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DOI: 10.1093/aob/mcw114

Example citation: Watts, S., Dormann, C. F., Gonzalez, A. M. M. and Ollerton, J. (2016) The influence of floral traits on specialisation and modularity of plant-pollinator networks in a biodiversity hotspot in the Peruvian Andes. *Annals of Botany.* **118**(3), pp. 415-429. 0305-7364.

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Version: Accepted version

Note: This is a pre-copyedited, author-produced version of an article accepted for publication in Annals of Botany following peer review. The version of record is available online at: http://dx.doi.org/10.1093/aob/mcw114.

http://nectar.northampton.ac.uk/8930/

Original Article

The influence of floral traits on specialisation and modularity of plant-pollinator networks in a biodiversity hotspot in the Peruvian Andes.

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Abstract

- *Background and Aims*. Modularity is a ubiquitous and important structural property of ecological networks which describes the relative strengths of sets of interacting species and gives insights into the dynamics of ecological communities. However this has rarely been studied in species rich, tropical plant-pollinator networks. Working in a biodiversity hotspot in the Peruvian Andes we assessed the structure of quantitative plant-pollinator networks in nine valleys, quantifying modularity among networks, defining the topological roles of species and the influence of floral traits on specialisation.
- *Methods* A total of 90 transects were surveyed for plants and pollinators at different altitudes and across different life zones. Quantitative modularity (QuanBiMo) was used to detect modularity and six indices were used to quantify specialisation.
- *Key Results* All networks were highly structured, moderately specialised and significantly modular regardless of size. The strongest hubs were *Baccharis* plants, *Apis mellifera, Bombus funebris,* and Diptera spp., which were the most ubiquitous and abundant species with the longest phenologies. Species strength showed a strong association with the modular structure of plant-pollinator networks. Hubs and connectors were the most centralised participants in the networks and were ranked highest (high generalisation) when quantifying specialisation with most indices. However, complimentary specialisation d' quantified hubs and connectors as moderately specialised. Specialisation and topological roles of species were remarkably constant across some sites, but highly variable in others. Networks were dominated by ecologically and functionally generalist plant species with open access flowers which are closely related taxonomically with similar morphology and rewards. Plants associated with hummingbirds had the highest level of complimentary specialisation and exclusivity in modules (functional specialists) and the longest corollas.

Conclusions We have demonstrated that the topology of networks in this tropical montane environment was non-random and highly organised. Our findings underscore that specialisation indices convey different concepts of specialisation and hence quantify different aspects, and that measuring specialisation requires careful consideration of what defines a specialist.

Key words: Asteraceae, *Baccharis,* floral traits, plant-pollinator networks, modularity, specialisation, *Apis mellifera, Bombus funebris,* biodiversity hotspot, hummingbirds, topological roles, Peruvian Andes.

INTRODUCTION

Ecological interactions between plants and their flower visitors are fundamental to the ongoing function of both natural and agricultural ecosystems (Klein *et al*., 2007; Ollerton *et al*., 2011). In the past decade network approaches have been developed that enable ecologists to probe these interactions in ever more detail, introducing many new indices to describe network topology, quantify the degree of specialisation between partners, and assess network stability, robustness and ecosystem function (Memmot *et al*., 2004; Fortuna and Bascompte, 2006; Dormann *et al.*, 2009).

Understanding the topology of ecological networks is fundamental when interpreting community and ecosystem responses to global change (Fortuna *et al*., 2010), and there is growing recognition of network structure, such as the distribution of strong and weak links and the presence of compartments or modules (Ings *et al*., 2009). Modularity is a ubiquitous and important structural property of ecological networks which describes the relationship between interacting species and gives insights into the dynamics of ecological communities. In modular networks subsets of species interact more frequently with each other than with species in other modules (Newman, 2004; Olesen *et al*., 2007).

The advent of sophisticated algorithms and indices for the analysis of quantitative networks also allows for comparisons of network-wide specialisation and modularity among communities with differing species richness (Dormann and Strauss, 2014; Schleuning *et al*., 2014; Martín González *et al*., 2015). In addition to comparisons of modularity among entire communities, each species can be classified into different functional roles according to their position within and among modules (Olesen *et al*., 2007; Martín González *et al*., 2012). For instance, module hubs are highly connected generalist species linked to many species within their own module, while connectors are species linking several modules. Network hubs are

generalist species, acting as both connectors and module hubs, and are thus important to the cohesiveness of both the network and its own module. Peripheral species are specialists, have few links, and are linked almost exclusively to species within their module (Olesen *et al*., 2007; Martín González *et al*., 2012).

Modularity tends to prevail towards the tropics in areas of high contemporary precipitation (Dalsgaard *et al*., 2013; Schleuning *et al*., 2014). Specialisation may also be expected in species rich tropical communities, given that more feeding niches may become available and inter-specific competition may increase (e.g. Dalsgaard *et al*., 2011; but see Ollerton and Cranmer, 2002; Schleuning *et al*., 2012; Moles and Ollerton, 2016). However, although modularity may be regarded as a sign of interaction specialisation, it does not necessarily involve highly specific links but rather a discrete partition of interactions among species in the network (Martín González *et al*., 2015). Ecological processes thought to shape network patterns and influence modularity include seasonal resource fluctuations, overlapping phenological schedules in highly seasonal climates, high productivity and resource diversity (Bosch *et al*., 2009; Martín González *et al*., 2012, 2015, Schleuning *et al*., 2012, 2014), and plant and animal traits (Donatti *et al*., 2011).

In this study we use a new method to detect modularity and to describe species' roles across nine valleys in the Peruvian Andes, investigating modularity, topological roles of species and specialisation of plant-pollinator communities. Specifically we addressed the following questions: (1) Network level traits: how are the regional plant-pollinator networks structured in terms of interaction specialisation and modularity? (2) Species level traits: which species have important topological roles in the networks (i.e. network and module hubs), does their position change across valleys, and are there similarities in module composition of widespread species among valleys?

(3) Dominant species: do widespread plant and pollinator species share similar traits, and is there evidence of taxonomic and functional clustering across valleys? (4) Generalists and specialists: are network hubs generalist, widespread species and do peripheral species such as hummingbirds tend to be more specialised? Are species consistently generalised or specialised across valleys?

MATERIALS AND METHODS

Study sites, sampling design and species traits

The Vilcanota Highlands of southeastern Perú contain a unique flora and fauna with high levels of diversity and endemism (Wege and Long, 1995; Stattersfield *et al*.,1998). A ten year study of the flora of this region in several ecosystems and life zones (2700m -4900m), revealed 145 plant families, 450 genera and 871 species (Tuypayachi, 2005). Despite being a biodiversity hotspot, no previous work has examined plant-pollinator networks in the region. Fieldwork was carried out in nine valleys of the Sacred Valley of the Incas, this region lies 60km north of the city of Cusco. These valleys differ in their development from valley floor to snow level in terms of river volume, amplitude, width and human occupation. Therefore the life zones are not uniform (Tuypayachi, 2005). Surveys were conducted between the villages of Pisac, Ollantaytambo and Chillca, in the provinces of Calca and Urubamba, Department of Cusco. The study sites spanned an area of ca. 60km in length along the Urubamba river, from Huaran to the eastern limits of the Historical Sanctuary of Machu Picchu at Piscacucho, situated between (13° 13'S, 72° 2'W and 13° 12'42' S, 72° 21' 41 W). The vegetation is dominated by deciduous shrubs, abundant annual herbs, small trees, spiny shrubs and stunted Elfin forest. The canopy is generally not tall and is mostly present in subtropical humid montane, comprising of approximately 10% of the vegetation. *Alnus acuminata* (Betulaceae) has a restricted distribution, surviving only as a few individuals strewn in steep ravines and along water courses. *Passiflora* grow in *Alnus* stands but was too

high up to include in surveys. *Myrcianthes oreophylla* (Myrtaceae) and *Escallonia resinosa* (Grossulariaceae) trees are small enough to survey at head height. *Eucalyptus* plantations were not present in transects and only the understory of *Polylepis* (Rosaceae) forests was surveyed given that *Polylepis* is a wind pollinated species. Anthropogenic pressures include livestock farming, agriculture, overgrazing, wide-spread planting of *Eucalyptus* and pine and the extraction of *Polylepis* wood by rural communities. A total of 390 honey bee hives are owned within the Sacred Valley, with an average of ten hives per keeper (The Association of Beekeepers, Urubamba, Department of Cusco, pers. comm.).

Transects

In each of the nine valleys we established ten transects covering a total altitudinal range of 1150 m. Each transect was subdivided at each altitude into two 500 x 3m sampling areas, running parallel either side of established trails and were marked with ten points at intervals of 50m.The topography of the mountain chain dictated where transects started and finished, and whether they were orientated horizontally across or vertically up the valleys. A total of 90 transects were surveyed once during the dry season, between April and October 2002 at five different altitudes and across different life zones (as defined by Holdridge, 1967) (Fig.1). Sampling effort focused on one valley at a time, rather than spreading the effort across all sites due to the logistical constraints encountered covering such a large sampling area. The order in which each transect was walked in each of the valleys was determined using random numbers (1-5), so that the timing of the transect surveys across valleys and elevations minimised biasing the results. Transects correspond approximately to the following life zones: subtropical montane thorn steppe (2700-3200 m; sampled between 3147 and 3235 m), subtropical montane dry forest (3000-3400 m, sampled 3351-3424 m), subtropical humid montane forest (3500-3800 m, sampled at 3653-3746 m) and *Polylepis* forests (the majority of the ca. 30 species are classified as vulnerable (IUCN, 2010) (3700-

4200 m, sampled at 3846-4003 m) (see Fig. 2 for plants and habitats). Surveys were undertaken between 08:00-17:00 h mostly under favourable conditions for a total of 90 h. Two observers slowly walked each 500 m transect belt (one surveying the left side of the trail and the other surveying the right side) for 60 minutes, recording only those visitors that while foraging for pollen and/or nectar made contact with either anthers or stigmas, i.e. potential pollinators. Those insects that could not be identified in the field were captured and deposited individually into labelled vials for later identification or assignment to morphospecies. Most bee and syrphid fly species were identified to species or genus; other groups were usually identified to family and assigned to morphospecies categories. Functional taxonomic groups of flower visitors (sensu Fenster *et al*., 2004; Ollerton *et al*., 2007) were identified as follows: Diptera were divided as Syrphidae, Tachinidae, and all other Diptera. Hymenoptera were divided as all other solitary bees, *Bombus* spp., Vespidae and *Apis*. Voucher specimens of insects and plants are retained at the University of San Antonio Abad, Cusco, Perú. Hummingbirds were identified in the field using the field guide *Birds of the High Andes* (Fjeldså and Krabbe, 1990).

Body length for 5-10 insects captured on flowers was measured representing the main functional groups (see Table 5). Measurements of hummingbirds' bills were taken from mist-net data collected in the field and from the literature. Corolla length for 10-20 flowers of each plant species was measured from the base of the calyx to the flower aperture using a digital calliper in the field. Plant species were identified using (Gentry, 1996) and with help from the staff from the Herbario Vargas, Universidad Nacional de San Antonio Abad del Cusco, Perú. Plants were assigned to floral traits and nectar was assessed following Ollerton and Watts (2000).

Data analysis

Data represent interaction frequency matrices for nine valleys. Cell values indicate the frequency of interaction between species pairs, and cells with zeros indicate no interaction. For each of the nine valleys, matrices of interaction between *P* plant and *A* pollinator species were created by pooling data across the altitudinal gradient (1-5) then each matrix was analysed separately. Additionally, we constructed the following two matrices: (1) Full matrix: a single plant-pollinator (*A x P*) network pooling all the data from nine valleys across the altitudinal gradient (110 plant and 143 pollinator species), (2) Reduced matrix: a single plant-pollinator (*A x P*) matrix (same as 1) but which excluded species with fewer than two interactions in at least two valleys. This exclusion reduced the total number of species to 26 plants and 39 pollinators. We used the R-package bipartite 2.03 (Dormann *et al*., 2009) to calculate all network indices. At the network level, we calculated complementary specialisation H_2' and quantitative modularity (QuanBiMo: Dormann and Strauss, 2014). At the species level we used five measures to quantify specialisation (species degree, weighted closeness, species strength, pollination service (*PSI*), and complimentary specialisation *d'*). We then focused on three widespread abundant species across valleys: the honey bee (*Apis mellifera*; Apidae), a bumblebee (*Bombus funebris*; Apidae) and the hummingbird (*Aglaeactis cupripennis*; Trochilidae) to illustrate how the indices reflect the actual degree of specialisation (niche partitioning between species), by contrasting observed visitations with expectations from a null model. These three species were selected because they were present in most valleys and at many altitudes so the sample sizes were sufficient. The measures of specialisation chosen are suitable for comparisons across networks (Dormann, 2011). We chose these particular species because *Apis mellifera* is an introduced species reported in the literature to be a super generalist and hence likely to have a strong impact on network structure (Dupont *et al*., 2003). Similarly, some *Bombus* spp. are reported as generalists (see

Dormann, 2011) and hummingbirds are predicted as specialists (Sonne *et al*., 2016). Thus, this presented an excellent opportunity to compare these predictions with our data. All statistical analyses were performed using R, version 3.1.0 (R Development Core Team, 2014). All means are ± SD and medians are indicated as required.

Network-level metrics

Quantitative modularity (QuanBiMo) (Dormann and Strauss, 2014) computes modules in weighted, bipartite networks. This algorithm follows the approach of Clauset *et al*., (2008) based on a hierarchical representation of interaction frequencies and optimal allocation of species into modules. A module is defined by species having more interactions within the module than among modules, thus modularity is the result of some degree of specialisation in species interactions (Martín González *et al*., 2015). Modularity Q ranges from 0 for randomly configured networks to 1 for networks composed of perfect modules. We searched for the best organisation of each network into modules in the best of five independent runs of the QuanBiMo algorithm following Schleuning *et al*., (2014). If no further improvement was recorded after 10^8 swaps, the run was terminated and the result interpreted as the optimum. QuanBiMo can be invoked recursively, searching for modules within modules (see Dormann and Strauss, 2014). Thus, to identify nested module structure at the highest level, we performed a separate modularity analysis focusing on hummingbirds using 10^6 steps. To determine whether hummingbirds and their plants were consistently ascribed to the same modules, we checked module identity by repeating the analysis 50 times and recorded the distribution of plants and hummingbirds across modules each time, following Gómez *et al*., (2013). To account for Q's dependence on network size and sampling intensity (Dormann and Strauss, 2014) absolute values were corrected using null models based on the random placement of interactions observing the same marginal totals (Patefield, 1981). Corrected

modularity *Q* was calculated as the difference between the value of the empirical network and the mean value obtained from 100 null models for QuanBiMo (Schleuning *et al*., 2014; Martín González *et al*., 2015).

To identify species with importance for modularity, *c*- and *z*- values were calculated for all species based on the number of links, where *c* refers to the even distribution of links within and across modules and *z* refers to the number of within-module interactions (Guimerà *et al*., 2005). Critical *c* and *z* values proposed by Olesen *et al*., (2007) were defined for binary networks and we thus adapted their approach by calculating weighted versions of *z* and *c* using species strength instead of species degree (*sensu* Bascompte *et al*., 2006). To objectively define thresholds we ran 100 null models for original networks and employed 95% quantiles as critical *c*- and *z*-values.

Complementary specialization H_2' (Blüthgen *et al*., 2006) is a network level index which measures the degree of complementary specialisation (or exclusiveness) of the interactions at the level of the entire matrix. Specifically, it quantifies the deviation of observed interactions from those expected given the species' abundances or interaction frequencies (measured as species' marginal totals), so that the more exclusive the interactions, the larger is the H_2' value for the web. Complimentary specialisation H_2' ranges from 0 for the most generalised networks to 1 for a completely specialised network. As H_2' accounts for variability in the species' total observation frequencies it can be used directly to make cross-network comparisons despite variation in total frequencies among communities (Blüthgen, 2010).

Species-level indices

Species' Degree (qualitative measure) (Jordano *et al*., 2003) is the number of species to which a species is linked. Degree is calculated based on a binary interaction matrix and thus describes specialisation in a qualitative way. Specialists have lower degree than generalists.

Complimentary Specialisation *d'* (Blüthgen *et al*., 2006) is a species-level specialisation index related to complimentary H_2' which estimates the complementarity of interactions based on the standardised Kullback-Lieber divergence (= relative entropy). As H_2' for the entire web, the complimentary d' index determines the extent to which the interaction specialization of a focal species may differ from null-model expectations in which species interact with partners in proportion to their availability, again measured as species' marginal totals (Blüthgen *et al*., 2006). It ranges from 0 (no specialisation) and 1 (perfect specialisation).

Species Strength (Bascompte *et al*., 2006). The strength of a species is defined as the sum of dependences of the plants relying on an animal or the animals relying on a plant. It is a measure of the importance of this animal from the perspective of the plant set and vice versa. This measure is a quantitative extension of the species degree, which is the number of interactions per species in qualitative networks (Jordano *et al*., 2003). The higher the value, the more generalised e.g. a plant species is, because more pollinator species depend on it (and vice versa).

Pollination Service Index (*PSI*) (Dormann, 2011) estimates the importance of a pollinator for all plant species; is hence an extension of the idea of species strength. Put simply, it measures the probability that *intraspecific* pollen is transferred to plant species *i*. This depends both on the proportion of visits a pollinator pays to species *i* and on the number of

pollinators that visit *i.* For *PSI*, importance of a pairwise interaction (for the plant) is calculated as: 'dependence' *i* on *j* multiplied by per visit efficiency *i* visited by *j*, where per visit efficiency *i* visited by *j* = (average proportion visits to *i* by *j* in all visits by *j*) ^ß. It assumes that the order of plant species visited is random (no mixing, no constancy). To account for that not being true, ß could be adjusted. We envisage a penalty for the fact that a pollinator has to make two (more or less successive) visits to the same plant species: the first to take the pollen up, the second to pollinate the next. Thus, using ß=2 as an exponent in step 1 would simulate that a pollinator deposits all pollen at every visit. In a sense, ß=2 represents a complete turnover of pollen on the pollinator from one visit to the next; only the pollen of the last-visited species is transferred. That is certainly a very strong penalisation. At present we set the exponent to ß=1, because the step of controlling for "pollen purity" is already a major improvement. It assumes, implicitly, that pollen is perfectly mixed on the pollinator and hence pollen deposited directly proportional to frequency of visits to the different plants. Also, the extent to which pollen gets mixed and/or lost during foraging flights is unknown, and hence the true exponent remains elusive. For a value of ß = 0, *PSI* simplifies (and is equal) to species strength. At its maximum, *PSI* = 1, it shows that all pollen is delivered to one plant species that completely depends on the monolectic pollinator. At its minimum, *PSI* = 0, it indicates that a pollinator is irrelevant to all plant species. To any of the target species: accounting for the proportion of pollen actually delivered (due to floral constancy, irreversible pollen compaction, pollen viability, etc.) by a modifying exponent, beta. A value of 1 (the default) makes pollen deposition proportional to the number of same-species visits, while a value of 2 would require the pollinator to have come from the same species the exact previous visit. We acknowledge that species will differ substantially in their beta-value, and at present use *PSI* largely as an index of pollen-purity-at-visit.

Weighted closeness centrality measures the proximity of a node to all other nodes in the network (Freeman, 1979) based on path lengths to other nodes, and has been proposed as measure of generalisation in pollination networks by Martín González *et al*., (2010) as it measures the connectivity of the entire community. Thus, for each individual species we measure its connectivity to all other species in the community and then average all the individual connectivities in order to obtain a value that describes the entire community. Weighted closeness centrality (Opsahl *et al*., 2010) calculates closeness, but based on weighted representation of the network. Low closeness scores indicate specialisation and high closeness scores indicate nodes (pollinators) are more "central", e.g. closer to all other species in the network.

As raw values for network indices may be affected by species frequencies and sampling intensities, network metrics were compared with an appropriate null model. We generated 1000 null models using the Patefield algorithm (Patefield, 1981) (method *r2d* implemented in the bipartite package of R), which generates null models with marginal totals identical to those of the observed matrix (see Blüthgen *et al*., 2008; Dormann *et al*., 2009). This null model redistributes interaction events among all the cells in the network randomly, while constraining the total number of interactions per species. It assumes that species interact randomly, without constraining the degree of specialisation in a network.

Following Ollerton *et al*., (2007) we categorised the plants according to their level of functional and ecological specialisation/generalisation. "Functional" refers to the number of functional groups (often higher taxonomic groups such as family) of pollinators which service a plant. "Ecological" refers to the species richness of pollinators. Clearly for both of these categories there is a continuum between specialisation and generalisation: for the purposes of this analysis we define a functional specialist as one that is pollinated by only a

single higher taxon (e.g. Trochilidae or Apidae); a strict ecological specialist is one that is pollinated by a single animal species.

RESULTS

A total of 1583 flower visits to 110 plant species from 143 animal species and morphospecies were recorded across all 9 valleys (Table 1). When pooled across all sites we observed a total of 719 species-species links. Thirty-three plant families were recorded, of which Asteraceae (43 species) was the most frequently visited family, receiving 65% of total visits, followed by Lamiaceae (10%) and Myrtaceae (6%). The highest diversity of flower visitors was on the dioecious flowers of *Baccharis*, receiving 29% of all visits by a total of 73 pollinator species. The most frequent flower visitors belonged to the orders Diptera (48%), Hymenoptera (33%), Coleoptera (8%), Trochilidae (6%) and Lepidoptera (5%). *Apis mellifera* dominated the bee fauna (26%) while Vespidae comprised less than 1% (see Tables S3 and S4 in Supplementary Data for a full species list of plants and pollinators).

Network complimentary specialisation (H_2') and modularity (Q)

All networks were significantly different from null models ($P < 0.0001$) (Supplementary Data Fig. S1), most of them being also moderately specialised (mean $H_2' = 0.39 \pm 0.10$). Huaran was the most specialised site ($H_2' = 0.58$). All networks were more modular than expected from null models and showed very low variability in Q among runs (Table 2). Q was positively correlated with the number of modules detected at each site (Pearson's correlation: $t = 2.83$; $r = 0.53$; $P = 0.02$). Q was negatively correlated with honey bee abundances across sites (Pearson's correlation: $t = -2.90$; $r = -0.73$; $P = 0.02$) but not with H_2' (Pearson's correlation: $t = -0.73$; $r = 0.26$; $P = 0.48$). Q and H_2' index values for the reduced matrix were similar to the other nine networks, suggesting that deleting species with fewer than two interactions in at least two valleys had little effect on index values (Table 2).

The role of individual species and functional groups in the network structure

The roles of functional groups and plant families in network structure across valleys are presented in Table 3. Hymenopterans and plants from the family Asteraceae played the most important topological roles (i.e. were network hubs, module hubs and connectors) across networks. The majority of species were peripheral (83%), with most of their links within their own module (Table 3, Figs. 3 and 4). Species strength was positively related to weighted measures of *c* and *z* values, particularly *z* values (*z* values: $r = 0.48$, $P < 0.000001$; *c* values: $r = 0.05$, $P < 0.00001$). Thus species with high species strength have many interactions within their own module. By contrast, *c* values, where *c* refers to the even distribution of links within and across modules, although significant, the correlation was very weak. Only 29 pollinator species (20%) and 19 plant species (17%) exceeded the threshold for *c*-values and *z*-values to be considered hubs or connectors. The strongest network and module hubs were *Baccharis* plants, *Apis mellifera, Bombus funebris,* and Diptera spp.; the most ubiquitous and abundant species with the longest phenologies, found at all altitudes, present in most valleys and covering several life zones (Supplementary Data Tables S1, S2, S3 and S4). Just three plants, *Baccharis salicifolia, Baccharis buxifolia* and *Jungia rugosa* (Asteraceae) and two flower visitors, the honey bee *Apis mellifera* and Syrphidae sp.2 exceeded both thresholds in eight valleys, and were thus network hubs (Supplementary Data Tables S1 and S2). Connectors were both plant and insect/bird species in approximately equal proportions. Introduced honey bees were hubs in 60% of networks, or acted as module hubs, i.e. species with many interactions within their own module (low *c*, high *z*), or connector species, i.e. linking several modules (high *c*, low *z*) in the remaining networks (see Supplementary Data Table S1). The bumblebee *Bombus funebris* was a module hub and connector in two networks. Syrphids (Diptera) were consistently connectors, while Lepidoptera, Coleoptera and Trochilidae were mostly peripheral. These functional groups had *c* and *z* values close to zero and were specialists, i.e., they had only a few links and almost always only to species

within their module. Lepidoptera, Coleoptera and Trochilidae were observed quite frequently across most valleys and at most altitudes (Table1, Supplementary Data Table S4). Across networks, the majority of interactions aggregated around two hub and two plant connector species belonging to the family Asteraceae (78%) (Fig. 4 and Supplementary Data Table S2, S3 and Figs S6 and S7). As with pollinators, plants changed roles across networks.

Module composition

A total of 69 modules were detected when summing the number of modules recorded in each of the nine valleys (see Table 2). Seventy percent of all those modules contained Diptera and 26% of all modules were isolated species groups without any links to the remaining network (z values = 0); of those, more than a quarter were hummingbirds (see Figs 3 and 4). Complementary specialisation d' for hummingbirds was significantly higher than all other functional groups of flower visitors (Wilcoxon signed rank test with continuity correction v = 50, $P < 0.01$) (Fig. 5A). Likewise, corolla length of flowers visited by hummingbirds was significantly longer than flowers visited by all other functional groups of flower visitors (Wilcoxon signed rank test with continuity correction $v = 273.5$, $P < 0.0001$) (Fig. 5B). Seven modules were exclusively represented by hummingbird species and the plant species they interacted with across valleys. The module identity of hummingbirds and plants was 100% consistent when the analysis was repeated across 50 independent algorithm runs (i.e. for each matrix, the same plants and hummingbirds were always members of the same module) (Table 4, Fig. 4 and Supplementary Data Fig. S7). Taxonomic and functional clustering in module composition was evident across sites. Modules consistently formed around similar hub plant and pollinator species mostly at the level of orders, but in some cases at the level of genus. Sets of interacting species which were repeatedly associated across valleys include the hummingbird *Aglaeactis cupripennis* which interacted with *Barnadesia horrida* (Asteraceae) in the same modules 75% of the time. *Apis mellifera,* which interacted in the same modules

with *B. buxifolia* and *Minthostachys spicata* (Lamiaceae) in 80% of cases, and in the same modules as *Myrsianthes oreophila* (Myrtaceae) in 67% of cases. *Bombus melaleucus* (Apidae), which interacted in the same modules with *Escallonia resinosa* (Grossulariaceae) 75% of the time (see Table 4, Fig. 4 and Supplementary Data Figs S6 and S7).

Morphological traits

The relevant morphological traits of plant families and functional groups of pollinators are presented in Table 5. There was significant variation among groups for the median number of pollinator species visiting flowers with different morphologies (χ^2= 7.841, $P < 0.05$) with up to 57 species visiting plants with open tube morphology. However, a Bonferroni adjustment for the six comparisons rendered this finding non-significant (Fig. 6). Thus, bowl shaped flowers or flowers with tubular, flag or gullet shaped corollas were not visited by significantly more species than flowers with open access tubular flowers. Hub, connector and peripheral insect flower visitors had short to medium mouthparts allowing easy access to both pollen and nectar to a wide range of corolla lengths. Peripheral, hub and connector hummingbirds had short to long bills (Table 4), which together with tongue maximal extension beyond bill tip (Watts *et al*., 2012) allowed legitimate and non-legitimate access to nectar from a wide range of corolla tube lengths (6 to >100 mm) (Fig. 5B). The majority of hub and connector plants (*Baccharis, Ageratina, Aristeguietia,* and *Jungia*) have numerous open tube flowers characterised by a head of small ray and disc flowers 5–10mm in length. The stamens and pistels are exposed, which allows easy access to pollen, while the corolla tubes are short enough to allow access to the small amounts of nectar contained at the base. The remaining connectors had small white tubular flowers (5-6 mm), or open dish or open bowl flowers which permitted easy access to the reward for a wide variety of flower visitors (see Table 5, Fig. 2B for *B. salicifolia* and Supplementary Data Table S2 for hub and connector plant species).

Specialisation indices and the role of individual species in the network structure

Network and module hub pollinators were ranked highly when quantifying species degree, species strength, weighted closeness and pollination service index (*PSI*) (Supplementary Data Tables S1 and S2). The strongest network and module hubs were the most centralised participants in the networks (high ranking weighted closeness values indicating generalisation). However, complimentary specialisation d' quantified network hubs, module hubs and connectors as moderately specialised: $d'_{flw.\ visitors} = 0.42 \pm 0.18$; $d'_{plants} = 0.43 \pm 0.16$). Thus, in some cases, although network hubs such as *Sciaria* sp.4 yielded high species degree and weighted closeness values (high generalisation), when measuring specialisation in terms of exclusiveness of interactions complimentary specialisation d' indicated a significant amount of specialisation (see Table S1). The *PSI* index also yielded relatively high values and rankings suggesting that network hubs and modules hubs were potentially important pollinators for the plant in the networks. Similarly, the same high rankings were also found for network and module hub plants when calculating specialisation indices (Supplementary Data Table S2). The strongest connector plant species (species linking several modules) also yielded high rankings for specialisation indices and were the most centralised participants in the networks (*Jungia rugosa* at Poques, *M. spicata* at Piscacucho and *M. oreophila* at Mantanay). The remaining connector species were still relatively central in the networks, but specialisation indices values and their rankings were lower than for hub species (Supplementary Data Tables S1 and S2). Both plant and pollinator network hubs and module hubs were some of the most abundant in terms of visitation and their presence in transects.

Hubs and connectors were generally more abundant and widespread than peripherals, but not always (Supplementary Data Tables S3 and S4). In some valleys, honey bees were peripherals, but were ranked highest in terms of visitation (Table 1). Similarly, *B. salicifolia* was the most visited plant in Pumamarca (46 visits), but was classified as a peripheral.

Hummingbird complimentary specialisation d' values indicated a relatively high level of specialisation ($d'_{flw.\ visitors}$ = 0.61 ± 0. 23; d'_{plants} = 0.60 ± 0.19). In 95% of cases, $d'_{flw.\ visitors}$ values were significantly different from null models. Likewise, d'_{plants} also yielded high values; in 74% of cases values were significantly different from null models (Table 4). At Huaran, the most specialised hummingbird *Aglaeactis castelnaudii* interacted within its own module with the most specialised plants, whereas the most generalised hummingbird *Metallura tyrianthina* interacted with the most generalised plant *Aegiphila mortoni* (Verbenaceae). At Chicon, module 2 included the addition of Diptera sp.11 and Hymenoptera sp.5 visiting plants to collect pollen (Table 4, Supplementary Data Fig. S6).

A summary of observed species level specialisation index values for the most relevant functional groups of pollinators are shown in Table S5 (Supplementary Data). Figures S2, S3 and S4 (Supplementary Data) show five specialisation indices and the position of the observed values relative to the null models for three widespread abundant species across valleys: *A. mellifera*, *B. funebris* and *A. cupripennis.* These represent random realisations of a perfect generalist. Thus, when the observed value is within the histogram of null models, species are classified as generalist. Honey bees were moderately specialised, but this was not consistent across sites (i.e. Choquebamba and Poques, Supplementary Data Fig. S2). The bumblebee *B. funebris* was the most generalist flower visitor; the observed values were consistently within the histogram of null models across most valleys (Supplementary Data Fig. S3). *Aglaeactis cupripennis* was the most specialised; the observed values were consistently on one side of the histogram, indicating consistent specialisation across valleys (Supplementary Data Fig. S4). The indices and null model correction can be used to further highlight these irregularities. The raw data, the difference between observed and mean null model values, and *z*-scores for five specialisation indices (degree, strength, *PSI*, weighted centrality and complimentary specialisation d') are presented in Supplementary Data Fig. S5).

The inconsistency for honeybees is reflected in the height of the summary box plots, for which *d′* is very small for *B. funebris* (always a generalist) and considerably larger for *A. mellifera* (sometimes a generalist, sometimes a specialist).

1 DISSCUSSION

2 In this work we investigated modularity, topological roles of species and specialisation of
3 plant-flower visitor networks in the tropical Peruvian Andes. Our results showed that all
4 plant-pollinator networks were highly structured, deviating significantly from random species
5 associations. For the network-wide complimentary specialisation index H_2', null models
6 were unable to capture the observed structure of networks, suggesting a network property
7 inexplicable merely from species abundances. Plant-flower visitor networks, especially those
8 containing hummingbirds, showed moderate to high levels of specialisation (or exclusiveness
9 of interactions) and modularity. Modularity was higher in networks where *A. mellifera*
10 numbers were generally lower, suggesting that in some sites subsets of species interact more
11 frequently with each other than with species in other modules where honey bees are less
12 dominant. All networks were significantly modular, regardless of size, which contrasts with
13 reports that networks with < 50 species were never modular (Olesen *et al*., 2007). This
14 incongruence may result from a lack of detecting power of the algorithm used by previous
15 studies at low network sizes (e.g. Guimerà *et al*., 2005; Olesen *et al*., 2007). On the other
16 hand, the new QuanBiMo algorithm is more sensitive and also more specific than current
17 binary algorithms (Dormann and Strauss, 2014).
18
19 On average, modularity in the nine valleys was neither high nor low and networks were only
20 moderately specialised. Observed modules represent communities of pollinators and plants
21 which were active in the same season. The networks were dominated by ecologically and
22 functionally generalist plant species which are closely related taxonomically (e.g. *Baccharis*,
23 *Ageratina* and *Aristeguietia*) with similar morphology and rewards. These plants exhibited
24 high plasticity by changing their topological roles across sites and serving as either network
25 hubs in some valleys, or switching to module hubs or connectors in other valleys
26 (Supplementary Data Table S2). Thus, our networks were structured mainly by hubs and

connector plants and pollinators which were functionally and ecologically equivalent. Asteraceae plant hubs were ubiquitous and abundant in most valleys; they flowered throughout the season and were present at each altitude and most life zones. A similar pattern was also evident for the dominant pollinators such as *A. mellifera,* Syrphid sp.2*, Sciaria* sp.4 (Diptera) and *B. funebris*. Such pollinators have the ability to "fill the gap" by changing topological roles, for example, where honey bees were less common (Pumamarca), bumblebees replaced them as module hubs. The weighted modularity analysis (which accounts for sampling bias with null-model corrections) also showed that modules were comprised of both plant hubs and flower visitor hubs, with more insects and hummingbirds than plants acting as hub or connector species. This is in contrast with other studies (Dupont and Olesen, 2008), where no insect species served as hubs and the majority of connectors were insects, or where all hubs were plant species (Bosch *et al*., 2009). Only 48 (19%) of all species played a significant role in shaping network structure, while the majority of species were peripheral, in line with other studies (Olesen *et al*., 2007; but see Bosch *et al*., 2009). In each network, plant, insect and hummingbird species served as connectors in equal proportions, suggesting they play an important role in linking different modules or by gluing peripheral species together into modules. Across networks, most modules were dominated by dipterans and social bees, particularly introduced honey bees. Taxonomic and functional clustering was also evident across sites, with some plant species and functional groups of flower visitors repeatedly associated. This further supports the conclusion that the topology of networks is non-random and highly organised.

The networks in the Sacred Valley were dominated by open-access flowers, which were visited by many small to medium sized insects, with few morphological restrictions for the insects to access the reward. This is in accord with findings of Kaiser-Bunbury *et al*., (2014), who also reported that flowers with a low complexity showed weak constraints in floral

resource accessibility and interacted with most pollinator species. Moreover, some hummingbirds, bees and syrphids were still able to access such flowers by robbing nectar and pollen. The highest diversity of flower visitors was on the dioecious flowers of *Baccharis*, which is not surprising given that the genus has the richest galling fauna of the neotropics (Boldt and Robbins, 1990), and the highest diversity of visiting flies (Souza-Silva *et al*., 2001). The abundance of dipterans on *Baccharis* plants may not only signify the importance of the flowers in their diet, but also their importance as potential pollinators, and hence play an important role in ecosystem function (Souza-Silva *et al*., 2001). This suggests that species strength and specific dietary requirements of functional groups, influences module structure in the Sacred Valley. Our networks were dominated by ecological and functional generalist plants, which were probably pollinated by whatever flower visitors were a suitable size and shape, and had appropriate behaviour.

Earlier binary modularity studies which implied that network hubs, module hubs and connectors are generalist species (e.g. Olesen *et al*., 2007) did not evaluate this using quantitative specialisation indices and null models. This study is one of the few to measure the level of specialisation for individual species with important topological roles within and across networks using quantitative data. We found that the strongest network hubs, module hubs and connectors were the most centralised participants in the networks and were ranked highest when quantifying specialisation across the five different (species level) specialisation indices. Moreover, many of these species were consistently the most centralised participants across networks, suggesting a high level of generalisation. Both plant and pollinator network hubs and module hubs were also the most abundant in terms of visitation and presence in transects. In contrast though, network hubs, module hubs and connectors all showed a moderate degree of specialisation (or exclusiveness) when measuring specialisation using complimentary specialization index d', and a few species were highly specialised. This

finding is in contrast with Olesen *et al*., (2007) who found that network hubs and connectors (i.e. species with both high *c* and *z* scores) were super-generalists. These differences are likely to be attributed to the SA algorithm (see Guimerà *et al*., 2005; Olesen *et al*., 2007) which analyses each trophic level separately and to the fact that in Olesen *et al*.'s study interactions are binary whereas in our study we use interaction strength. Finally, species strength is closely related to species abundance (Bascompte and Jordano, 2007) and was positively related to weighted measures of within-module degree. This suggests that species strength and factors relating to abundance were the main determinants of the modular structure of plant-pollinator networks, in concordance with Schleuning *et al*., (2014). In contrast, the relationship between species strength and the even distribution of links across modules, although significantly positive, was weak suggesting that links are not uniformly distributed among all of the communities.

In the Sacred valley, specialisation varied along a continuum between moderate generalisation to moderate specialisation, concurrent with other work (Waser *et al*., 1996; Johnson and Steiner, 2000). One interesting finding was how much the specialisation of some species changed across sites, and how constant it remained in other species, a trend also evident in terms of the topological roles of plants and flower visitors. Across all seven sites where present, *B. funebris* was consistently a generalist flower visitor, but served as hub, connector or peripheral species. Degree is the number of plant links and is consistent with a strict definition of specialisation, but it makes no use of the number of visits recorded for each interaction. Surprisingly, although honey bees recorded the highest number of links and visits of all flower visitors, when describing niche properties, they showed a moderate degree of complementary specialisation (or exclusiveness of species interactions). These findings underscore that specialisation indices convey different concepts of specialisation and hence quantify different aspects (Dormann, 2011). Hummingbirds and the plants they visited had

the highest level of complimentary specialisation and exclusivity in modules (functional specialist). At the same time, the majority of plants visited and probably pollinated by hummingbirds (but see Watts *et al.*, 2012), were usually visited by several species of hummingbirds and so in that sense could be considered as ecological generalists. Yet again, this highlights that measuring specialisation requires careful consideration of what defines a specialist (Ollerton *et al*., 2007; Dormann, 2011).

The variability in specialisation described above could be attributed to any of a number of factors including: a response of flower visitors to low plant diversity at some sites (Schleuning *et al*., 2012), community and geographical context of plant populations (Ollerton *et al*., 2007), spatio-temporal variation in pollinator abundance (Johnson and Steiner, 2000; Watts *et al*., 2013), variability in pollinator distribution and morphology (Newman *et al*. 2014), geographical phenotypic variation (Cosacov *et al*., 2014), or variation in flower visitors and floral and pollinator community composition (Kaiser-Bunbury *et al*., 2014). Finally, the changes in specialisation across sites could also be explained by flower visitors switching to more rewarding plants throughout their activity periods.

A number of potential biases are important in to highlight. Since the pollinator assemblages studied were taxonomically very different in life histories, nesting preferences and behaviour, the transect census method undertaken may not have been appropriate to adequately characterise some of the taxa, particularly solitary bees and hummingbirds. For example, hummingbirds may have been under-represented in different samples because the composition and the relative abundance of hummingbird species is likely to be affected by their morphological-behavioural attributes, available resources, distributional/altitudinal limits or habitat affinities of a particular bird species and gradients in local climate (Borgella *et al*., 2001). Furthermore hummingbirds were easily disturbed from foraging by observers

walking transects and did not tend to visit many plants within the sampling area, but instead either remained on the periphery or in the canopy. However most parts of the valleys did not have a high canopy, thus we estimate that approximately 10% of plant-hummingbird interactions were missed from the canopy in subtropical humid montane forests. These plants include *Passiflora* spp. which climbs up trees such as *Alnus, Duranta* spp*., Fuchsia* spp. and *M. oreophila*.

Micro-climatic differences among these valleys and changes in weather along the altitudinal gradient may have affected local distributions of butterfly species. Flower visiting beetles can be inactive and infrequent visitors, whereas some small solitary bees are short-lived, have short flight ranges and are not easily detected (Gathmann and Tscharntke, 2002). For future work a number of alternative sampling designs might be incorporated in conjunction with the transect method to eliminate some of the potential biases such as data aggregation, one of which could have included fixed observation plots, which might also generate sufficient data to avoid pooling data.

In conclusion, during a single season snapshot in time, we have demonstrated that the topology of networks in this tropical montane environment was non-random and highly organised. Although we acknowledge that some taxa may have been under-represented in different samples and lacked sampling replication, the weighted modularity analysis (which accounts for sampling bias with null-model corrections) showed some remarkable consistency with many plant species and functional groups of flower visitors repeatedly associated. We used six different specialisation indices to show that in the Sacred Valley, specialisation varied along a continuum between moderate generalisation to moderate specialisation. Our findings also underscore that specialisation indices convey different

concepts of specialisation and hence quantify different aspects, and that measuring specialisation requires careful consideration of what defines a specialist.

SUPPLEMENTARY DATA

Supplementary data are available online at www.aob.oxfordjournals.org and consist of the following. Figure S1: Histograms for H_2' values for the analysis of each network. Figure S2: Histograms of observed and null model specialisation values of *Apis mellifera,* for the analysis of specialisation shift. Figure S3: histograms of observed and null model specialisation values of *Bombus funebris* for the analysis of specialisation shift. Figure S4: histograms of observed and null model specialisation values of *Aglaeactis cupripennis* for the analysis of specialisation shift. Figure S5: histograms showing specialisation index values (species degree, species strength, Pollination Service Index (*PSI*), weighted centrality (WC) and complimentary specialisation *d'*) for *Bombus funebris, Apis mellifera* and *Aglaeactis cupripennis*. Figure S6: Chicon featuring seven modules identified by QuanBiMo. Figure S7: Mantanay featuring seven modules identified by QuanBiMo. Table S1: Connection (*c*) and participation (*z*) values and complimentary specialisation *d'* for pollinators in 10 networks based on weighted strength from 100 null models. Table S2: Connection (*c*) and participation (*z*) values and complimentary specialisation *d'* for plants in 10 networks based on weighted strength from 100 null models. Table S3: Full list of plant species surveyed in the Sacred Valley. Table S4: Full list of pollinator species surveyed in the Sacred Valley. Table S5: Summary of observed species level specialisation index values for the most relevant functional groups of pollinators.

ACKNOWLEDGEMENTS

We thank Federico and Fatty Argandoña, Carmen Aparicio, Carlos Calvo, Rossemeri Cuéllar, Rosa and Herbert Duran, Juan Flores, Marcela Moreno Herrera, David Huamàn Ovalle, Ramon Ipanaque, Karin Nuñez, Berioska Quispe Estrada, Mireya Natividad Raurau Quisiyupa, Javier Saldivar and Celia Zuñiga for field assistance; the staff from Universidad Nacional de San Antonio Abad del Cusco, Perú; Permission to undertake fieldwork was granted by the Director of the National Institute of Natural Resources (INRENA)—Permit numbers: 008799 and 0001982. This research was self-funded by SW and by grants from The British Ecological Society, Idea Wild, The Biodiversity Trust, The Anglo Peruvian Society and The Leslie Church Bursary Fund of the University of Northampton.

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Table 1. Total number of flower visitors for each functional group in each of the 9 valleys starting from Huaran to the eastern limits of the Historical Sanctuary of Machu Picchu at Piscacucho, situated between (13° 13'S, 72° 2'W and 13° 12'42' S, 72° 21' 41 W).

	Apis	Lepidoptera	*Bombus*	Solitary bees	Diptera	Syrphidae	Tachinidae	Coleoptera	Trochilidae	Hemiptera	Vespidae
Huaran	40	0	3	0	4	8	1	0	26	0	0
Yanacocha	79	41	0	1	114	25	10	4	4	0	2
Chicon	104	4	5	1	26	20	4	10	33	0	0
Mantanay	47	5	20	2	12	32	21	5	19	0	0
Pumamarca	24	2	21	3	53	21	0	42	0	0	1
Choquebamba	7	0	19	1	84	24	3	14	1	15	3
Poques	29	5	10	0	50	43	4	37	0	0	3
Tiaparo	74	2	0	4	46	35	5	7	4	0	0
Piscacucho	24	14	4	0	22	61	14	16	0	0	0
Total	428	73	82	12	411	269	62	135	87	15	9

Table 2. Network modularity and complimentary specialisation H_2' for the 9 valleys and the combined networks (full and reduced matrices– see Methods). Modularity related measures given are (1) by the number of detected modules, (2) by observed modularity Q with its standard deviation across five independent algorithm runs and (3) by the null-model corrected modularities using Patefield algorithm (null model PA) (ΔQPA), given by Q – mean QNULL for the respective null model.

Networks	A	P	Network size	H_2'	Number of modules	Weighted Q	s.d.(w. Q)	PA	ΔQPA	Null model z score s.d.	P value
Huaran	16	8	24	0.59	5	0.39	0.01	0.25	0.14	6.26	<< 0.001
Yanacocha	51	22	73	0.37	6	0.37	0.00	0.12	0.25	6.95	<< 0.001
Chicon	32	18	50	0.46	7	0.35	0.01	0.17	0.18	6.00	<< 0.001
Mantanay	34	24	58	0.39	7	0.50	0.00	0.26	0.24	9.22	<< 0.001
Pumamarca	36	26	62	0.40	10	0.48	0.00	0.31	0.17	6.03	<< 0.001
Choquebamba	43	25	68	0.43	10	0.55	0.00	0.21	0.34	6.19	<< 0.001
Poques	47	32	79	0.26	7	0.46	0.00	0.39	0.07	2.94	< 0.01
Tiaparo	32	25	57	0.52	9	0.48	0.00	0.24	0.24	8.07	<< 0.001
Piscacucho	38	27	65	0.36	8	0.47	0.01	0.34	0.13	6.07	<< 0.001
Reduced matrix	39	26	65	0.27	5	0.30	0.00	0.13	0.17	22.52	<< 0.001
Full	143	110	253	0.31	9	0.31	0.00	0.10	0.21	5.46	<< 0.001

Table 3. The role of functional groups of pollinators and plant families in the nine networks. Numbers indicate the number of species per order. Species numbers do not add up to the total number of pollinator species (143) since some species acted as both network hubs, module hubs, connectors and periphery species depending on the site. Only those plant families with the most important topological roles are shown.

Order	Network hub	Module hub	Connector	Periphery	Valleys present
Coleoptera	0	1	3	25	8
Diptera	0	4	7	57	9
Hemiptera	0	1	0	0	1
Hymenoptera	1	3	3	16	9
Lepidoptera	0	1	1	13	7
Syrphidae	1	3	4	18	9
Trochilidae	0	1	1	7	6
Family					
Apocynaceae	0	0	1	0	2
Asteraceae	3	7	9	44	9
Gentianaceae	0	1	1	2	2
Lamiaceae	0	0	1	3	6
Myrtaceae	0	0	1	1	3
Verbenaceae	0	0	1	3	3

Table 4. Connection (*c*) and participation (*z*) values, complimentary specialisation *d′* for hummingbirds and their plant species in six networks based on weighted strength from 100 null models, identifying species with important topological roles in the networks and how they change across valleys. Frequency of each hummingbird and plant belonging to each module when the modularity analysis is repeated 50 times. Module ascription was always the same for each plant and pollinator (100% or 1.00) for each of the 50 runs.

Valley	Hummingbird species	*d′*	*c*	*z*	Network role	Module ascription	Frequency of belonging to each module	Plant species	*d′*	*c*	*z*	Network role	Module ascription
Huaran	*Metallura tyrianthina*	0.31**	0.47	0.15	Connector	Module 1	1	*Aegiphila mortoni*	0.26*	0.58	-0.54	Connector	Module 1
	Colibri coruscans	0.06 NS	0.00	-0.34	Periphery	Module 1	1						
	Oreonympha nobilis	0.51*	0.00	-0.71	Periphery	Module 2	1	*Barnadesia horrida*	0.73***	0.26	0.71	Periphery	Module 2
	Aglaeactis cupripennis	0.62***	0.06	1.14	Periphery	Module 2	1	*Duranta mandonii*	0.74 NS	0.00	-0.71	Periphery	Module 2
	Aglaeactis castelnaudii	1.00***	0.00	0.00	Periphery	Module 5	1	*Fuchsia apetala*	0.70 NS	0.00	-0.70	Periphery	Module 5
								Passiflora tripartita	0.86*	0.00	0.70	Periphery	Module 5
Yanacocha	*Metallura tyrianthina*	1.00***	0.00	0.00	Periphery	Module 6	1	*Barnadesia horrida*	0.74 NS	0.00	0.71	Periphery	Module 6
								Fuchsia apetala	0.58 NS	0.00	-0.70	Periphery	Module 6
Chicon ‡	*Aglaeactis cupripennis*	0.66***	0.03	2.13	Module hub	Module 2	1	*Gynoxys longiflora*	0.60***	0.27	0.63	Periphery	Module 2
	Aglaeactis castelnaudii	0.66*	0.00	-0.35	Periphery	Module 2	1	*Brachyotum nutans*	0.78***	0.00	1.07	Periphery	Module 2
	Pterophanes cyanopterus	0.45**	0.05	0.24	Periphery	Module 2	1	*Barnadesia horrida*	0.54*	0.00	-0.84	Periphery	Module 2
	Oreonympha nobilis	*0.52*	0.00	-0.76	Periphery	Module 2	1	*Puya ferruginea*	0.77***	0.00	0.86	Periphery	Module 2
	Oretrochilus estella	0.47 NS	0.00	-0.11	Periphery	Module 2	1						
Mantanay	*Metallura tyrianthina*	0.64*	0.00	-0.90	Periphery	Module 5	1	*Passiflora tripartita*	0.39 NS	0.16	-0.23	Periphery	Module 5
	Aglaeactis castelnaudii	0.80***	0.00	1.08	Periphery	Module 5	1	*Barnadesia horrida*	0.60***	0.14	1.02	Periphery	Module 5
	Aglaeactis cupripennis	0.50***	0.13	-0.18	Periphery	Module 5	1	*Duranta mandonii*	0.73*	0.00	0.49	Periphery	Module 5
						Module 5	1	*Siphocampylus actinothrix*	*0.62*	0.00	-1.28	Periphery	Module 5
Choquebamba	*Aglaeactis cupripennis*	1.00***	0.00	0.00	Periphery	Module 8	1	*Brachyotum nutans*	1.00***	0.00	0.00	Periphery	Module 8
Reduced	*Aglaeactis castelnaudii*	0.69***	0.00	0.28	Periphery	Module 4	1	*Barnadesia horrida*	0.61*	0.32	2.12	Module hub	Module 4
	Metallura tyrianthina	0.61***	0.00	-0.02	Periphery	Module 4	1	*Fuchsia apetala*	0.54*	0.00	-0.78	Periphery	Module 4
	Oreonympha nobilis	0.52*	0.00	-1.33	Periphery	Module 4	1	*Gynoxys longiflora*	0.42***	0.40	-0.59	Periphery	Module 4
	Aglaeactis cupripennis	0.66***	0.10	1.06	Periphery	Module 4	1	*Passiflora tripartita*	0.26 NS	0.13	-0.70	Periphery	Module 4
								Duranta mandonii	0.56***	0.00	0.07	Periphery	Module 4
								Brachyotum nutans	0.55***	0.12	0.02	Periphery	Module 4
								Aegiphila mortoni	0.25***	0.44	0.00	Periphery	Module 4

Values significantly different from1000 null models using Patefield algorithm as follows < 0.05*; < 0.01**; < 0.001***, NS = Not significant. Marginal values shown in ita

‡Module also comprised of Diptera sp.11 visiting *B. horrida* and Hymenoptera sp.5 visiting *G. longiflora*.

1 Table 5. Summary of the main morphological traits of plants and flower visitors in the Sacred Valley.
2

Plant family/genera	Flower morphology	Accessibility to nectar and pollen	Flower orientation
Apocynaceae, Caryophyllaceae, Ranunculaceae, Rosaceae	Dish shaped or bowl shaped: actinomorphic (with several symmetry planes) 2–5 mm deep	Open access flowers with exposed nectar and pollen, or pollen presented as pollinia. Nectar volume small.	Upright or horizontal (0–90°)
Asteraceae: *Bidens, Baccharis, Senecio, Ageratina, Aristeguietia*	Open tube: actinomorphic characterised by a head of small ray and disc tubular flowers mostly 5–10mm in length. Stamens and pistels exposed	Easy access to both pollen and nectar. Nectar volume small, concealed at the base of narrow tubes. Pollen exposed	Upright or horizontal (0–90°)
Fabaceae, Gentianaceae, Lamiaceae	Flag or gullet: bilaterally symmetrical, zygomorphous flowers 4–35 mm. Mechanically strong. Stamens and pistils exposed	Nectar concealed at the bottom of narrow or wide tubes. Nectar volume moderate and concentration high. Pollen exposed or absent	Horizontal (90°)
Verbenaceae, Passifloraceae, Melastomataceae,Bromeliaceae, Onagraceae	Tube: bilaterally symmetrical, zygomorphous flowers 5–135 mm in length. Some flowers mechanically strong. Stamens and pistels exposed	Nectar concealed in mostly deep narrow tubes. Pollen hidden or located anterior to the corolla, large amounts of nectar. Nectar concentration low	Horizontal to pendant (90–180°)

Pollinator functional group	Families/genera	Body/bill length	Resource
Diptera	Muscidae, Sphaeroceridae, Tachinidae, Sciariadae, Scianidae and Anthomyiidae	4–10 mm	Mostly nectar
Syrphidae	*Eristalis,Copestylum,Toxomerus, Platycheirus* and *Tuberculanostoma*	> 9 mm	Nectar and pollen
Trochilidae	*Aglaeactis, Metallura, Colibri, Pterophanes, Oreotrochilus* and *Oreonympha*	13–32 mm	Nectar only; also nectar robbers
Hymenoptera: Apidae	*Apis mellifera* and several *Bombus* spp.	10–16 mm; proboscis 6–10 mm	Pollen and nectar
Hymenoptera: Vespidae	Small to medium wasps	< 10 mm	Pollen and nectar
Coleoptera	Chrysomelidae, Bruchidae, Curculionidae and Melyridae	5–10 mm	Pollen and nectar
Lepidoptera	Hesperiidae and some small diurnal moths	5–10 mm	Nectar
Hemiptera	All *Lygaeus albornatus*	> 10 mm	Nectar

Fig. 1: Schematic diagram representing the nine valleys surveyed in the Sacred Valley in terms of different habitats encountered along an elevational gradient from 2900-4100 m and their quantitative bipartite graphs. Pollinators are arranged on the left and plants on the right. The number of interactions is indicated by the width of the bars.

Fig. 2. Plant species and habitats surveyed in the Sacred Valley: (A) *Barnadesia horrida* (Asteraceae); (B) *Baccharis salicifolia* (Asteraceae); (C) *Passiflora tripartita* var. *mollissima* (Passifloraceae); (D) *Polylepis* (Rosaceae) woodlands 3700-4200 m; (E) subtropical montane dry forest (3000-3400 m), characterised by steep rocky slopes with spiny shrubs such as *Duranta mandonii* (Verbenaceae) and many *Puya* sp.; (F) *Lupinus mutabilis* (Fabaceae); (G) *Oreocallis grandiflora* (Proteaceae); Photographs: (A, C, F,G) Stella Watts, (D,E) Jeff Ollerton, (B) Lynn Watson.

Fig. 3. Scatterplot of species roles for the reduced matrix. The coefficients *z* and *c* refer to among-module connectivity and within-module degree, respectively. Dashed grey lines indicate 95% quantiles from 100 null models and indicate the topographical space of network hubs (top right-hand rectangle, high *z* and *c* values), module hubs (top left-hand rectangle, high *z* and low *c* values), connectors (bottom right-hand rectangle, low *z* and high *c* values) and peripheral species (bottom left-hand rectangle, low *z* and *c* values). The top graph represents the role of functional groups of pollinator species, showing the presence of two bees in the role of module and network hubs, and two flies (one of them a syrphid) acting as connectors. For the purposes of this analysis, solitary bees and wasps are included within Hymenoptera and Tachinidae are included within Diptera. The bottom graph illustrates plant species, showing that the family Asteraceae has two module hubs and one connector species, the latter together with a Grossulariaceae species. No plant takes the role of network hub.

Fig. 4. Reduced pooled matrix featuring five modules identified by QuanBiMo (with steps = 1e8; $Q = 0.30$; $n = 5$ independent runs). Species are sorted according to their modular affinity, plants as rows and pollinators as columns. Darker squares indicate more frequent interactions. Red boxes delineate the five modules and cells inside the boxes are the links within modules. As can be seen, *Apis mellifera* is clearly not randomly distributed over the five modules, thus linking modules five, four, three, two and one (bottom to top right) into a coherent network. The dominant pollinator and flower type are: Module 1: large syrphids, a large butterfly and a large long-billed hummingbird visiting open access flowers; Module 2: small flies and syrphid flies visiting open access Asteraceae flowers; Module 3: large bumblebees, large syrphids, large flies and beetles visiting open access and flag/gullet flowers; Module 4: medium sized hummingbirds with relatively short bills visiting long tubular flowers, Module 5: honey bees and mainly large flies, tachinid flies and syrphids visiting open access and flag/gullet flowers. Asteraceae plants are as follows: *Ageratina sternbergiana*, *Aristeguietia anisodonoton*, Asteraceae sp. 2, Asteraceae sp. 4, *Baccharis buxifolia*, *Baccharis salicifolia*, *Barnadesia horrida*, *Cronquistianthus urubambensis*, *Gynoxys longiflora*, *Senecio panticallensis*.

Fig. 5. Complimentary specialisation d' (A) and corolla length (B) for hummingbirds *versus* all other functional groups of flower visitors. Data pooled across the five valleys: Huaran, Yanacocha, Chicon, Mantanay and Choquebamba in which hummingbirds were observed. Box plots show the median (horizontal line) and ranges from the 25th and 75th percentiles, the solid square is the mean, and the tips of the whiskers indicate the fifth and 95th

percentiles. Circles represent outliners. Different letters denote significant differences at $P < 0.01$.

Fig. 6. Number of pollinator species visiting plant species with open tube, open access, gullet/flag and tubular flowers. Data pooled across all valleys. Box plots show the median (horizontal line) and ranges from the 25th and 75th percentiles, the solid square is the mean, and the tips of the whiskers indicate the fifth and 95th percentiles. Circles represent outliners. Bars with the same letters indicate no significant difference, $P > 0.05$ after Bonferroni adjustment.

SUPPLEMENTARY DATA

Table S1. Connection (*c*) and participation (*z*) values for each species to describe their role in 10 plant–pollinator networks in the Sacred Valley. Specialisation indices: species degree, species strength, pollination service index (*PSI*) and complimentary specialisation *d′* for flower visitors based on weighted strength from 100 null models, identifying insect and hummingbird species with important topological roles. Superscripts indicate ranks with 1 for the highest generalisation down to 42 for lowest. Index values and rankings also show how network positions change across some valleys and how constant they remain in others. For species degree, values in bold are unique (all others are ties). Abbreviations as follows: Nh = network hub; Mh = Module hub and C = connector. Complimentary specialisation *d′* values significantly different from 1000 null models using Patefield algorithm as follows: < 0.05*, < 0.01**, < 0.001***. Marginal values are shown in italics.

Table S2. Connection (*c*) and participation (*z*) values for each species to describe their role in 10 plant–pollinator networks in the Sacred Valley. Specialisation indices: species degree, species strength, pollination service index (*PSI*) and complimentary specialisation *d′* for plants based on weighted strength from 100 null models, identifying plant species with important topological roles. Superscripts indicate ranks with 1 for the highest generalisation down to 26 for lowest. Index values and rankings also show how network positions change across some valleys and how constant they remain in others. For species degree, values in bold are unique (all others are ties). Abbreviations as follows: Nh = network hub; Mh = Module hub and C = connector. Complimentary specialisation *d′* values significantly different from 1000 null models using Patefield algorithm as follows: < 0.05*, < 0.01**, < 0.001***. Marginal values are shown in italics.

Table S3. Full list of plant species surveyed in the Sacred Valley and the total number of plants found in transects for each plant species, in which valleys, altitudes, life zones and months. Life zones abbreviations are as follows: mts-S = subtropical montane thorn steppe; mdf-S = subtropical montane dry forest; hmf-S = subtropical humid montane forest; *p*-S = *Polylepis* forests.

Table S4. Full list of pollinator species surveyed in the Sacred Valley and the total number of visits recorded in which valleys, altitudes, life zones and months. Life zones abbreviations are as follows: mts-S = subtropical montane thorn steppe; mdf-S = subtropical montane dry forest; hmf-S= subtropical humid montane forest; *p*-S – *Polylepis* forest.

Table S5. Summary of observed species level specialisation index values for the most relevant functional groups of pollinators reporting species degree, species strength, Pollination Service Index (*PSI*) weighted closeness and complimentary specialisation *d′*.

Figure S1. Complimentary specialisation H_2' values for the analysis of each network. Red triangles indicate observed values whereas histograms represent the distribution of 1000 null models using the Patefield algorithm in the bipartite package R. All values significantly different from 1000 null models using Patefield algorithm: $P < 0.001$.

Figure S2. Observed and null model specialisation values of *Apis mellifera,* for the analysis of specialisation shift. Histograms illustrate the distribution of 1000 null models and represent the position of a perfect generalist. Red triangles indicate the observed value.

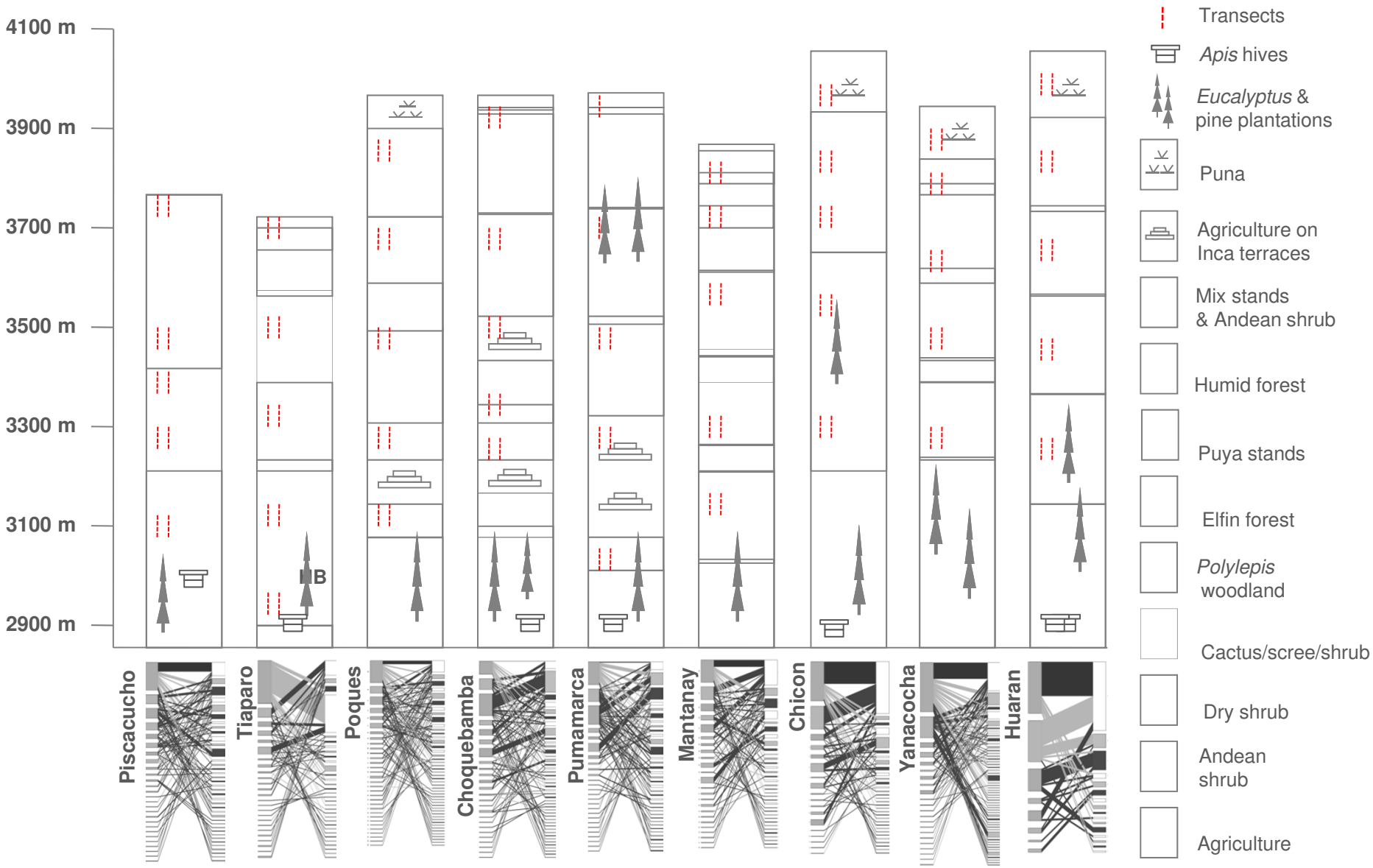
Figure S3. Observed and null model specialisation values of *Bombus funebris* for the analysis of specialisation shift. Histograms illustrate the distribution of 1000 null models and represent the position of a perfect generalist. Red triangles indicate the observed value.

Figure S4. Observed and null model specialisation values of *Aglaeactis cupripennis* for the analysis of specialisation shift. Histograms illustrate the distribution of 1000 null models and represent the position of a perfect generalist. Red triangles indicate the observed value.

Figure S5. Specialisation index values (degree, strength, Pollination Service Index (*PSI*), Weighted Centrality (WC) and complimentary specialisation *d'*) for *Bombus funebris, Apis mellifera* and *Aglaeactis cupripennis.* The first box represents the raw index values, as computed from the networks. The second box represents corrected values, i.e. differences between raw values and the mean of the null models. They position the boxes relative to a perfect generalist (value of 0). The third is the *z*-scores (divided by a constant for more convenient comparison in the plots).

Fig. S6. Chicon featuring seven modules identified by QuanBiMo (with steps = 1e8; Q = 0.30; n = 5 independent runs). Species are sorted according to their modular affinity, plants as rows and pollinators as columns. Darker squares indicate more frequent interactions. Red boxes delineate the seven modules and cells inside the boxes are the links within modules. As can be seen, *Baccharis buxifolia* is clearly not randomly distributed over the seven modules, thus linking modules six modules (left to right) into a coherent network. There were no network hubs in this valley. The main pollinator and flower type (left to right): Module 2: medium sized hummingbirds with relatively short bills visiting long tubular flowers; Module 3: dominated by honey bees (module hub) a bumblebee, large flies, tachinid flies, large syrphids and a large hummingbird with a long bill visiting open access and gullet flowers; Module 6: dominated by Syrphid sp. 2 (connector) and Syrphid sp. 3 visiting open access Asteraceae flowers.

Fig. S7. Mantanay featuring seven modules identified by QuanBiMo (with steps = 1e8; Q = 0.30; n = 5 independent runs). Species are sorted according to their modular affinity, plants as rows and pollinators as columns. Darker squares indicate more frequent interactions. Red boxes delineate the seven modules and cells inside the boxes are the links within modules. As can be seen, *Apis mellifera* is clearly not randomly distributed over the seven modules, thus linking five modules (bottom to top) into a coherent network. The main pollinator and flower type (left to right): Module 1: large bumblebee, a butterfly and Syrphid fly visiting small tubular flowers of *Escallonia resinosa* (module hub) and *Duranta armata*; Module 4: dominated by honey bees (network hub), a large syrphid and small beetles visiting mostly open access flowers; Module 5: exclusively medium sized hummingbirds with relatively short bills visiting long tubular flowers; Module 6: dominated by the plant *Myrsianthes oreophila* (connector) and bumble bee, butterflies, large tachinid flies, large flies and a large hummingbird with a long bill visiting mostly long tubular and open access flowers.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Chicon
Yanacocha
Huaran
Transects
Apis hives
Eucalyptus & pine plantations
Puna
Agriculture on Inca terraces
Mix stands & Andean shrub
Humid forest
Puya stands
Elfin forest
Polylepis woodland
Cactus/scree/shrub
Dry shrub
Andean shrub
Agriculture

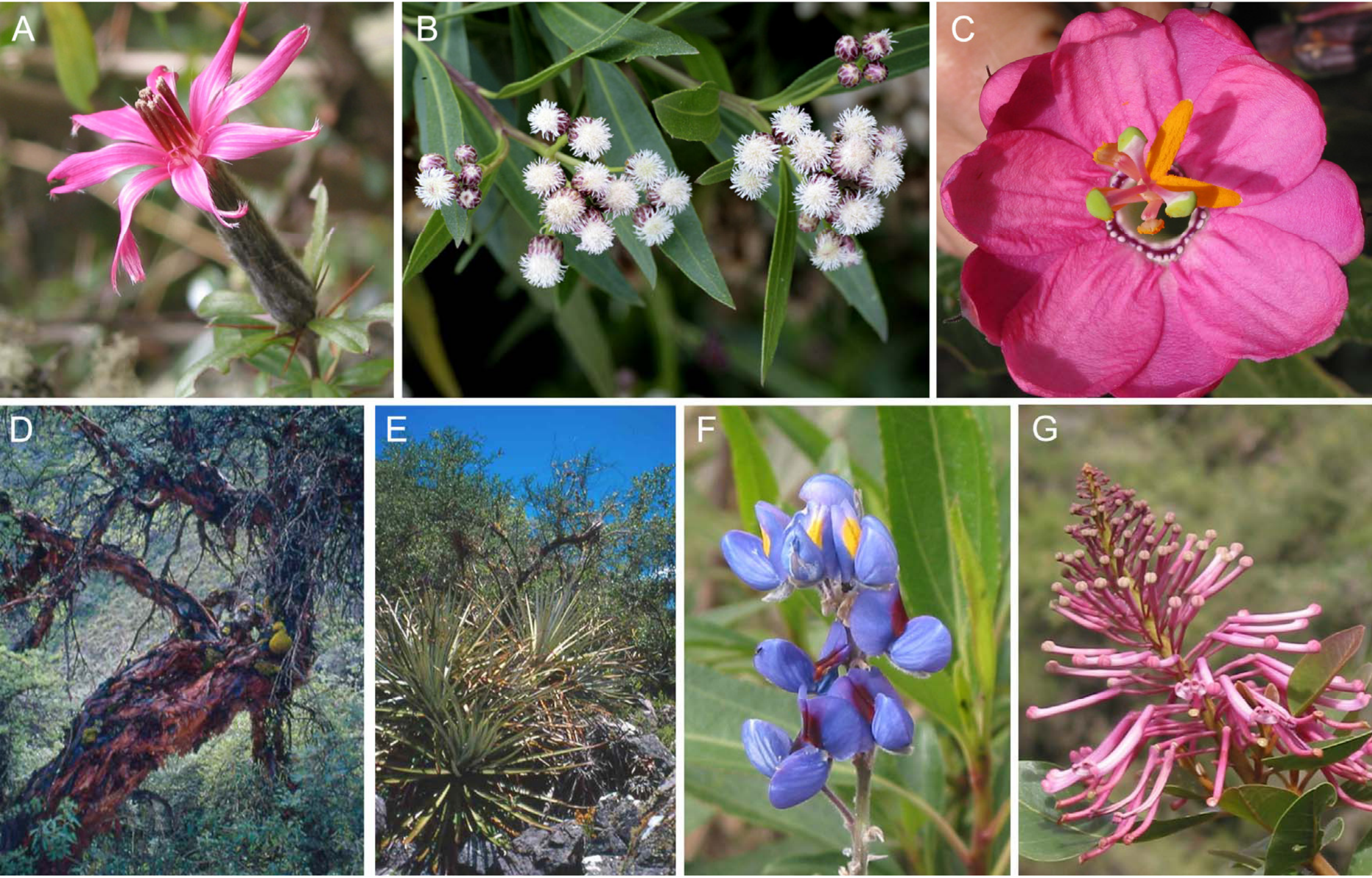
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Table S1. Connection (*c*) and participation (*z*) values for each species to describe their role in 10 plant–pollinator networks in the Sacred Valley. Specialisation indices: species degree, species strength, pollination service index (*PSI*) and complimentary specialisation *d′* for flower visitors based on weighted strength from 100 null models, identifying insect and hummingbird species with important topological roles. Superscripts indicate ranks with 1 for the highest generalisation down to 42 for lowest. Index values and rankings also show how network positions change across some valleys and how constant they remain in others. For species degree, values in bold are unique (all others are ties). Abbreviations as follows: Nh = network hub; Mh = Module hub and C = connector. Complimentary specialisation *d′* values significantly different from 1000 null models using Patefield algorithm as follows: < 0.05*, < 0.01**, < 0.001***. Marginal values are shown in italics.

Flower visitor species	Order	Network position	*c*	*z*	Species Degree	Species Strength	*PSI*	Weighted Closeness	*d′*
Apis mellifera	Hymenoptera	Nh	0.51	2.04	**10** [1]	5.66 [1]	0.52 [3]	0.06 [1]	0.39*** [22]
Apis mellifera	Hymenoptera	Nh	0.48	2.47	**8** [1]	3.37 [2]	0.36 [7]	0.03 [1]	0.33** [21]
Apis mellifera	Hymenoptera	Nh	0.65	1.78	**9** [1]	3.08 [2]	0.33 [9]	0.02 [1]	*0.21* [15]
Apis mellifera	Hymenoptera	Nh	0.67	3.45	**18** [1]	7.18 [1]	0.47 [2]	0.16 [1]	0.18*** [18]
Apis mellifera	Hymenoptera	Mh	0.00	2.66	**3** [7]	2.12 [5]	0.67 [5]	0.12 [2]	0.43*** [7]
Apis mellifera	Hymenoptera	Mh	0.27	2.46	**5** [1]	3.43 [1]	0.67 [2]	0.71 [1]	0.40*** [21]
Apis mellifera	Hymenoptera	C	0.71	1.23	4 [3]	2.21 [3]	0.67 [4]	0.01 [2]	0.50*** [20]
Bombus funebris	Hymenoptera	C	0.54	-0.33	4 [2]	0.26 [14]	0.06 [20]	0.01 [6]	0.07 [7]
Bombus funebris	Hymenoptera	Mh	0.20	1.58	**7** [1]	2.87 [2]	0.28 [11]	0.02 [3]	0.24 [14]
Bombus funebris	Hymenoptera	Mh	0.57	2.26	**15** [2]	2.54 [2]	0.16 [6]	0.06 [3]	0.21*** [21]
Eriopis sp.2	Coleoptera	Mh	0.00	1.78	2 [6]	0.65 [13]	0.32 [9]	0.02 [6]	*0.52* [30]
Eriopis sp.2	Coleoptera	C	0.61	-0.68	3 [6]	0.20 [23]	0.06 [23]	0.01 [6]	0.58* [11]
Lygaeus albornatus	Hemiptera	Mh	0.00	1.37	3 [5]	2.62 [2]	0.75 [3]	0.01 [5]	0.85*** [42]
Metardaris cosinga	Lepidoptera	Mh	0.12	3.24	**8** [2]	4.61 [2]	0.32 [4]	0.03 [3]	0.23*** [32]
Muscidae sp.1	Diptera	Mh	0.00	2.12	3 [3]	1.57 [5]	0.24 [10]	0.02 [3]	0.32* [17]
Muscidae sp.1	Diptera	Mh	0.09	1.98	3 [5]	1.18 [8]	0.21 [14]	0.02 [6]	0.55* [16]
Muscidae sp.1	Diptera	Mh	0.10	2.26	5 [4]	2.34 [4]	0.33 [6]	0.01 [9]	*0.34* [19]
Sciaria sp.4	Diptera	Mh	0.12	2.04	**8** [1]	5.26 [5]	0.69 [3]	0.01 [1]	0.75*** [28]
Sciaria sp.4	Diptera	Mh	0.15	1.72	6 [3]	3.97 [1]	0.50 [5]	0.03 [3]	0.65*** [33]

Sciaria sp.4	Diptera	Mh	0.46	2.06	9 [3]	1.75 [4]	0.25 [4]	0.08 [2]	0.30[*** 29]
Sciaria sp.4	Diptera	C	0.65	1.15	6 [3]	1.68 [5]	0.58 [2]	0.02 [4]	0.50[*** 28]
Syrphidae sp.2	Syrphidae	Nh	0.42	3.24	4 [3]	0.80 [7]	0.11 [14]	0.02 [6]	0.15 [26]
Syrphidae sp.2	Syrphidae	C	0.58	-0.60	4 [2]	0.79 [2]	0.18 [11]	0.03 [2]	0.26[* 14]
Syrphidae sp.2	Syrphidae	Mh	0.22	2.02	**8** [2]	3.22 [2]	0.36 [10]	0.03 [3]	0.41[** 24]
Syrphidae sp.2	Syrphidae	C	0.64	-0.33	4 [3]	1.19 [7]	0.16 [16]	0.01 [4]	0.18 [10]
Syrphidae sp.2	Syrphidae	C	0.71	0.00	7 [5]	1.09 [7]	0.10 [8]	0.06 [3]	0.16[*** 15]
Syrphidae sp.3	Syrphidae	C	0.59	-0.40	3 [5]	0.20 [22]	0.06 [24]	0.00 [15]	0.16 [7]
Syrphidae sp.3	Syrphidae	Mh	0.00	1.88	5 [4]	2.32 [4]	0.37 [4]	0.01 [10]	0.56[** 36]
Syrphidae sp.3	Syrphidae	C	0.50	1.48	3 [5]	0.58 [12]	0.25 [11]	0.03 [4]	0.28 [18]
Toxomerus sp.2	Syrphidae	C	0.64	0.06	3 [5]	0.41 [14]	0.15 [14]	0.03 [2]	0.13 [11]
Toxomerus sp.2	Syrphidae	C	0.60	0.10	3 [5]	0.28 [19]	0.11 [21]	0.01 [4]	0.12 [8]
Toxomerus sp.2	Syrphidae	C	0.74	1.34	6 [3]	2.29 [5]	0.24 [14]	0.02 [2]	0.30 [24]
Metallura tyrianthina	Trochilidae	C	0.47	0.15	3 [1]	0.66 [4]	0.23 [5]	0.06 [2]	0.31[** 7]
Aglaeactis cupripennis	Trochilidae	Mh	0.03	2.13	9 [3]	2.49 [3]	0.53 [3]	0.03 [8]	0.66[*** 28]

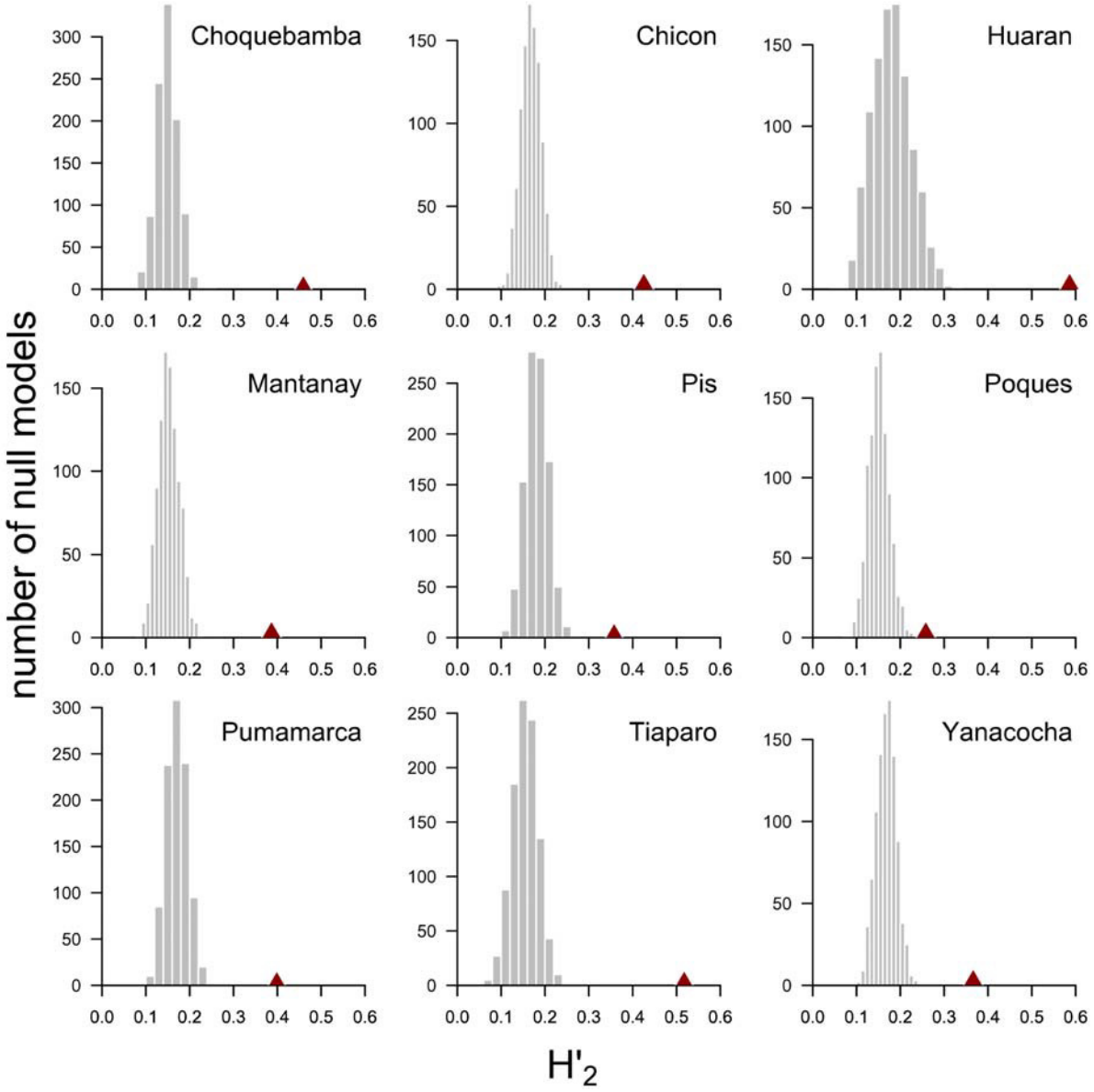

Figure S1. Complimentary specialisation H_2' values for the analysis of each network. Red triangles indicate observed values whereas histograms represent the distribution of 1000 null models using the Patefield algorithm in the bipartite package R. All values significantly different from 1000 null models using Patefield algorithm: $P < 0.001$.

Table S2. Connection (*c*) and participation (*z*) values for each species to describe their role in 10 plant–pollinator networks in the Sacred Valley. Specialisation indices: species degree, species strength, pollination service index (*PSI*) and complimentary specialisation *d′* for plants based on weighted strength from 100 null models, identifying plant species with important topological roles. Superscripts indicate ranks with 1 for the highest generalisation down to 26 for lowest. Index values and rankings also show how network positions change across some valleys and how constant they remain in others. For species degree, values in bold are unique (all others are ties). Abbreviations as follows: Nh = network hub; Mh = Module hub and C = connector. Complimentary specialisation *d′* values significantly different from 1000 null models using Patefield algorithm as follows: < 0.05*, < 0.01**, < 0.001***. Marginal values are shown in italics.

Network	Plant species	Family	Network position	*c*	*z*	Species Degree	Species Strength	Weighted Closeness	*d′*
Choquebamba	*Baccharis salicifolia*	Asteraceae	Nh	0.71	1.49	11 [2]	4.53 [4]	0.02 [1]	0.39*** [6]
Mantanay	*Baccharis salicifolia*	Asteraceae	Mh	0.30	1.7	**8** [2]	4.58 [2]	0.04 [2]	0.32** [11]
Poques	*Baccharis salicifolia*	Asteraceae	Mh	0.29	2.43	10 [3]	4.75 [2]	0.04 [2]	0.41* [15]
Reduced	*Baccharis salicifolia*	Asteraceae	C	0.63	1.45	**29** [1]	11.08 [1]	0.07 [1]	0.16*** [7]
Chicon	*Baccharis buxifolia*	Asteraceae	Mh	0.31	1.78	17 [1]	11.67 [1]	0.02 [2]	0.21*** [4]
Huaran	*Baccharis buxifolia*	Asteraceae	Mh	0.17	1.15	**8** [1]	7.16 [1]	0.14 [1]	0.46*** [4]
Pumamarca	*Baccharis buxifolia*	Asteraceae	Mh	0.24	1.5	3 [5]	0.87 [8]	0.02 [5]	0.44 [13]
Choquebamba	*Ageratina sternbergiana*	Asteraceae	Mh	0.19	1.89	2 [6]	0.64 [13]	0.01 [10]	0.44*** [11]
Tiaparo	*Ageratina sternbergiana*	Asteraceae	Mh	0.36	1.74	5 [2]	3.11 [2]	0.01 [4]	0.64*** [17]
Poques	*Ageratina sternbergiana*	Asteraceae	C	0.74	-0.41	10 [3]	2.58 [5]	0.03 [5]	0.29 [8]
Tiaparo	*Aristeguietia discolor*	Asteraceae	C	0.45	0.85	5 [2]	2.05 [4]	0.01 [5]	0.79** [8]
Piscacucho	*Aristeguietia discolor*	Asteraceae	C	0.55	0.00	**9** [3]	4.18 [3]	0.03 [2]	0.54*** [19]
Yanacocha	Asteraceae sp.2	Asteraceae	Mh	0.07	2.15	**6** [4]	3.75 [3]	0.04 [3]	0.38* [10]
Pumamarca	Asteraceae sp.2	Asteraceae	Mh	0.22	1.49	15 [1]	6.47 [3]	0.02 [4]	0.36** [7]
Choquebamba	Asteraceae sp.2	Asteraceae	Mh	0.38	1.49	4 [4]	1.46 [7]	0.01 [9]	0.65*** [15]
Yanacocha	Asteraceae sp.4	Asteraceae	C	0.39	-0.45	3 [6]	0.37 [11]	0.04 [4]	0.23 [5]
Piscacucho	Asteraceae sp.4	Asteraceae	C	0.56	0.58	**7** [3]	1.65 [3]	0.02 [5]	0.33 [5]
Reduced	*Barnadesia horrida*	Asteraceae	Mh	0.32	2.12	**8** [8]	1.93 [6]	0.02 [8]	0.61*** [26]
Mantanay	*Cynanchum tarmense*	Apocynaceae	C	0.46	0.08	**4** [3]	1.27 [7]	0.03 [3]	*0.32* [12]

Mantanay	*Escallonia resinosa*	Grossulariaceae	Mh	0.34	1.61	8 [2]	2.72 [3]	0.03 [5]	0.28 [8]
Reduced	*Escallonia resinosa*	Grossulariaceae	C	0.64	-0.53	**13** [5]	1.67 [7]	0.03 [6]	0.28*** [6]
Tiaparo	*Eupatorium* sp.2	Asteraceae	Mh	0.00	1.5	2 [5]	0.25 [16]	0.01 [11]	0.63 [16]
Piscacucho	*Gentiana postrata*	Gentianaceae	Mh	0.18	2.18	**10** [2]	4.85 [2]	0.03 [3]	0.47*** [19]
Tiaparo	*Gentiana postrata*	Gentianaceae	C	0.46	-0.85	2 [5]	0.19 [18]	0.01 [9]	0.42 [4]
Pumamarca	*Jungia rugosa*	Asteraceae	Nh	0.63	1.77	**14** [2]	6.50 [2]	0.02 [2]	0.34** [6]
Reduced	*Jungia rugosa*	Asteraceae	Mh	0.31	1.63	11 [6]	1.93 [5]	0.05 [3]	0.22*** [11]
Choquebamba	*Jungia rugosa*	Asteraceae	C	0.57	0.71	1 [7]	0.14 [17]	0.00 [14]	0.45*** [12]
Poques	*Jungia rugosa*	Asteraceae	C	0.54	1.5	**22** [1]	13.82 [1]	0.05 [1]	0.31** [10]
Chicon	*Minthostachys spicata*	Lamiaceae	C	0.46	-0.97	2 [6]	0.24 [14]	0.02 [4]	0.09 [1]
Piscacucho	*Minthostachys spicata*	Lamiaceae	C	0.51	1.15	**16** [1]	9.71 [1]	0.04 [1]	0.47*** [16]
Mantanay	*Myrsianthes oreophila*	Myrtaceae	C	0.39	0.71	**17** [1]	11.17 [1]	0.04 [1]	0.31*** [14]

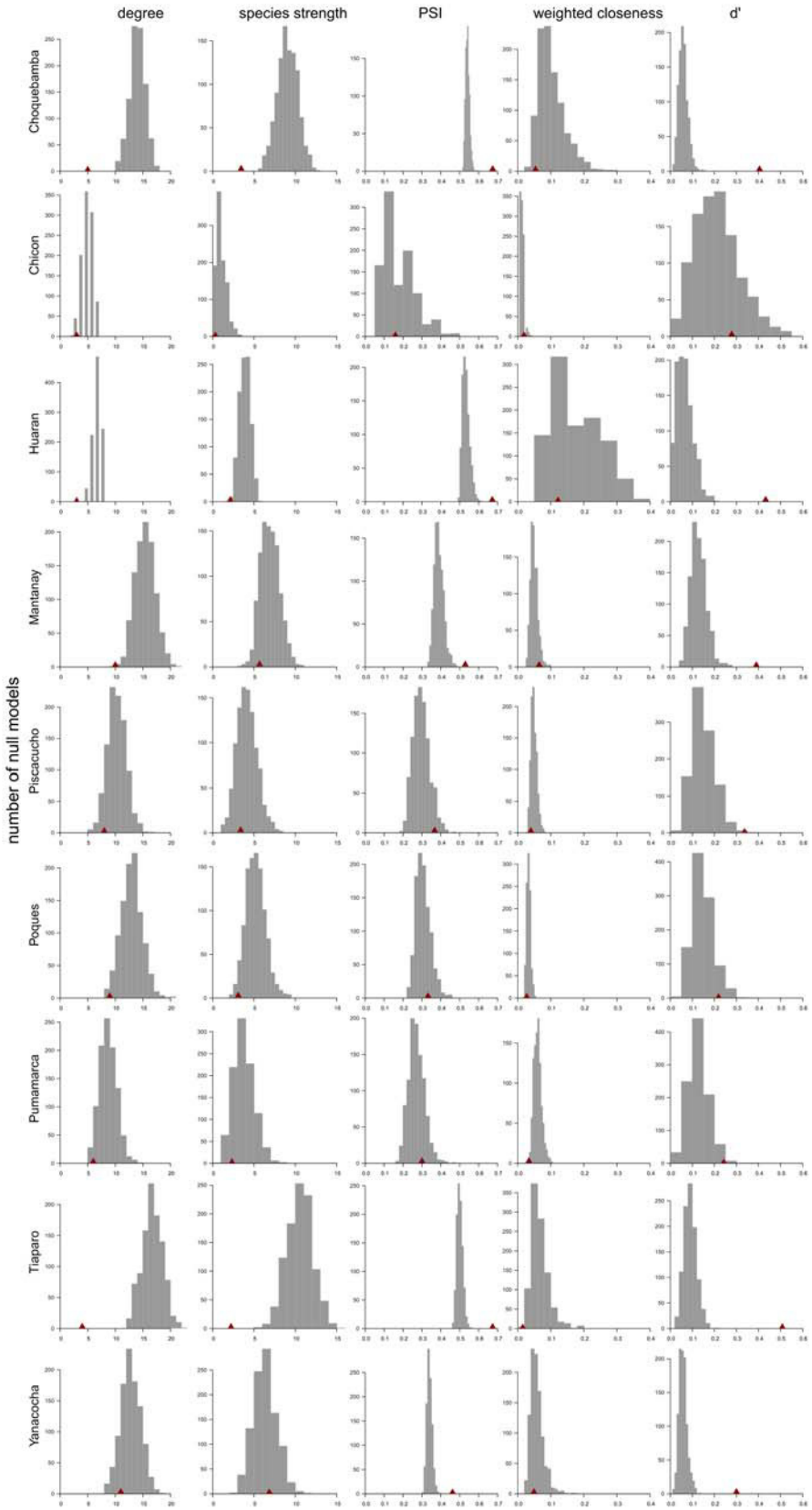

Figure S2. Observed and null model specialisation values of *Apis mellifera,* for the analysis of specialisation shift. Histograms illustrate the distribution of 1000 null models and represent the position of a perfect generalist. Red triangles indicate the observed value.

Table S3. Full list of plant species surveyed in the Sacred Valley and the total number of plants found in transects for each plant species, in which valleys, altitudes, life zones and months. Life zones abbreviations are as follows: mts-S = subtropical montane thorn steppe; mdf-S = subtropical montane dry forest; hmf-S = subtropical humid montane forest; *p*-S = *Polylepis* forests.

Family	Scientific name	Number of plants	Huaran	Yanacocha	Chicon	Mantanay	Pumamarca	Choquebamba	Poques	Tiaparo	Piscacucho	Altitude 1	Altitude 2	Altitude 3	Altitude 4	Altitude 5	mts-S	mdf-S	hmf-S	*p*-S	April	June	July	August	October
Apocynaceae	Asclepiadoideae sp1	1		X								X					X								X
	Asclepiadoideae sp2	1		X										X			X								X
	Cynanchum tarmense	14				X						X					X							X	
Asteraceae	*Ageratina sternbergiana* (D. C.) King & H. Robinson	54			X		X	X	X	X		X	X	X	X	X		X		X	X	X	X	X	
	Ageratina sp.1	2									X	X	X	X	X			X				X			
	Ageratina sp.2	1								X					X			X				X			
	Aristeguietia anisodonoton (D. C.) King H. Robinson	13			X	X		X	X	X		X	X	X	X				X		X	X	X	X	
	Aristeguietia discolor (D. C.) King H. Robinson	25								X	X	X	X		X	X			X			X			
	Asteraceae sp. 2	59		X	X	X	X	X	X		X	X		X	X	X	X	X	X		X	X	X	X	X
	Asteraceae sp. 4	22		X	X	X			X		X		X	X	X	X	X	X	X		X	X	X	X	X
	Asteraceae sp. 5	49		X				X				X		X	X	X	X	X	X		X				X
	Asteraceae sp. 6	10		X				X				X		X			X	X			X				X
	Asteraceae sp. 7	5		X					X						X	X			X		X				X
	Asteraceae sp. 8	7		X					X						X	X			X		X				X
	Asteraceae sp. 14	6							X				X	X				X			X				
	Asteraceae sp. 15	1							X					X					X		X				
	Asteraceae sp. 16	2							X				X		X			X	X		X				
	Asteraceae sp. 17	2							X	X			X					X			X	X			
	Asteraceae sp. 35	4					X		X						X	X			X		X				
	Asteraceae sp. 37	3						X	X						X				X		X				

	Asteraceae sp. 63	2					X									X			X		X					
	Asteraceae sp. 45	2							X					X					X		X					
	Baccharis boliviensis (Weddell) Cabrera	5							X		X					X		X			X	X				
	Baccharis buxifolia (Lamarck) Persoon	79	X		X	X	X		X			X	X	X	X	X		X	X	X	X	X	X	X		
	Baccharis odorata H.B.K.	4			X						X			X		X			X	X						
	Baccharis salicifolia (R. & P.) Persoon	262	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	
	Baccharis sp.4	1						X				X							X		X					
	Baccharis sp.6	1					X					X							X		X					
	Barnadesia horrida Muschler	27	X	X	X	X				X		X	X	X	X	X		X	X	X		X	X	X	X	
	Bidens andicola H.B.K.	3			X					X				X								X	X			
	Bidens pilosa L.	1			X										X				X				X			
	Bidens triplinervia H.B.K.	6								X	X		X	X	X	X			X			X				
	Cronquistianthus cf. *urubambensis* King H. Robinson	7								X		X		X		X		X	X			X				
	Cronquistianthus sp.1	1					X							X					X		X					
	Cronquistianthus sp.2	2								X				X				X	X			X				
	Cronquistianthus sp.3	1									X					X			X			X				
	Eupatorium sp.1	4					X							X	X	X			X		X					
	Eupatorium sp. 2	6								X	X			X					X			X				
	Gynoxys longiflora Sch.Bip. ex Wedd.	9			X	X									X	X				X			X	X		
	Jungia rugosa Lessing	76			X	X	X	X	X	X		X	X	X	X	X	X	X	X		X	X	X	X		
	Senecio panticallensis Cabrera	15						X	X		X	X				X			X	X	X	X				
	Senecio sp.1	1					X									X			X		X					
	Senecio sp.2	1					X								X				X		X					
	Senecio sp.3	1					X								X				X		X					
	Senecio sp.4	1							X					X					X		X					
	Taraxacum sp.1	3		X				X				X				X		X	X		X					X
	Verbesina sp.	3							X					X	X				X		X					
Berberidaceae	*Berberis humbertiana* J. F. Macbride	7		X				X	X			X	X			X		X	X		X					X
Bignoniaceae	*Tecoma sambucifolia* H.B.K.	2				X						X						X						X		
Brassicaceae	Brassicaceae sp.	1							X							X			X			X				
Bromeliaceae	*Puya ferruginea* (R. & P.) L. D. Smith	1			X											X		X					X			

Campanulaceae	*Lobelia tenera* H. B. K.	3					X				X	X				X		X	X		X	X			
	Siphocampylus actinothrix E. Wimm.	3				X										X			X				X		
	Siphocampylus sp.	1									X					X			X		X				
Caryophyllaceae	*Arenaria lanuginosa* (Michaux) Rohrbach	1									X					X				X		X			
	Drimaria sp.	2								X				X	X				X	X		X			
	Stellaria media (L.) Cirillo	5					X	X	X			X	X		X	X			X						
Convolvulaceae	*Cuscuta grandiflora* H.B.K.	1							X			X						X			X				
Cunoniaceae	*Weinmannia pentaphylla* R.& P.	9				X								X	X				X					X	
Fabaceae	*Desmodium rotundifolium* (Michaux) D.C.	1									X		X									X			
	Fabaceae sp.	1		X								X						X							X
	Lupinus aridulus C.P.Sm.	2					X					X						X			X				
	Lupinus mutabilis (Sweet)	7				X									X	X			X					X	
	Lupinus paniculatus Desr.	8								X	X				X	X			X			X			
	Lupinus sp.	1					X									X			X		X				
	Melilotus alba Medikus	10			X			X	X					X	X				X		X		X		
	Platymiscium sp.	1		X									X					X							X
	Senna birostris (Vogel) H. S. Irwin & Barneby	5						X				X			X			X	X		X				
	Trifolium amabile var. *pentlandii* Ball	6					X		X			X	X		X			X	X		X				
Gentianaceae	*Gentiana prostrata(*Haenke) Á. Löve & D. Löve	12								X	X		X					X				X			
	Gentiana sp.1	1									X				X				X			X			
Geraniaceae	*Geranium* sp.1	2									X				X				X			X			
Grossulariaceae	*Escallonia resinosa* (Ruiz & Pav.)	28		X	X	X	X	X	X	X		X	X	X	X	X			X		X	X	X	X	X
Lamiaceae	*Lamium amplexicaule* L.	1						X							X				X		X				
	Minthostachys spicata (Bentham) Epling	103	X		X	X				X	X	X	X	X	X	X		X	X			X	X	X	
	Salvia oppositiflora R. & P.	4						X		X			X			X		X	X		X	X			
Lythraceae	Lythraceae sp.	2							X			X		X					X		X				
Loasaceae	*Mentzelia fendleriana* Urban & Gilg	3							X							X			X		X				
Loranthaceae	*Gaiadendrum* cf. *punctatum* (R. & P.) G. Don	1									X				X				X			X			
Melastomataceae	*Brachyotum naudinii* Triana	2						X			X					X			X	X	X	X			
	Brachyotum nutans Gleason	21		X	X					X	X				X	X			X			X	X		X
Myrtaceae	*Myrcianthes oreophila* (Diels) McVaugh	83			X	X		X				X	X	X	X	X			X		X		X	X	

Onagraceae	*Fuchsia apetala* R.& P.	4	X	X									X	X	X			X	X					X	X
	Fuchsia boliviana Carriere	3						X				X		X	X			X		X					
	Oenothera rosea Aiton	1				X						X						X						X	
	Oenothera versicolor Lehman	1						X						X				X		X					
Oxalidaceae	*Oxalis lotoides* (Knuth)	2					X	X				X						X		X					
	Oxalis urubambensis R. Knuth	5					X	X	X			X		X	X				X		X					
Passifloraceae	*Passiflora* sp.	1				X						X							X					X	
	Passiflora trifoliata Cav.	2		X		X								X					X					X	X
	Passiflora tripartita var. mollissima (A. L. Jussieu) Poiret	3	X			X						X	X	X					X					X	
Polygalaceae	*Monnina salicifolia* R. & P.	1		X									X					X							X
Proteaceae	*Oreocallis grandiflora* (Lamarck) R. Brown	4								X						X			X			X			
Ranunculaceae	*Ranunculus praemorsus* H.B.K.	3					X		X		X			X	X	X			X		X	X				
Rhamnaceae	*Colletia spinosissima* J. Gmelin	3		X										X				X							X
Rosaceae	*Prunus serotina* subsp. *serotina*	2				X						X					X							X	
Rubiaceae	*Fragaria* sp.	1								X			X					X				X			
Scrophulariaceae	*Agallinis lanceola*	1								X				X					X			X			
	Scrophulariaceae sp.	1			X							X						X					X		
Solanaceae	*Saracha punctata* Ruiz & Pav.	1									X					X			X			X			
	Solanaceae sp.	2				X								X					X					X	
	Solanum sp.1	1								X		X						X				X			
	Solanum sp.2	1									X		X					X				X			
Undetermined	Undetermined Species 22	4					X			X	X	X	X			X		X	X		X	X			
Undetermined	Undetermined Species 24	1					X					X						X			X				
Urticaceae	*Urtica echinata* Bentham	1					X								X				X		X				
Verbenaceae	*Aegiphila mortonii* Moldenke	22	X			X						X	X	X					X					X	
	Duranta armata Moldenke	8		X		X						X	X	X				X						X	X
	Duranta mandonii Moldenke	9	X	X		X						X		X		X		X	X					X	X
Apiaceae	Apiaceae sp.	1						X								X			X		X				
	Total	1235																							

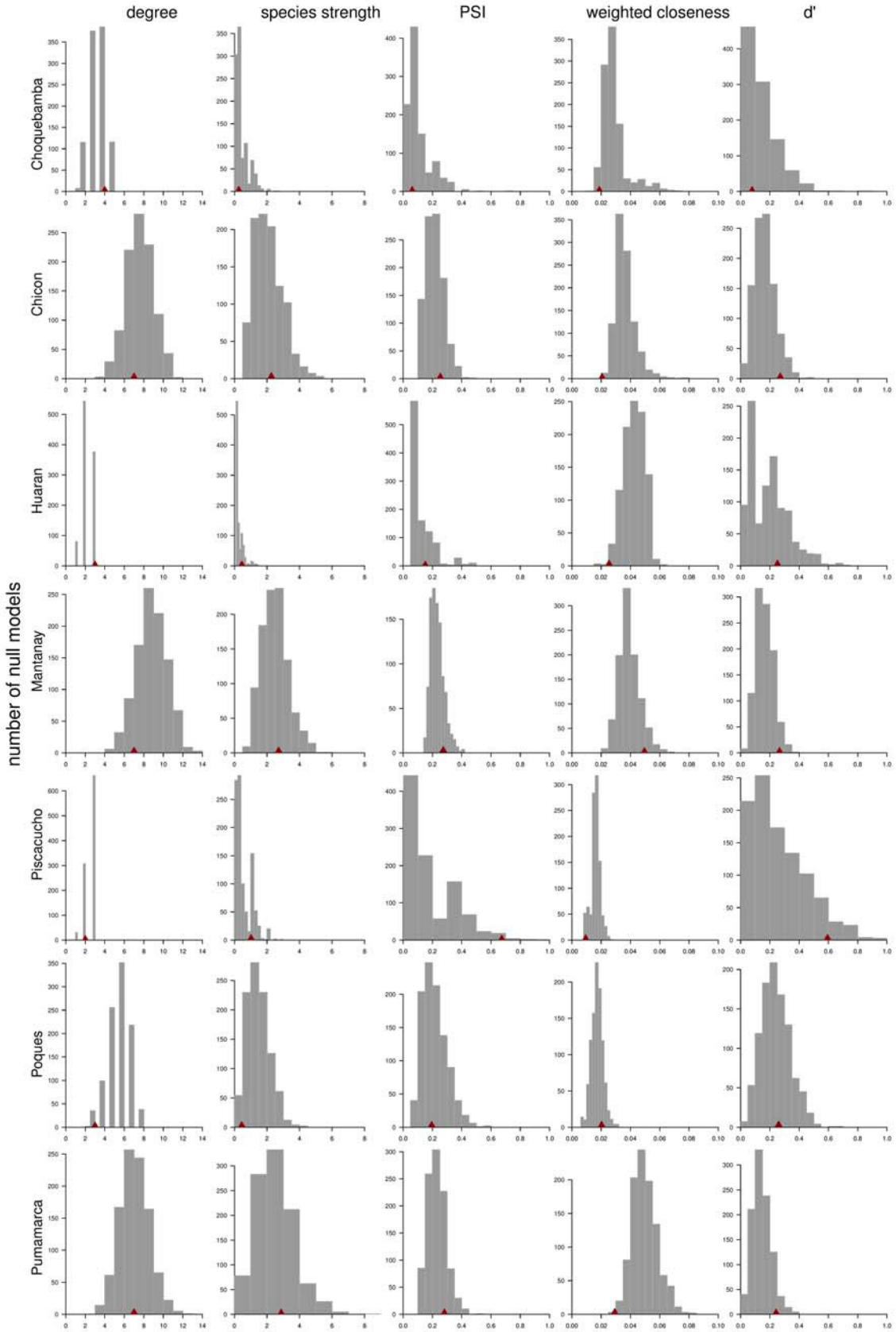

Figure S3. Observed and null model specialisation values of *Bombus funebris* for the analysis of specialisation shift. Histograms illustrate the distribution of 1000 null models and represent the position of a perfect generalist. Red triangles indicate the observed value.

Table S4. Full list of pollinator species surveyed in the Sacred Valley and the total number of visits recorded in which valleys, altitudes, life zones and months. Life zones abbreviations are as follows: mts-S = subtropical montane thorn steppe; mdf-S = subtropical montane dry forest; hmf-S= subtropical humid montane forest; *p*-S – *Polylepis* forest.

Family	**Scientific name**	**Number of visits**	**Huaran**	**Yanacocha**	**Chicon**	**Mantanay**	**Pumamarca**	**Choquebamba**	**Poques**	**Tiaparo**	**Piscacucho**	**Altitude 1**	**Altitude 2**	**Altitude 3**	**Altitude 4**	**Altitude 5**	**mts-S**	**mdf-S**	**hmf-S**	***p-S***	**April**	**June**	**July**	**August**	**October**
Diptera	Diptera sp. 1	36		X	X		X	X	X			X	X	X	X	X	X	X	X		X		X		X
	Diptera sp. 2	3		X	X						X		X	X	X				X			X	X		X
	Diptera sp. 3	5		X		X			X				X		X	X		X	X		X			X	X
	Diptera sp. 4	1		X								X						X							X
	Diptera sp. 5	7				X			X	X	X	X	X	X		X		X	X		X	X		X	
	Diptera sp. 6	2		X	X								X					X						X	X
	Diptera sp. 7	1									X			X					X			X			
	Diptera sp. 8	2		X								X						X							X
	Diptera sp. 9	1		X									X					X							X
	Diptera sp. 10	2		X								X													X
	Diptera sp. 11	7		X	X	X		X		X		X	X		X	X	X	X	X		X	X			X
	Diptera sp. 12	1		X									X					X							X
	Diptera sp. 13	3		X										X		X			X						X
	Diptera sp. 14	9		X						X			X	X								X			X
	Diptera sp. 15	11	X		X	X		X		X	X	X	X	X	X	X	X	X	X		X	X	X	X	
	Diptera sp. 16	2		X		X						X					X							X	X
	Diptera sp. 17	5		X						X		X				X		X	X			X			X
Anthomyiidae	Anthomyiidae sp. 1	3						X	X						X			X			X				
	Anthomyiidae sp. 2	7		X				X					X	X	X				X		X				
Bibionidae	Bibionidae sp.	2							X					X		X			X		X				
Chironomidae	Chironomidae sp.	1						X				X						X			X				

Muscidae	*Muscina* sp. 1	25	X	X						X		X	X		X	X	X	X	X			X		X	X
	Muscidae sp. 1	45		X	X	X	X	X				X	X	X	X	X	X	X	X		X		X	X	X
	Muscidae sp. 2	1								X			X				X					X			
	Muscidae sp. 3	1		X								X						X							X
	Muscidae sp. 4	9					X	X	X					X	X	X			X		X				
	Muscidae sp. 5	24		X			X	X	X			X	X	X	X	X		X	X		X				X
	Muscidae sp. 6	10			X		X	X	X				X	X	X	X		X	X		X		X		
	Muscidae sp. 7	1						X								X			X		X				
Sciaridae	Sciaria sp. 1	1			X									X					X			X			
	Sciaria sp. 2	14			X			X	X	X		X	X	X	X	X	X	X	X		X	X	X		
	Sciaria sp. 3	19		X				X			X	X		X	X	X			X		X	X			X
	Sciaria sp. 4	133			X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X
	Sciaria sp. 5	5					X	X					X		X	X		X	X		X				
Sphaeroceridae	Sphaeroceridae sp. 1	5		X			X	X				X		X				X	X		X				X
	Sphaeroceridae sp. 2	5					X		X		X	X		X	X	X		X	X		X	X			
Sarcophagidae	*Helicobia* sp.	2								X						X			X			X			
Syrphidae	Syrphidae sp. 1	2	X	X								X		X				X						X	X
	Syrphidae sp. 2	64	X	X	X	X		X		X	X	X	X	X	X	X	X	X	X		X	X	X	X	X
	Syrphidae sp. 3	54			X	X		X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	
	Syrphidae sp. 4	1		X									X					X							X
	Syrphidae sp. 5	4									X					X			X			X			
	Syrphidae sp. 6	1			X								X					X					X		
	Syrphidae sp. 7	2	X								X				X	X			X			X		X	
	Copestylum sp. 1	6	X	X		X				X	X			X	X	X			X				X	X	X
	Copestylum sp. 2	11		X						X	X	X	X	X	X	X	X	X	X				X		X
	Eristalis sp. 1	5	X	X			X		X				X		X	X			X		X			X	X
	Eristalis sp. 2	16				X	X		X	X	X	X	X	X	X	X	X	X	X		X	X		X	
	Platycheirus sp.1	20						X			X	X	X			X		X	X		X	X			
	Platycheirus sp.2	19		X	X			X	X	X	X	X	X	X	X	X	X	X	X		X	X	X		X
	Platycheirus sp.3	6		X					X				X		X	X		X	X		X				X
	Toxomerus sp. 1	7					X	X	X		X			X	X	X			X		X	X			
	Toxomerus sp. 2	39		X	X	X	X	X	X			X	X	X	X	X	X	X	X		X		X	X	X

	Toxomerus sp. 3	3	X						X					X		X			X		X			X	
	Tuberculanostoma sp.1	9							X		X	X	X	X	X	X	X	X	X		X	X			
Tachinidae	Tachinidae sp. 1	4			X	X					X	X	X	X		X		X	X			X	X	X	
	Tachinidae sp. 2	5				X				X			X		X				X			X		X	
	Tachinidae sp. 3	3	X						X				X	X					X		X			X	
	Tachinidae sp. 4	1		X								X						X							X
	Tachinidae sp. 5	1				X								X					X					X	
	Tachinidae sp. 6	8				X							X	X				X						X	
	Tachinidae sp. 7	1									X	X						X				X			
	Tachinidae sp. 8	13		X		X				X	X	X	X	X	X	X	X	X	X			X		X	X
	Tachinidae sp. 9	2				X								X					X					X	
	Tachinidae sp. 10	8		X		X		X	X	X		X	X	X				X	X		X	X		X	X
	Tachinidae sp. 11	1							X			X						X			X				
	Tachinidae sp. 12	1			X											X			X				X		
	Tachinidae sp. 13	6		X				X					X			X			X		X				X
	Tachinidae sp. 14	2				X								X					X					X	
	Tachinidae sp. 15	1		X								X						X							X
	Tachinidae sp. 16	1									X		X					X				X			
	Tachinidae sp. 17	1			X											X			X						X
	Tachinidae sp. 18	2									X			X					X			X			
	Tachinidae sp. 19	1						X					X					X			X				
Hymenoptera	Hymenoptera sp. 1	1						X					X						X	X					
	Hymenoptera sp. 2	2								X			X		X			X				X			
	Hymenoptera sp. 3	2				X									X	X			X					X	
	Hymenoptera sp. 4	1								X					X				X			X			
	Hymenoptera sp. 5	1			X								X					X					X		
Apidae	*Apis mellifera*	428	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
	Bombus (*Funebribombus*) *funebris* Smith, 1854	66	X		X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	
	Bombus (*Robustobombus*) *melaleucus* Handlirsch, 1888	14				X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X		X	
	Bombus sp.	2						X					X			X			X	X					
Halictidae	*Lasioglossum* sp.1	4		X			X						X					X							X
Ichneumonidae	*Ophion* sp.	1								X					X				X		X				

Vespidae	Vespidae sp. 1	1						X			X						X		X				
	Vespidae sp. 2	1	X								X						X						X
	Vespidae sp. 3	2						X			X		X				X		X				
	Vespidae sp. 4	2					X							X									
	Vespidae sp. 5	1	X								X												X
	Vespidae sp. 6	1					X					X					X		X				
	Vespidae sp. 7	1				X					X								X				
Coleoptera	Coleoptera sp. 1	5		X		X	X	X			X			X	X		X	X	X		X		
	Coleoptera sp. 2	7			X		X			X	X		X	X	X		X	X	X	X		X	
	Coleoptera sp. 3	9		X	X	X	X	X	X		X	X		X	X			X	X	X	X	X	
	Coleoptera sp. 4	2	X			X					X						X		X				X
	Coleoptera sp. 5	3				X		X			X				X		X		X				
	Coleoptera sp. 6	1							X						X			X		X			
	Coleoptera sp. 7	7				X	X				X	X		X	X		X	X	X				
	Coleoptera sp. 8	1	X										X					X					X
	Coleoptera sp. 9	1							X		X						X			X			
	Coleoptera sp. 10	3						X		X	X			X				X	X	X			
	Coleoptera sp. 11	3							X		X						X			X			
	Coleoptera sp. 12	2	X									X					X						X
	Coleoptera sp. 13	2						X				X		X				X		X			
	Coleoptera sp. 14	1					X								X			X	X				
	Astylus sp. 1	5						X	X	X		X					X		X	X			
Melyridae	*Astylus* sp. 2	4				X	X						X	X	X		X		X			X	
	Astylus sp. 3	15				X		X			X	X	X	X	X		X	X	X			X	
Bruchidae	Bruchidae sp. 1	1						X			X						X		X				
	Bruchidae sp. 2	1						X			X						X		X				
	Bruchidae sp. 3	1								X				X				X		X			
Chrysomelidae	Chrysomelidae sp. 1	1						X			X						X		X				
	Chrysomelidae sp. 2	32		X	X	X		X		X	X	X		X	X	X	X	X	X	X	X	X	
Curculionidae	Curculionidae sp. 1	6				X	X	X				X		X				X	X				
	Curculionidae sp. 2	4				X	X				X			X	X			X	X				
	Curculionidae sp. 3	3				X	X					X		X				X	X				

Coccinellidae	*Eropis* sp. 1	5					X	X	X			X	X			X		X	X		X					
	Eropis sp. 2	9					X		X			X			X				X		X					
	Eropis sp. 3	1							X			X						X			X					
Hemiptera																											
Lygaeidae	*Lygaeus albornatus* Blanchard	15						X				X			X		X	X			X					
Lepidoptera	Lepidoptera sp. 1	5		X					X			X						X			X					X
	Lepidoptera sp. 2	4		X		X							X	X				X							X	X
	Lepidoptera sp. 3	1		X										X					X							X
	Lepidoptera sp. 4	3									X	X						X				X				
	Lepidoptera sp. 5	1		X								X						X								X
	Lepidoptera sp. 6	9			X	X					X	X	X	X	X			X	X			X	X	X		
	Lepidoptera sp. 7	2									X		X					X				X				
	Lepidoptera sp. 8	1								X		X						X				X				
	Lepidoptera sp. 9	1									X				X				X			X				
	Lepidoptera sp.10	1			X								X	X												
	Lepidoptera sp.11	6				X			X	X	X	X		X	X	X		X	X		X	X		X		
	Lepidoptera sp.12	1									X				X				X			X				
	Lepidoptera sp.13	3					X		X			X						X			X					
	Lepidoptera sp. 14	1					X					X						X			X					
Hesperiidae	*Metardaris cosinga* (Hewitson 1874)	34		X								X	X	X	X	X		X	X							X
Trochilidae	*Colibri coruscans (*Gould 1846*)*	7	X		X	X				X		X		X		X		X	X			X	X	X		
	Oreotrochilus estella (D'Orbigny and Lafresnaye 1838)	1			X											X			X			X				
	Aglaeactis cupripennis (Bourcier 1843)	44	X	X	X	X		X		X		X	X	X	X	X		X	X	X	X	X	X	X	X	X
	Aglaeactis castelnaudii (Bourcier and Mulsant 1848)	12	X		X	X								X		X			X	X			X	X		
	Pterophanes cyanopterus (Fraser 1839)	6			X							X				X		X	X				X			
	Metallura tyrianthina (Loddiges 1832)	13	X	X		X						X	X	X		X		X	X	X				X	X	
	Oreonympha nobilis (Gould 1869)	4	X		X								X		X	X			X	X				X		
	Total	1485																								

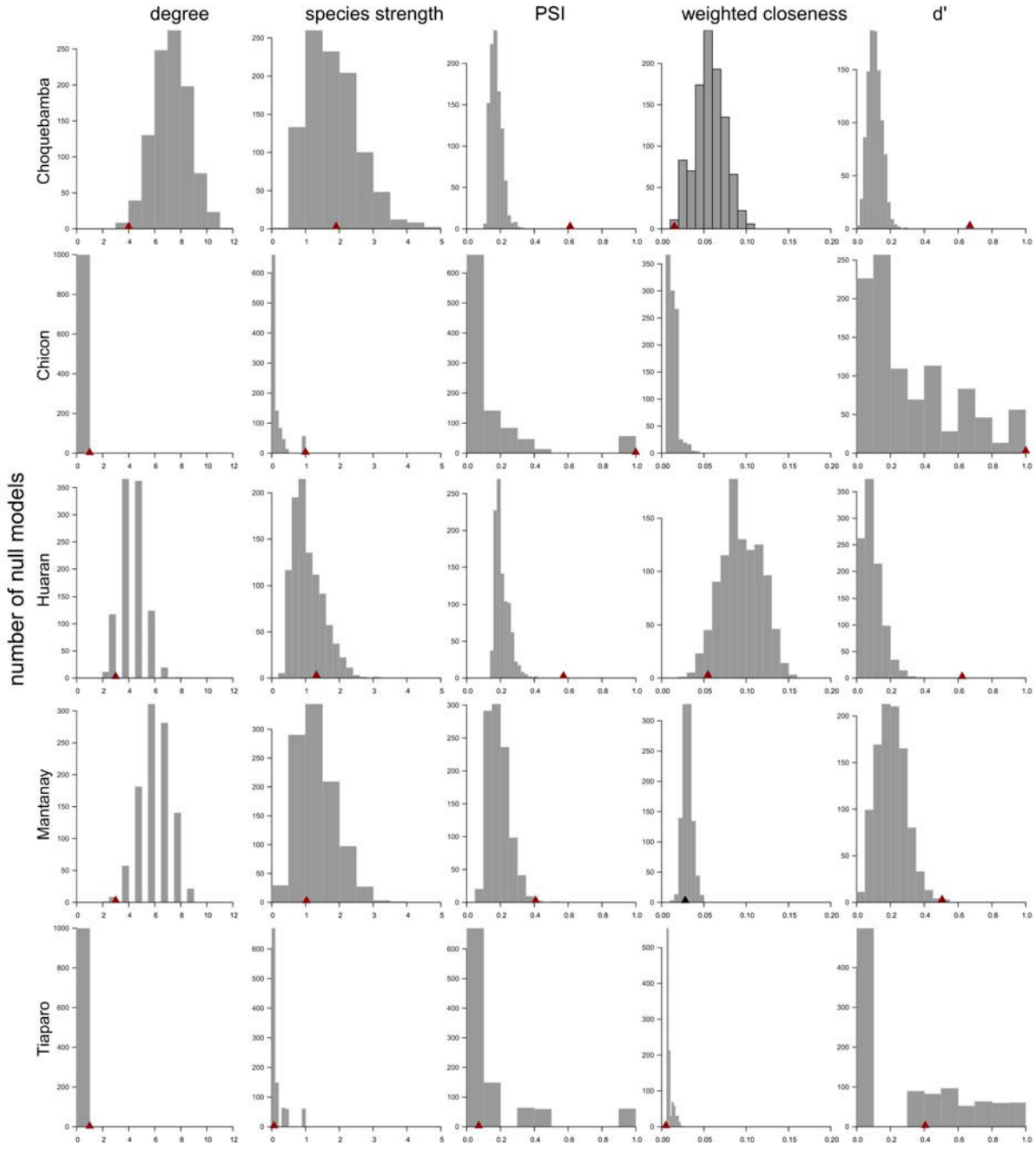

Figure S4. Observed and null model specialisation values of *Aglaeactis cupripennis* for the analysis of specialisation shift. Histograms illustrate the distribution of 1000 null models and represent the position of a perfect generalist. Red triangles indicate the observed value.

Table S5. Summary of observed species level specialisation index values for the most relevant functional groups of pollinators reporting species degree, species strength, Pollination Service Index (*PSI*) weighted closeness and complimentary specialisation *d'*.

		Species Degree	Species Strength	Pollination Service Index (*PSI*)	Weighted Closeness	Complimentary Specialisation *d'*
Diptera	Mean	2.00	0.660	0.210	0.012	0.352
	Median	2.00	0.260	0.140	0.009	0.338
	SD	1.79	0.940	0.200	0.008	0.260
	Maximum	8.00	5.267	1.000	0.030	1.000
	Minimum	1.00	0.000	0.000	0.000	0.000
Apis mellifera	Mean	7.00	3.264	0.463	0.121	0.340
	Median	6.00	3.080	0.463	0.039	0.330
	SD	3.04	1.950	0.180	0.220	0.090
	Maximum	11.00	6.830	0.674	0.716	0.508
	Minimum	3.00	0.310	0.159	0.010	0.219
Coleoptera	Mean	2.00	0.290	0.153	0.011	0.319
	Median	1.00	0.120	0.092	0.008	0.281
	SD	1.80	0.300	0.197	0.006	0.248
	Maximum	7.00	1.634	1.000	0.027	1.000
	Minimum	1.00	0.010	0.010	0.000	0.000
Bombus	Mean	4.00	1.176	0.246	0.020	0.330
	Median	3.00	0.449	0.196	0.020	0.283
	SD	2.22	1.198	0.182	0.012	0.138
	Maximum	7.00	3.071	0.673	0.050	0.594
	Minimum	1.00	0.125	0.062	0.007	0.078
Tachinidae	Mean	1.00	0.171	0.105	0.011	0.223
	Median	1.00	0.259	0.050	0.009	0.123
	SD	0.65	0.259	0.129	0.006	0.244
	Maximum	3.00	1.048	0.500	0.028	0.815
	Minimum	1.00	0.007	0.007	0.004	0.000
Lepidoptera	Mean	2.00	0.313	0.168	0.009	0.344
	Median	1.00	0.125	0.100	0.009	0.386
	SD	0.82	0.395	0.164	0.005	0.264
	Maximum	3.00	1.167	0.583	0.017	0.753
	Minimum	1.00	0.007	0.007	0.000	0.000
Trochilidae	Mean	1.88	0.714	0.349	0.017	0.524
	Median	1.00	0.583	0.244	0.010	0.519
	SD	1.05	0.719	0.317	0.018	0.277
	Maximum	4.00	2.000	1.000	0.064	1.000
	Minimum	1.00	0.024	0.024	0.000	0.000

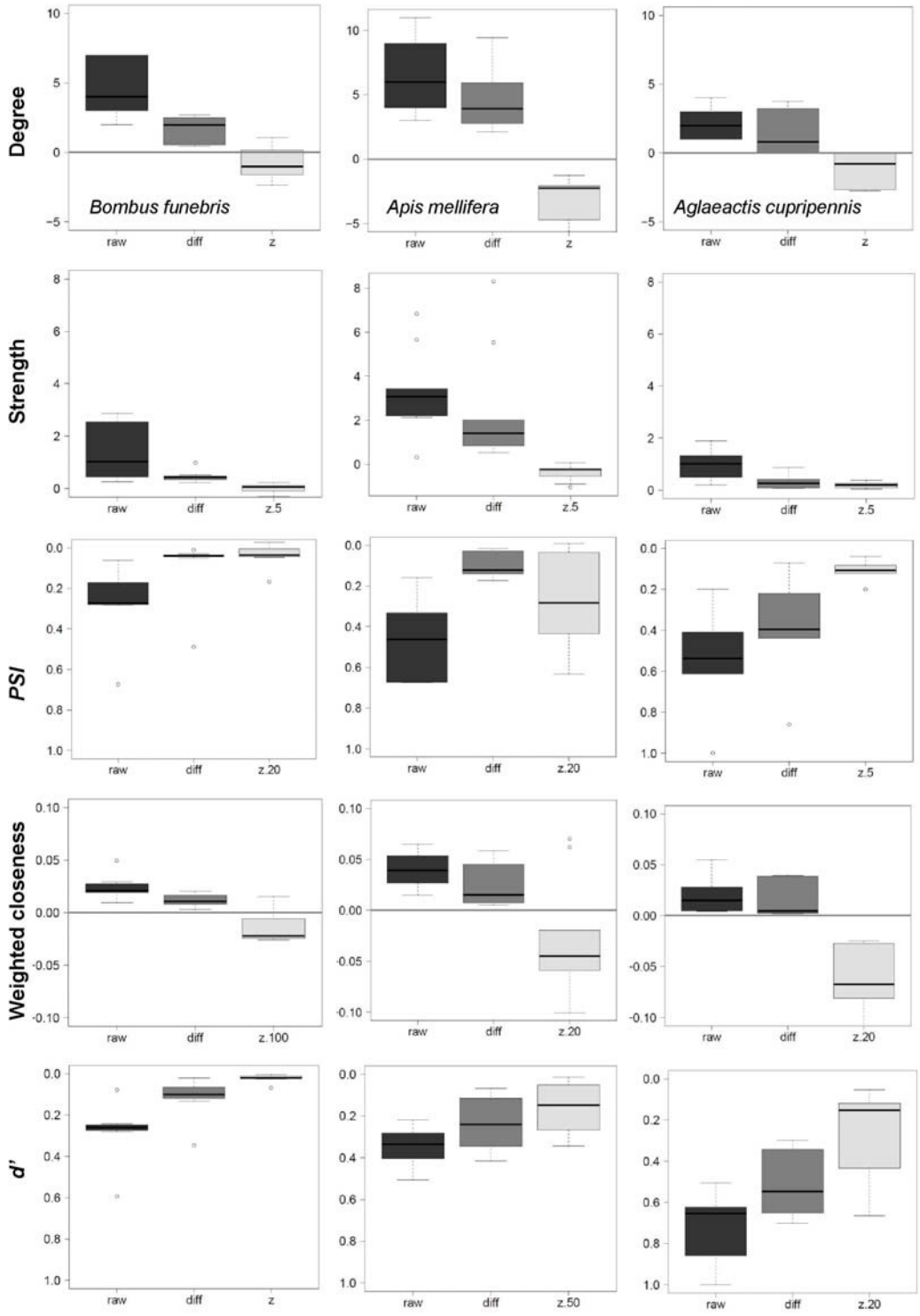

Figure S5. Specialisation index values (degree, strength, Pollination Service Index (*PSI*), Weighted Centrality (WC) and complimentary specialisation *d'*) for *Bombus funebris, Apis mellifera* and *Aglaeactis cupripennis.* The first box represents the raw index values, as computed from the networks. The second box represents corrected values, i.e. differences between raw values and the mean of the null models. They position the boxes relative to a perfect generalist (value of 0). The third is the *z*-scores (divided by a constant for more convenient comparison in the plots).

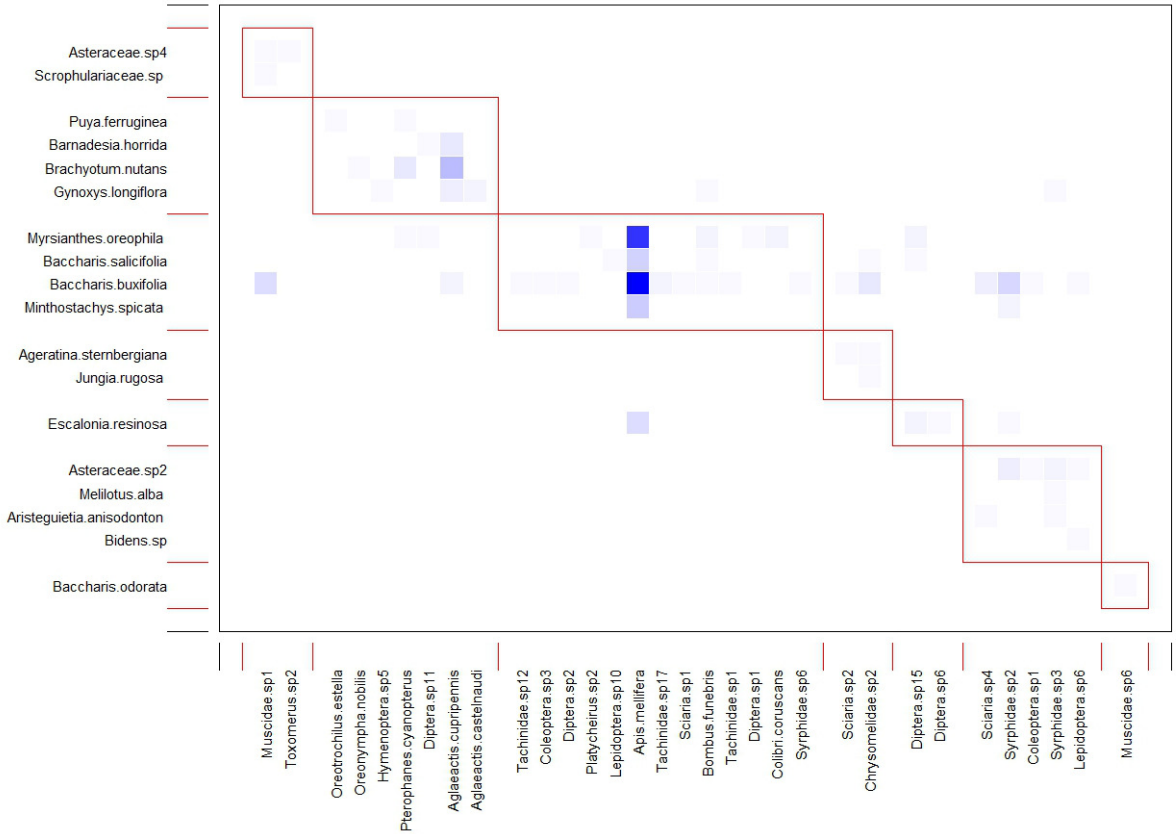

Fig. S6. Chicon featuring seven modules identified by QuanBiMo (with steps = 1e8; $Q = 0.30$; $n = 5$ independent runs). Species are sorted according to their modular affinity, plants as rows and pollinators as columns. Darker squares indicate more frequent interactions. Red boxes delineate the seven modules and cells inside the boxes are the links within modules.
As can be seen, *Baccharis buxifolia* is clearly not randomly distributed over the seven modules, thus linking modules six modules (left to right) into a coherent network. There were no network hubs in this valley. The main pollinator and flower type (left to right): Module 2: medium sized hummingbirds with relatively short bills visiting long tubular flowers; Module 3: dominated by honey bees (module hub) a bumblebee, large flies, tachinid flies, large syrphids and a large hummingbird with a long bill visiting open access and gullet flowers; Module 6: dominated by Syrphid sp. 2 (connector) and Syrphid sp. 3 visiting open access Asteraceae flowers.

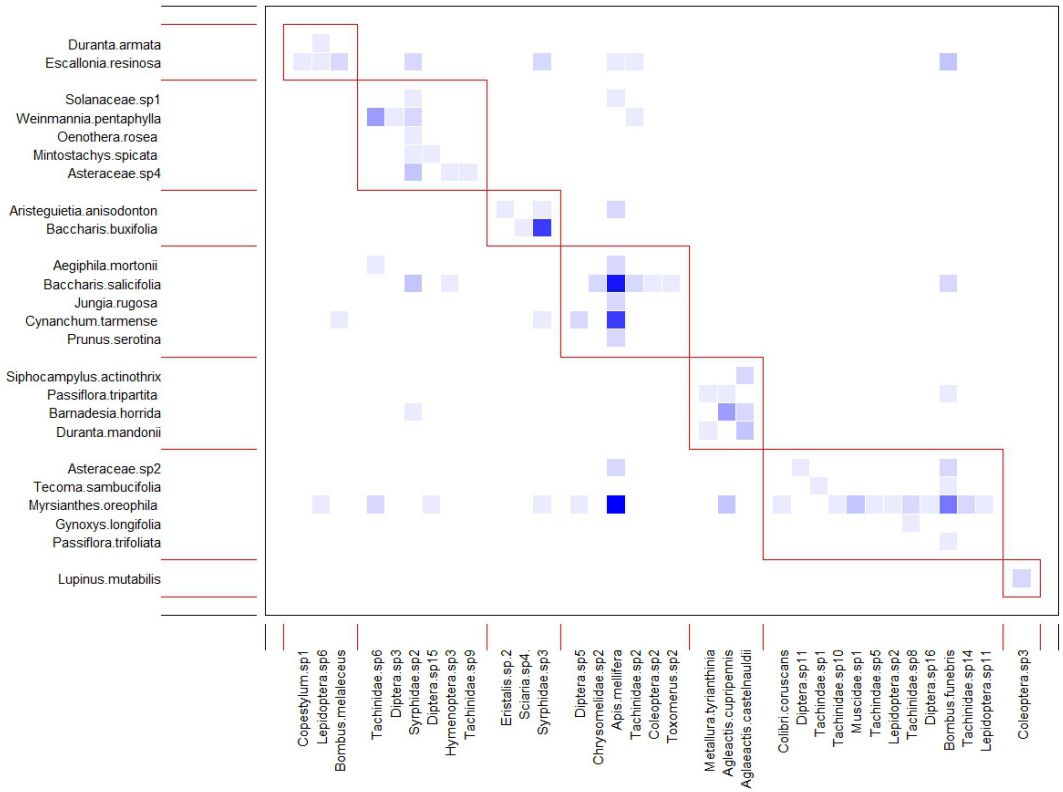

Fig. S7. Mantanay featuring seven modules identified by QuanBiMo (with steps = 1e8; $Q = 0.30$; $n = 5$ independent runs). Species are sorted according to their modular affinity, plants as rows and pollinators as columns. Darker squares indicate more frequent interactions. Red boxes delineate the seven modules and cells inside the boxes are the links within modules.

As can be seen, *Apis mellifera* is clearly not randomly distributed over the seven modules, thus linking five modules (bottom to top) into a coherent network. The main pollinator and flower type (left to right): Module 1: large bumblebee, a butterfly and Syrphid fly visiting small tubular flowers of *Escallonia resinosa* (module hub) and *Duranta armata*; Module 4: dominated by honey bees (network hub), a large syrphid and small beetles visiting mostly open access flowers; Module 5: exclusively medium sized hummingbirds with relatively short bills visiting long tubular flowers; Module 6: dominated by the plant *Myrsianthes oreophila* (connector) and bumble bee, butterflies, large tachinid flies, large flies and a large hummingbird with a long bill visiting mostly long tubular and open access flow