) prevents them from expanding their range. Each side of the interaction must
14 therefore be responding to a different balance of forces shaping their overall degree of
15 specialisation.

16 Previous studies investigating the relationship between pollinator range size and
17 generalisation have tended to focus on oceanic islands, where endemic bees have been
18 shown to visit a higher diversity of plants than non-endemic and exotic bees (Olesen et al.
19 2002; Travaset et al. 2013). In this mountain system, range-restricted bees were abundant
20 and involved in a large proportion of interactions, but showed no evidence of the super-
21 generalism associated with oceanic islands. Islands and mainland systems inevitably differ
22 in the causal forces leading to range restriction, and these shaping forces may exert
23 contrasting pressures on how species form their interactions. On islands, endemic species
24 are forced to become generalised because they have limited partner choice and nowhere
25 else to go. This extreme isolation rarely occurs in mainland systems (other than for strict
26 habitat specialists), so species are able to move and seek preferred interactions rather than
27 being forced into super-generalism.

1 4.1 Geographic range size and species roles

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

16 Evidence of whether pollination can actively limit range-expansion is mixed. Although
17 some research has shown pollen limitation towards the edge of the range (Moeller et al.
18 2012), other studies have shown no change in visitation rate (Hargreaves et al. 2015) and no
19 consistent decrease in pollen limitation towards the (altitudinal) range limits (Theobald et al.
20 2016). Our study does not assess whether plant generalisation is cause or a response to
21 range size, but the results do provide novel insight into the potential vulnerability of
22 specialised range-restricted plants within visitation networks.

23 Despite being the most species-rich group, widespread plants received fewer visits
24 and exhibited lower linkage levels than those with regional distributions. Some of these
25 widespread plants are historically introduced crop species (*Allium*, *Curcubita*, *Eruca*,
26 *Solanum*, *Nicotiana*), which are maintained by active management and irrigation. Introduced

1 plants often exhibit high levels of generalisation and frequently act as species-hubs in their
2 non-native range (Bartomeus et al. 2008; Vilà et al. 2009; Traveset et al. 2013), but super-
3 generalism in plants is associated with a tendency to become invasive (Emer et al. 2016)
4 and community-level studies have shown that alien plants have lower linkage levels than
5 native plants (Memmott & Waser 2002). The fact that many widespread plants in this study
6 are cultivated, rather than invasive, may contribute towards the lower linkage levels
7 observed.

8 4.2 Impact of the introduced honeybee on network structure

9 Unlike widespread plants, the honeybee stood out as a super-generalist interacting with half
10 of all available plant species. The low mountain network was dominated by honeybee
11 interactions (27% of all interactions) and exhibited significantly lower specialisation and
12 higher nestedness than the high mountain network. The observed difference in network-level
13 specialisation is likely to be influenced by the presence/absence of the super-generalist
14 honeybee, but may also reflect underlying variation in the environmental conditions of the
15 low and high mountains. The characteristics of visitation networks are known to be
16 influenced by altitudinal and environmental variation, with higher altitude networks typically
17 containing fewer interactions and partners (Olesen and Jordano 2002), so the higher
18 specialisation of the high mountain network may simply be a consequence of altitudinal
19 isolation. However the simulated removal of honeybees from the network led to equivalent
20 changes in network structure, suggesting that the higher nestedness observed in the low
21 mountain network is at least partially attributable to the introduction of the super-generalist
22 honeybee.

23 Similar trends have been observed in Spain, where competition with managed
24 honeybees has been shown to decrease wild pollinator niche breadth and increase overall
25 network specialisation (Magrach et al. 2017), and in Brazil where the presence of the
26 Africanised honeybee has been linked to increased nestedness (Santos et al. 2012).

1 Comparative studies in Brazil have shown that native super-generalist bees are not
2 associated with the same increases in nestedness, suggesting that exotic generalists do not
3 integrate into networks in the same way as native generalists (Giannini et al. 2015).
4 Increased nestedness could be considered positive, because nestedness is associated with
5 higher levels of robustness in scenarios when the least-linked species go extinct first
6 (Burgos et al. 2007). However, since honeybees tended to link with regional and widespread
7 plants, the least-connected endemic plants become those with the highest extinction risk and
8 so do not benefit from any increase in nestedness in this system.

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

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

25 4.3 Conservation implications

1 In this mountain network, range-restricted plants exhibit much higher levels of specialisation
2 than their pollinators, suggesting that they may be more vulnerable to extinction. Range-
3 restricted pollinators were abundant and visited a variety of plant species with wider
4 distributions; however they exhibited high resource overlap with the super-abundant
5 honeybee, which could lead to resource competition. Even a small reduction in the
6 population size of range-restricted bees could be detrimental for the reproductive success of
7 range-restricted plants, which depend on low numbers of specialised interactions. At a local
8 level this study highlights the potential vulnerability of local range-restricted species in
9 response to an introduced super-generalist. More generally, this system provides evidence
10 that range-restricted plants are more specialised in their interactions than range-restricted
11 pollinators, and that the forces shaping the structure of interaction networks vary between
12 partners.

13 **DATA ACCESSIBILITY**

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

15 **AUTHOR CONTRIBUTIONS**

16 O.N., F.G. and M.E. conceived the ideas; O.N. analysed the data

17 and led the writing of the manuscript; all authors contributed to revision of the text.

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22

1 **Table 1.** The impact of plant and pollinator geographic range size on species-level network
 2 metrics. N = number of species, I = number of realised interactions. L = linkage level and
 3 d' = specialisation. In all cases X represents the mean across all species (\pm standard error).
 4 Significant differences between range size categories are indicated by different letters ($P <$
 5 0.05).

6

POLLINATORS	N	$I(X \pm \text{s.e.})$	$L(X \pm \text{s.e.})$	L_{\max}	$d'(X \pm \text{s.e.})$
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	N	$I(X \pm \text{s.e.})$	$L(X \pm \text{s.e.})$	L_{\max}	$d'(X \pm \text{s.e.})$
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 2. Topology descriptors of the visitation networks in the low and high mountains of the St Katherine region. *P* and *A*, the number of plant and animal species respectively; *I*, the number of realised interactions; *C*, connectance ($I/AP*100$); *L*, linkage level, *IE*, interaction evenness; H_2 , 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 ($p < 0.05$).

	<i>P</i>	<i>A</i>	<i>I</i>	<i>C</i>	$L_p (X \pm s.d.)$	$L_a (X \pm s.d.)$	<i>G_p</i>	<i>G_a</i>	<i>IE</i>	H_2	$d_p (X \pm s.d.)$	$d_a (X \pm s.d.)$	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

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 3 times.

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.

Fig 1

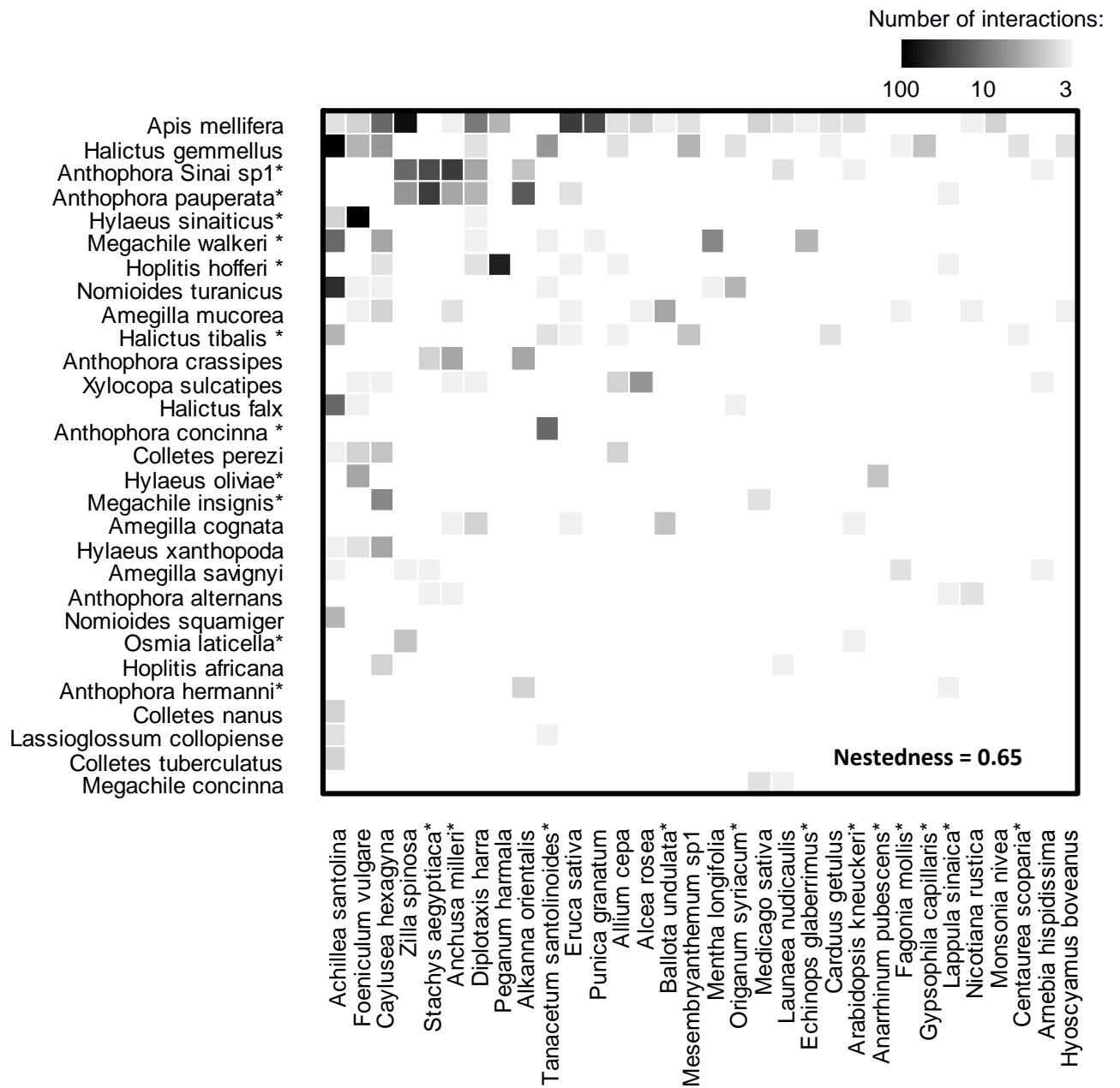


Fig 2

