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Research article

Flower-visitor and pollen-load data provide complementary insight into species and individual network roles

Alyssa R. Cirtwill[1], Helena Wirta[1,2], Riikka Kaartinen[1,3], Gavin Ballantyne[4], Graham N. Stone[3], Helen Cunnold[5], Mikko Tiusanen[1,6] and Tomas Roslin[7,8]

[1]Faculty of Agricultural Sciences, University of Helsinki, Helsinki, Finland
[2]Department of Ecology and Environmental Science, Umeå University, Umeå, Sweden
[3]Institute of Ecology and Evolution, University of Edinburgh, Edinburgh, UK
[4]Centre for Conservation and Restoration Science, Edinburgh Napier University, Edinburgh, UK
[5]University of Bath, Bath, UK
[6]Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zürich,Switzerland
[7]Department of Ecology, Swedish Agricultural University, Uppsala, Sweden
[8]Faculty of Biological and Environmental Sciences, University of Helsinki, Helsinki, Finland

Correspondence: Alyssa R. Cirtwill (alyssa.cirtwill@gmail.com)

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Most animal pollination results from plant–insect interactions, but how we perceive these interactions may differ with the sampling method adopted. The two most common methods are observations of visits by pollinators to plants and observations of pollen loads carried by insects. Each method could favour the detection of different species and interactions, and pollen load observations typically reveal more interactions per individual insect than visit observations. Moreover, while observations concern plant and insect individuals, networks are frequently analysed at the level of species. Although networks constructed using visitation and pollen-load data have occasionally been compared in relatively specialised, bee-dominated systems, it is not known how sampling methodology will affect our perception of how species (and individuals within species) interact in a more generalist system. Here we use a Diptera-dominated high-Arctic plant–insect community to explore how sampling approach shapes several measures of species' interactions (focusing on specialisation), and what we can learn about how the interactions of individuals relate to those of species. We found that species degrees, interaction strengths, and species motif roles were significantly correlated across the two method-specific versions of the network. However, absolute differences in degrees and motif roles were greater than could be explained by the greater number of interactions per individual provided by the pollen-load data. Thus, despite the correlations between species roles in networks built using visitation and pollen-load data, we infer that these two perspectives yield fundamentally different summaries of the ways species fit into their communities. Further, individuals' roles generally predicted the species' overall role, but high variability among individuals means that species' roles cannot be used to predict those of particular individuals. These findings emphasize the importance of adopting a dual perspective on bipartite networks, as based on the different information inherent in insect visits and pollen loads.

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Introduction

Pollination is an essential ecosystem service, providing economic value to humans (Klein et al. 2007, Porto et al. 2020) and maintaining populations of many plant and insect species (Kearns et al. 1998). Successful interactions between plants and insects provide plants with pollen transport between conspecific individuals (Miller-Rushing et al. 2010, Schmidt et al. 2016) and insects with food or other resources (e.g. nectar, pollen, scents used to attract mates, or heat; Simpson and Neff 1981). In order to predict the quality of these benefits and their vulnerability to disturbances, there has been longstanding interest in plants and insects' roles within networks, including the extent to which pollinators tend to specialise on particular plants (Blüthgen et al. 2007, Olesen et al. 2010, Potts et al. 2010, Rosas-Guerrero et al. 2014).

In general, most insects visit few plants and most plants are visited by few insects (Bascompte et al. 2003, Jordano et al. 2006, Schleuning et al. 2012). The few generalist species in the community tend to interact with many of the specialists, leading to a nested network structure (Bascompte et al. 2003, Jordano et al. 2006, Vázquez and Aizen 2006, Traveset et al. 2016). Multiple causes have been proposed for the relatively low numbers of plants visited by each insect species (Latty and Trueblood 2020). Insects may visit only the most abundant and rewarding flowers, as predicted by optimal diet theory (MacArthur and Pianka 1966, Waser 1986). Alternatively, insects may be constrained to few plant species based on their morphological or behavioural features, or insects may simply visit few plants despite the presence of apparently viable alternatives, perhaps due to focus on specific search images (Waser 1986, Chittka et al. 1999, Vázquez and Aizen 2006). Abiotic factors such as temperature, productivity, and elevation have also been investigated as drivers of specialisation, albeit with contrasting results (Schleuning et al. 2012, Brimacombe et al. 2022a, b, Luna et al. 2022b, Luna et al. 2022a, Gorostiague et al. 2023). For some species, particularly social bees, floral constancy has been observed in individuals of more generalist species, with each bee tending to visit a consistent small subset of the plants visited by the hive as a whole (Heinrich 1979, Amaya-Márquez 2009, Tur et al. 2014, Brosi 2016).

The perception of relatively specialised communities is largely based upon observations of insects visiting flowers rather than on observations of pollination per se (Bosch et al. 2009, Ballantyne et al. 2015). Flower-visitor sampling typically reveals only a single interaction per individual insect, although in rare cases individuals can be tracked over multiple visits in a small area (Heinrich 1979, Couvillon et al. 2015). An alternative approach which reliably records many interactions per individual is to use the composition of pollen loads carried by insects to infer their recent visits to plants (Bosch et al. 2009, Alarcón 2010, Popic et al. 2013, Bell et al. 2017). Networks of plants and pollinators constructed based on pollen-load data tend to suggest that insects are more generalist than is indicated by visitation data (Bosch et al. 2009, Ritchie et al. 2016), with few insects visiting only one plant species (Lucas et al. 2018). Nonetheless, a few studies suggest no change in specialisation until pollen deposition is taken into account (Alarcón 2010, Ballantyne et al. 2015, Zhao et al. 2019). Importantly, pollen-load data comes with one added feature, which is capturing variation in individual insects' visitation patterns (Tur et al. 2014, Lucas et al. 2018). Such added resolution allows investigation into individual-level specialisation across a community.

Despite these advantages of pollen-load data, it is not clear whether the greater apparent generality of pollinators based on pollen-load data simply reflects the greater amount of information per individual or whether the shift from observing focal plant individuals (i.e. visitation data) to analysing focal insect individuals (i.e. pollen-load data) has additional effects on the interactions observed. Sampling intensity is known to affect network structure, including measures of specialisation (Nielsen and Bascompte 2007, Bosch et al. 2009, Alarcón 2010, Kaiser-Bunbury et al. 2011, Ferrero et al. 2013, Trøjelsgaard and Olesen 2013, Ballantyne et al. 2015). Moreover, in one recent comparison of the same network sampled using visitation and pollen-load data, both approaches missed similar numbers of interactions, particularly involving rare species (Bosch et al. 2009). When combined with varying results of earlier comparisons of specialisation based on visitation or pollen-load data, it remains unclear how the choice between visitation or pollen-load sampling will affect our perception of each species' role in any particular plant–pollinator system.

Here we explore how sampling method affects our understanding of the interactions and the level of specialisation of species in a High Arctic plant–pollinator community (Olesen et al. 2008, Rasmussen et al. 2013). In contrast to previous studies which focus on bee-dominated systems, including specialist species (Bosch et al. 2009, Alarcón 2010, Ritchie et al. 2016, Zhao et al. 2019), this is a notably generalist fly-dominated system (Tiusanen et al. 2016). Previously characterised using visitation data (Olesen et al. 2010, Tiusanen et al. 2016), this system has recently been re-examined using both visitation and pollen-load data in the same year (Cirtwill et al. 2022). Having both types of data collected simultaneously in the same community allows us to compile two versions of the observed interaction network for this community. Using these complementary networks, we compare species' roles in the community, referring both to specialisation and the identity of their interaction partners, and describing direct and indirect patterns of interactions (Fig. 1, Cirtwill et al. 2018a). Using pollen-load data, we also calculate measures of individual insects' roles in the network and contrast these with our species-level measures. We then test to what extent our perception of the

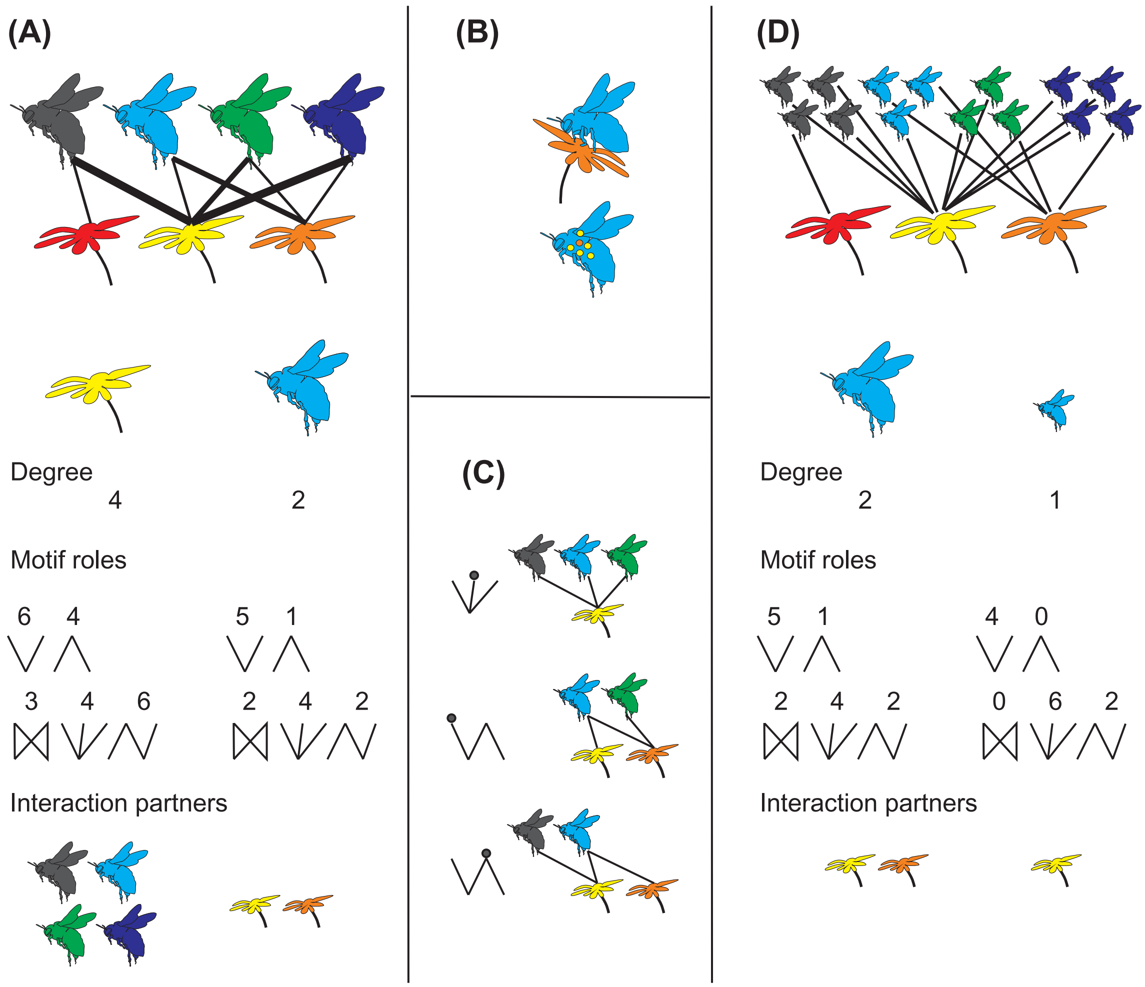

Figure 1. Conceptual illustration of three measures of species and individual roles within networks. Each colour indicates a different species; we take the yellow plant and blue pollinator as examples for more detailed descriptions. (A) We begin by comparing networks of plant taxa interacting with pollinator taxa. Interactions have different strengths (indicated by line widths) depending on how many times we observe the interaction. We describe species' roles in their communities using degree (top; number of interaction partners), motif roles (middle), and the list of interaction partners (bottom). The yellow plant has a degree of four and interacts with all of the available pollinators while the blue bee has a degree of two and interacts with the yellow and orange plants. Each group of n interacting species can be assigned to a motif (C for two examples), with each species taking a particular position within the motif. A species' motif role is the vector of frequencies with which the species takes each unique position within motifs containing 2–5 species (Simmons et al. 2019a) for a full dictionary of motifs and positions). In the interest of space, we show only those motifs with 3–4 species in which the yellow plant or blue pollinator appear. (B) These networks can be constructed based on flower visitation (bee on flower in inset) or insect pollen loads (coloured circles on pollinator in inset). Note that while each insect had only one observed visit, there could be many types of pollen per insect (indicated by different coloured circles). (C) Three pollinators that all interact with the same plant correspond to a different motif (top) than two pollinators and two plants, where one pollinator visits both plants and the other visits only one (middle and bottom). Note that some motifs include more than one position a plant or pollinator can take. For example, the blue pollinator can appear in the lower motif visiting both plants (middle) or only one (bottom). The number of times the species appears in each position is recorded separately in the motif role. (D) When using pollen-load data, we can also construct a network of individual insects visiting plant taxa. Here, we compare individuals' roles in this network to other individuals and to the species' overall role. As all individuals were only observed once, we do not consider interaction strengths in these comparisons. We describe each individual's role in the community using the same metrics as for species. Note that, because the structures of species-species and individual-species networks differ in many ways, we do not compare species and individuals' motif roles.

true interaction network for the community will vary with the perspective assumed. Specifically, we test 1) whether species tend to assume similar roles across method-specific network versions, 2) whether individual conspecific pollinators have similar roles, and 3) whether individual and species-level roles are broadly consistent.

In comparing these networks, it is important to remember that while both insects visiting target flowers and carrying target pollen on their bodies are prerequisites for pollination, both are ultimately proxies and do not provide 'true' pollination networks. To arrive at the latter, one would have to demonstrate the actual transfer of pollen to stigmas (King et al.

2013), but also (ideally) successful fertilization and production of seeds (Inouye et al. 1994, Ne'eman et al. 2010). Given the enormous challenges involved in achieving these steps for a full plant–pollinator network, we are explicitly comparing a visitation and a pollen-load network. Both approaches primarily provide information as to resources used by the animal visitors, albeit in different ways. The visitation network likely reflects nectar/pollen collection by insects, whereas the pollen network is also a function of insect morphology (size, hairiness, etc. Stavert et al. 2016) and flower-handling behaviour.

Although incorporating pollen deposition, fruit set, etc., is required to construct a true pollination network (Ballantyne et al. 2015), visitation and pollen-load data are likely – due to the massive effort involved in collecting these extra data – to remain the most common proxies for pollination. It is therefore essential to understand how observed measures of specialisation differ between these two sampling approaches.

Material and methods

Study site and network construction

Insects (primarily Diptera) visiting flowers were collected in 2016 from the Zackenberg Valley (74°30′N, 21°00′W; northeast Greenland; Schmidt et al. 2019). This sampling used the same sampling protocol as in previous studies (Olesen et al. 2008, Rasmussen et al. 2013, Cirtwill et al. 2022). Sampling targeted the same 500 × 500 m plot as surveyed in previous years, as well as a supplemental plot nearby (see the Supporting information for location). In general, insect visitors to focal plant individuals were captured and identified using DNA barcoding. The pollen carried by these insects was then visually identified. Visitation and pollen-load networks were constructed as in Cirtwill et al. (2022, Supporting information). Note that identifiable pollen was not recovered from all insects. In total, we successfully identified 163 368 pollen grains from 737 out of 1176 insects; the other 439 specimens were included in the visitation network only. See Supporting information for further details on the study site and data collection.

Defining network roles

Here we use three role definitions that describe the number and arrangement of a species' interaction partners in different levels of detail (Fig. 1). Most coarsely, we quantify each species' degree, i.e. the number of interaction partners. At the other extreme, we define each species' role as its exact set of interaction partners. As well as the set of interaction partners, we estimate the strength of each link between a pair of species. For the visitation network, strength was defined as the number of times the interaction was observed. For the pollen-load network, strength was defined as the total number of pollen grains of plant *i* observed on insect species *j*.

To describe species' interactions at an intermediate level of detail, we calculate each species' motif role (Simmons et al. 2019b). Motifs are unique patterns of *n* interacting species that can be seen as one of the 'building blocks' of a network (Milo et al. 2002); all networks can be decomposed into the set of their component motifs, where each set of n interacting species corresponds to exactly one instance of one motif. The frequencies of motifs within a network provides a meso-scale description of network structure (Milo et al. 2002) and a species' participation in these motifs provides a more detailed description of how it fits into the network than degree alone (Cirtwill et al. 2018a).

Here, we consider motifs with two, three, four, and five species (16 motifs in total) in order to provide a reasonably nuanced description of network structure. Within each motif, a species can appear in one or more unique positions. For example, in the four-species motif with two plants and two pollinators where one of each pair is a specialist and one a generalist (creating an 'N'-shaped motif), each plant can occupy either the specialist or generalist position (Fig. 1). To define a species' motif role with the most detail available, we therefore define the motif role as the frequency with which the focal taxon appeared in each position in all two, three, four, and five-species motifs (normalised by the total count across all positions in all motifs). Motif roles were computed using the R (www.r-project.org) function *node_positions* from the package 'bmotif' (Simmons et al. 2019a).

Does each species have a similar role across network representations?

To compare degree (i.e. number of interaction partners), we fit Poisson regressions for plants and insects relating degree in the pollen-load network to degree in the visitation network using the R (www.r-project.org) function *glm* from the package 'lmerTest' (Kuznetsova et al. 2017). As a less-restrictive test, we also fit Kendall correlation tests for the rank of degree of plants and insects (using the R (www.r-project.org) base function *cor.test*). Similarly, we calculated the Kendall rank correlation between link strengths in both networks. We did not test whether link strengths per se were correlated because the weights have different meanings in different network representations (number of observed visits in the visitation network and number of pollen grains carried in the pollen-load network). To compare each species' set of interaction partners between network representations, we calculated Jaccard similarity (union divided by intersection) of partners in each network representation. For easier interpretation, we subtracted this similarity score from 1 to obtain a Jaccard dissimilarity score (J) where higher values mean larger differences, as when comparing degrees between networks. For motif roles, we calculated Bray–Curtis dissimilarity following Baker et al. (2015). Plants included in only one network were omitted from these analyses as it is impossible to compare roles for a species that only appears once. While the above tests give some idea of the absolute differences between species' roles in different representations of the interaction network, they cannot tell us whether these correlations are significant. To do that, we must compare the observed differences to a null model.

Testing whether differences between network representations are significant

To test whether descriptors of species' roles differed more among the two method-specific versions of the network than expected by chance alone, we used a null network approach to obtain a distribution of differences that might be expected if the two observed networks (i.e. visitation and pollen-based) were simply two random draws from the same true network. To do this, we first pooled all observations into a metaweb including all interactions from either observed network. To adjust for differences in numbers of observations per network version, we standardised all link strengths (based on number of insect individuals and number of pollen grains, respectively) within each observed network versions to proportions, thus summing to one. Link strengths in the pooled network were assigned as the average of each such frequency across the two network versions.

From this metaweb including both visitation and pollen-load data, we then recreated 10 000 pairs of 'visitation' and 'pollen-load' networks. Each simulated network was assembled by randomly drawing links (with probabilities weighted by interaction strength) until the number of interactions included in the original network was reached (1176 for the visitation network and 3222 for the pollen-load network). This approach preserves differences in the network that are derived from the greater amount of information obtained per insect individual in pollen-load data, while removing any potential effect of capturing different interactions with different types of sampling.

To next establish whether the metric-specific observed difference between network versions was larger than expected by chance alone, we calculated the difference in species roles between each pair of simulated networks. We then compared the observed difference between the two empirically derived networks (the real visitation-based network and the real pollen-based network) to the distribution of 10 000 differences obtained from pairs of simulated networks. The p-value for the observed difference is simply, by definition, the proportion of null differences more extreme than the observed value.

Finally, we corrected for multiple hypothesis testing. As we expect the p-values for each species to be correlated (that is, we expect that either most species will have more different specialisation between networks than expected or that most species will not have significantly different specialisation between networks), we applied the correlated Bonferroni correction (Drezner and Drezner 2016). When applying the correction, we considered plants and insects separately.

How are species and individual roles related?

While network representations are typically focused on species as nodes, it is the behaviour of individuals that determines pollen transfer patterns. For this reason, we need to validate whether species-level descriptions capture the essential of individual behaviour – i.e. whether roles characterised at the level of species and individual match each other. From this perspective, one key benefit of pollen-load data is that they reveal individual variation in insects' interaction partners through the composition of individual pollen loads. In principle, the same could be achieved in visitation data if many individuals were observed for each plant species, but this is rarely achievable due to time and personnel constraints. We therefore use the pollen-load network to test 1) whether individuals' roles are predictable based on the overall role of their species and 2) whether individuals within a species tend to have similar roles. Note that we have individual-level data for insects only and therefore exclude plants from the following analyses.

Are individual roles predicted by species roles?

To test whether individual degree is predicted by species degree, we fit a Poisson regression relating individual degrees to species degrees for all insects. This regression was fit using the R (www.r-project.org) base function *glm*. Predicting multi-dimensional measures of individuals' roles based on multi-dimensional species roles is more complicated. In general, we expect that individuals' roles should reflect random sub-samples of the roles of their species.

In terms of interaction partners, this suggests that an individual's interaction partners should be more similar to the set of interaction partners for the whole species than to the set of interaction partners for another species. To test this, we calculated Jaccard dissimilarities (1-Jaccard similarity, as above) between each individual's set of interaction partners and 1) the interaction partners of its own species and 2) the interaction partners of all other species. We then used a two-sample t-test to determine whether the individual-own species dissimilarities were smaller than the individual-other species dissimilarities, fit using the R (www.r-project.org) base function *t.test*. As there will be some difference in individual and species-level partners purely due to differences in degree (an individual always interacts with the subset of the partners of the species, and the dissimilarity in interaction partners will be large if this subset is small), we fit an additional model relating Jaccard dissimilarity to comparison type (individual to same species or other species), individual degree, and their interaction. This model took the form of a general linear model with binomial error distribution, fit using the R base function *glm*.

Do individuals have similar roles within a species?

We are also interested in whether individuals of the same species tend to be more similar than expected by chance. As we have an unbalanced sample (i.e. some species with very few or only one individual and hence non-homogeneous variance within groups), traditional ANOVA-based tests are unsuitable. We therefore compare the observed mean differences in role among individuals within a species to a distribution obtained by randomising species identities across roles. This approach avoids the need for any test statistic that relies upon assumptions about the underlying data or their homoscedasticity. As conducting separate tests for each species increases the likelihood of obtaining significant results by chance, we apply the correlated Bonferroni correction to all tests for a given role measure, as above.

For degree, we calculated the mean of absolute differences in degree among all individuals in a species. For interaction partners, we calculated the mean Jaccard dissimilarity (1-Jaccard similarity) among all individuals in a species. For motif roles, we calculated the mean Bray–Curtis dissimilarity among all individuals in a species. In each case, we then compared the observed mean for each species to a distribution obtained by randomising species identities across roles (degree, partners, or motifs) and re-calculating within-species mean differences 10 000 times. The p-value for each difference is the proportion of randomised differences that is less than the observed difference.

We supplemented these comparisons to randomised data by testing whether the amount of within-species variability (where this could be calculated, i.e. where there were multiple individuals) was related to the number of individuals sampled. For degree variability, this took the form of a linear model with Gaussian error distribution. As Jaccard and Bray–Curtis dissimilarities both range 0–1, we fit general linear models with binomial error distribution for dissimilarities in interaction partners and motif roles.

Results

Most species had similar roles in both network representations

Species' specialisation tended to be similar in the visitation and pollen-load networks. A species' degree per se and, for insects, rank of degree were significantly and positively correlated between network representations (Fig. 2; degree per se: $R^2=0.649$, $\beta=0.077$, $p < 0.001$ for plants and $R^2=0.801$, $\beta=0.121$, $p < 0.001$ for insects. Rank of degree: $z=1.68$, $p=0.093$, $\tau=0.230$ for plants and $z=7.23$, $p < 0.001$, $\tau=0.634$ for insects; note that the p-value for plants could not be exactly computed due to tied ranks). Similarly, the rank of link strength was significantly and positively correlated, although the correlation was weaker than for rank of species degrees (Fig. 2, $\tau=0.322$, $z=5.57$, $p < 0.001$; $n=162$ links included in both network representations). When links supported by only one data type (visitation or pollen load) were also included (with link strength set to 0 in the data type where the link was not observed), the correlation was weaker but still significant ($z=2.80$, $p=0.005$, $\tau=0.107$; $n=394$, 158 links were supported by pollen only and 74 by visits only).

Species degrees (number of interaction partners) were significantly higher in the pollen-load network than in the visitation network for six (43%) plants and 25 (36%) insects (Fig. 3). All differences remained significant after applying the correlated Bonferroni correction. Greater degrees based on pollen-load data were expected given the larger number of interactions per individual insect detected by pollen-load sampling. However, after accounting for this difference in the number of interactions per individual, absolute differences in degrees were significantly greater than expected for nine (64%) plants and 28 (40%) insects, all of which remained significant after applying the correlated Bonferroni correction. Thus, for many species the differences in degree that we observe between networks cannot be explained by the greater number of interactions obtained per individual insect in pollen-load data.

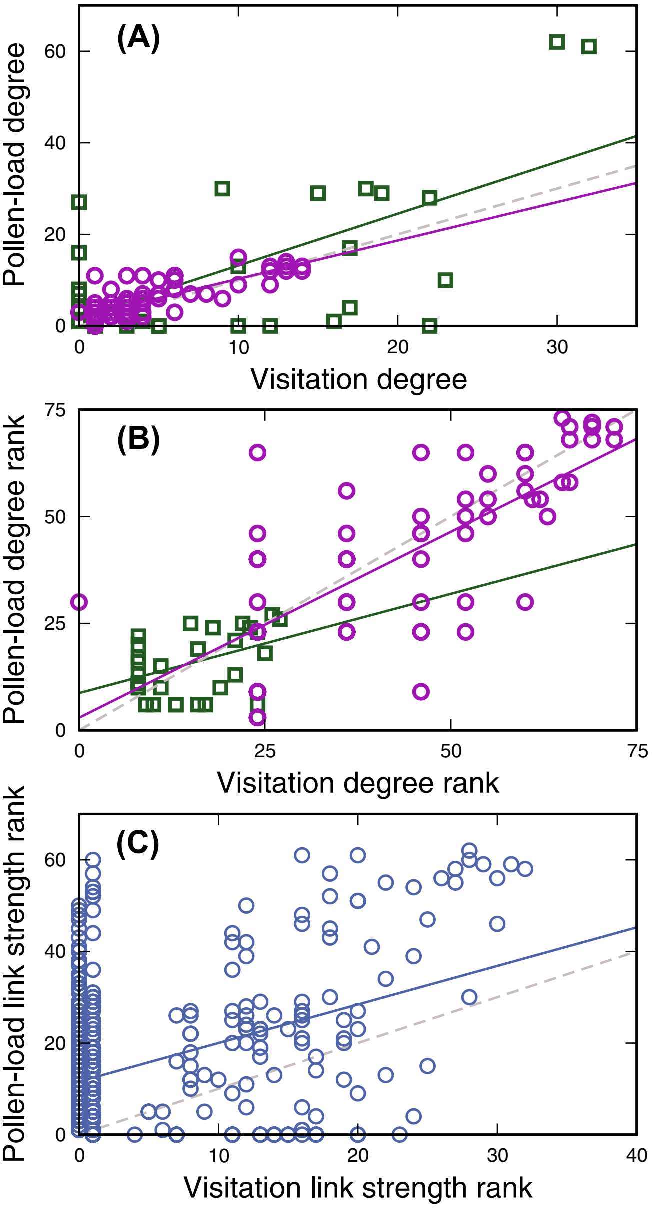

Figure 2. (A) High-degree plants (green squares) and insects (purple circles) in the visitation network tended to also be high-degree species in the observed pollen-load network. (B) Rank of degree was also significantly correlated for plants and insects. (C) The strongest interactions in visitation networks also tended to be the strongest interactions in pollen-load networks (although some rare visitors did have high pollen loads). In each panel, we show the rank of link strength: a higher rank indicates that an insect made more visits or carried more pollen (to/of the focal plant) than other insects. In all panels, the grey dotted line indicates a 1:1 relationship between axes.

Although both networks were sampled simultaneously and continuously over the whole active period, species tended to have quite different sets of interaction partners

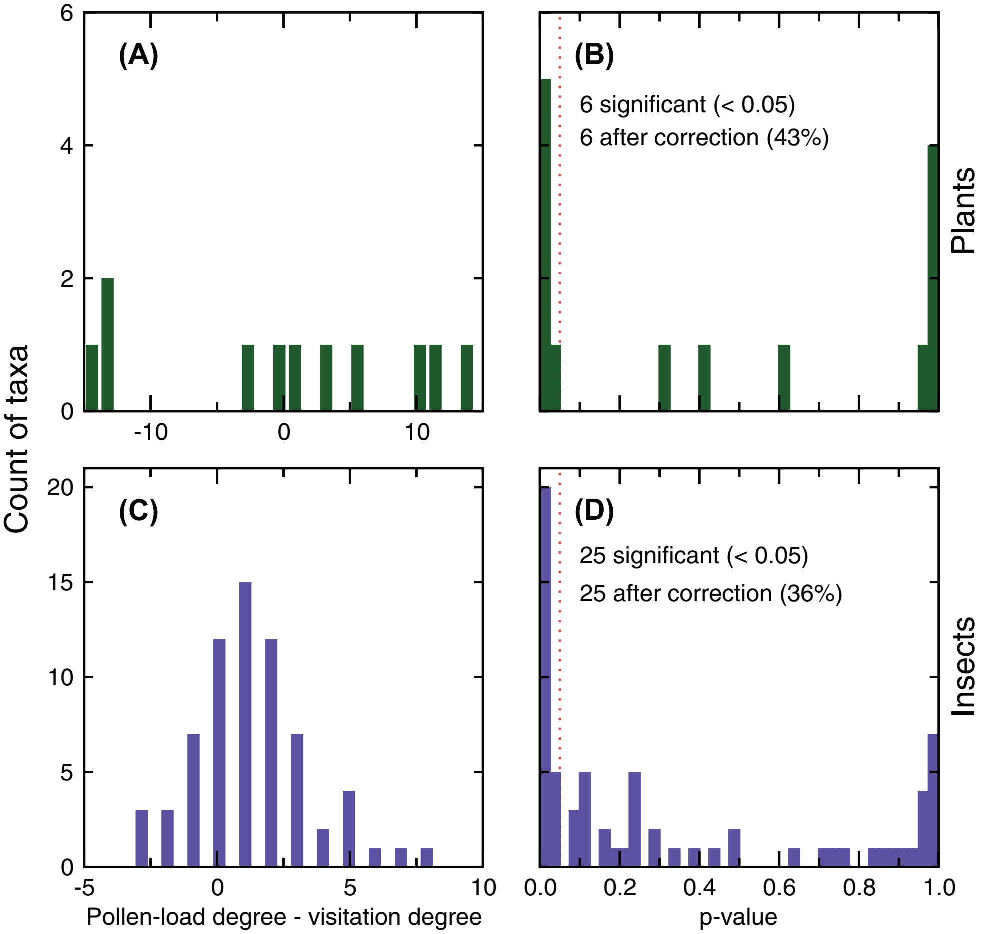

Figure 3. Distributions of differences in degree in visitation and pollen-load networks and distributions of the p-values of these differences. (A–B) for plants, differences in degree could be large but only 6/14 species had significantly more different degrees than expected if visitation and pollen-load networks were drawn from the same distribution of links. (C–D) For insects, differences in degree tended to be smaller, and even fewer (25/69) were significantly more different than expected. p-values were calculated by comparing the observed differences to those obtained when comparing null networks of the same size as the observed networks; the red, dotted line indicates $p = 0.05$.

in the visitation and pollen-load networks (Fig. 4). In several cases, over half of the interaction partners differed between the two network representations. Despite these occasionally large differences, most taxa did not exhibit significantly greater differences in interaction partners than expected by chance. For plants, no taxa showed significant differences. For insects, five taxa (7%) displayed significantly greater differences than expected by chance, all of which remained significant after applying the correlated Bonferroni correction.

Motif roles, however, tended to be significantly different between network representations for plants but not insects. For plants, 12 (86%) species had significantly greater dissimilarity in motif roles than expected by chance (Fig. 5; all remained significant after applying the correlated Bonferroni correction). For insects, 51 species had significantly greater dissimilarity in motif roles than expected by chance (49, 71% remained significant after applying the correlated Bonferroni correction). This means that the apparent motif roles of plants are influenced by differences in which interactions are detected using each type of sampling and not simply the greater number of interactions per individual insect obtained from pollen-load sampling, which also affects insects' roles.

Individual roles were linked to species roles but highly variable

Individual degrees and partners matched species roles

While individual degrees tended to be lower than species degrees, more-generalist species tended to be made up of more-generalist individuals ($\beta = 0.037$, $Z = 5.20$, $p < 0.001$ for a glm of species degree against individual degree). Individuals' sets of interaction partners tended to be more similar to the set of interaction partners for their own species than those of other species ($t_{606} = 2.20$, $p = 0.028$). However, the absolute difference in Jaccard dissimilarities was small (mean of 0.680 for individual to same species versus mean of 0.701 for individual to other species).

The frequently large dissimilarities in interaction partners were partially due to the smaller degrees of individuals than

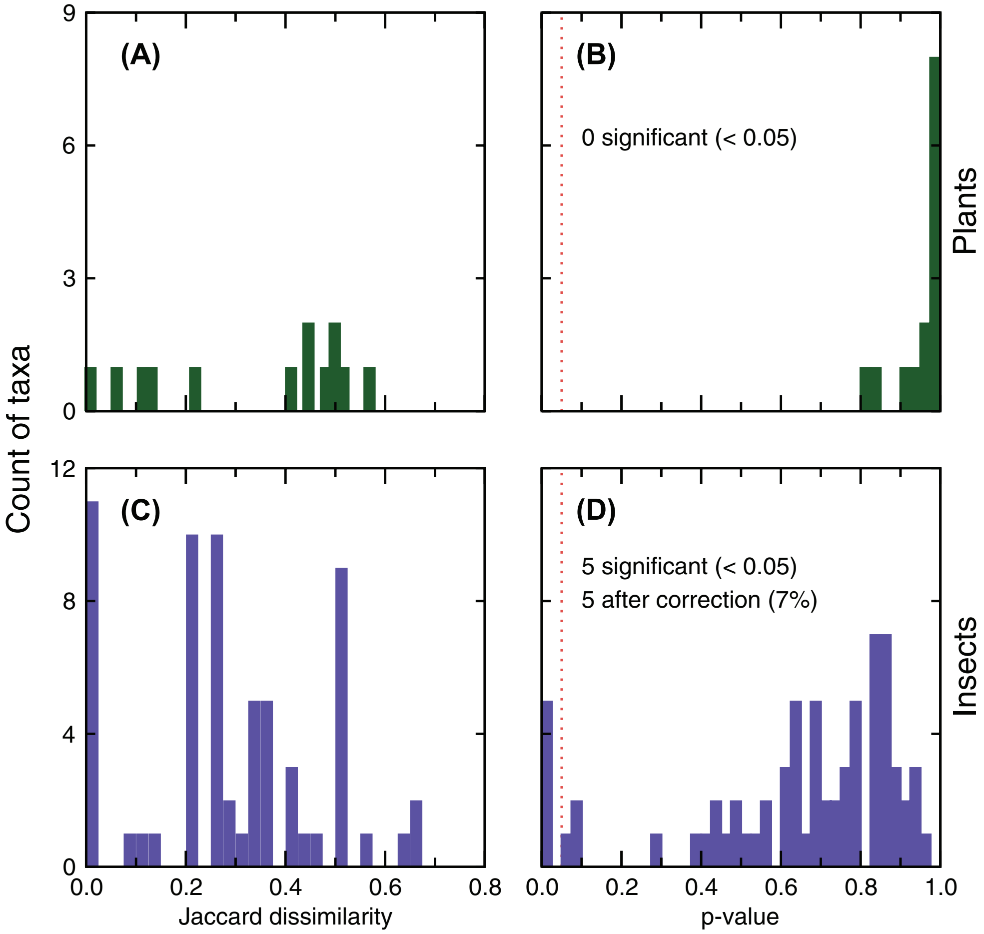

Figure 4. Distributions of Jaccard dissimilarities (1-Jaccard similarity) between species' interaction partners in visitation and pollen-load networks and distributions of the p-values of these dissimilarities. (A–B) For plants, Jaccard dissimilarities were generally small and no species had significantly more different sets of interaction partners than expected if visitation and pollen load networks were drawn from the same distribution of links. (C–D) For insects, Jaccard dissimilarities tended to be larger, but few species (5.69) had significantly more different sets of interaction partners than expected. p-values were calculated by comparing the observed dissimilarities to those obtained when comparing null networks of the same size as the observed networks; the red, dotted line indicates $p = 0.05$.

species (an individual always interacts with some subset of the partners of the species). Dissimilarity between an individual's interaction partners and a species' interaction partners decreased with increasing individual degree ($\beta_{degree} = -0.145$, $p < 0.001$) and this decrease was more than twice as steep when comparing individuals to the partners for their own species ($\beta_{degree:same} = -0.157$, $p = 0.009$; Fig. 6). Thus, high-degree individuals tend to converge on the interaction partners of their species much faster than on the interaction partners of other species.

Individual roles were generally not consistent within species

There were 31 insect species where at most one individual had observed interactions, for which we could not calculate within-species variability for any role measure. Of the remaining 44 species, 20 showed greater intraspecific similarity in degrees than expected, with 14 (31.8%) remaining significant after applying the correlated Bonferroni correction. Even fewer species (11) had significantly greater similarity in interaction partners than expected, with only nine species (20.5%) having significantly greater similarity in sets of partners after applying the correlated Bonferroni correction. Only five species had significantly greater motif-role similarity than expected (11%; all remained significant after correlated Bonferroni correction). Species with more individuals sampled tended to have larger within-species variability in degree ($\beta_N = 0.132$, $p = 0.0449$) but did not show any significant trend in the dissimilarity of their interaction partners ($\beta_N = 0.00258$, $p = 0.903$) or motif role dissimilarity ($\beta_N = -0.00922$, $p = 0.804$).

Discussion

Characterising the roles of plants and insects within pollination networks is an important step towards understanding population dynamics of, and services provided by, both taxonomic groups. However, these characterisations are likely to depend both on whether sampling targets visitors to focal plants (visitation data) or pollen on focal insects (pollen-load data) and on whether species or individuals are considered.

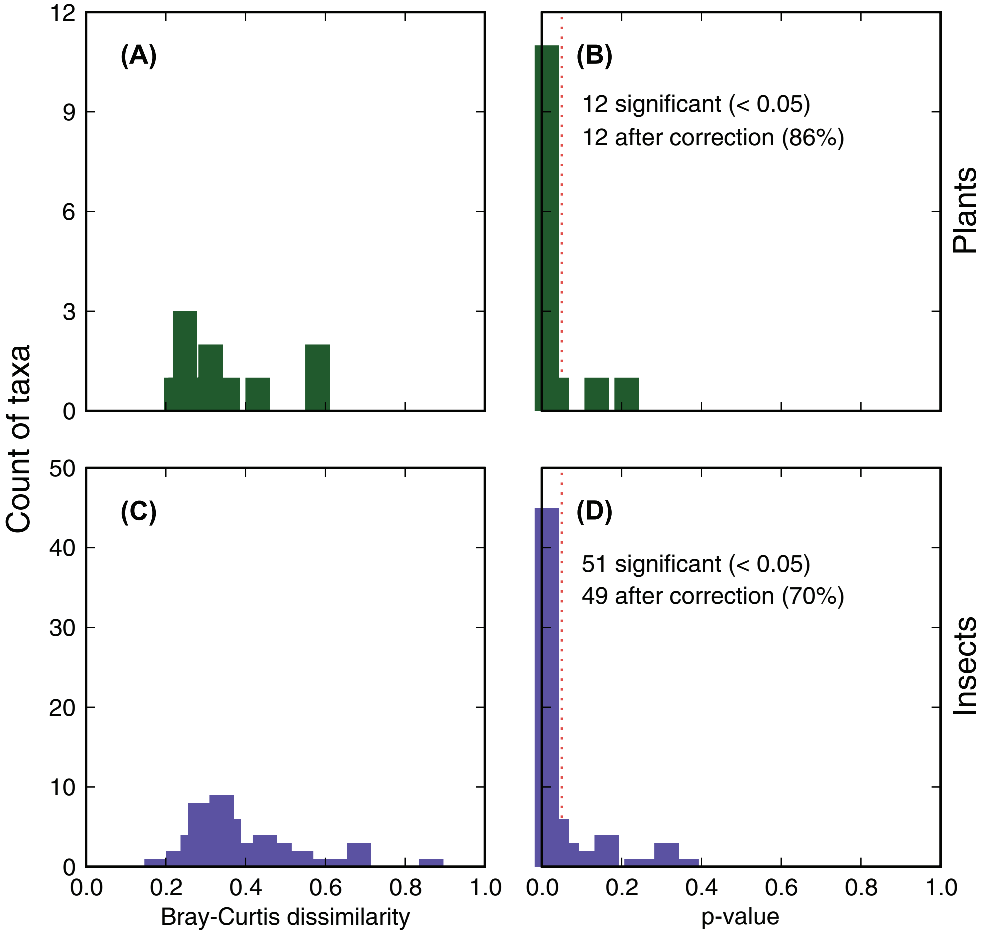

Figure 5. Distributions of Bray–Curtis dissimilarities between species' motif roles in visitation and pollen-load networks and distributions of the p-values of these dissimilarities. (A–B) Most plants (12/14) had significantly more dissimilar roles than expected if visitation and pollen-load networks were drawn from the same distribution of links. (C–D) Most insects (51/69) also had significantly more dissimilar roles than expected. p-values were calculated by comparing the observed dissimilarities to those obtained when comparing null networks of the same size as the observed networks; the red, dotted line indicates $p = 0.05$.

Using a Diptera-dominated pollination network from the Zackenberg valley (northeast Greenland) as a case study, we find that species roles are similar (with some important exceptions) when characterised by different sampling strategies, even when both types of sampling were conducted throughout the whole active season. We also find that individuals' degrees and sets of interaction partners (but not motif roles) tend to be highly variable within a species but tended to converge on the species-level role, especially for individuals with many observed interactions. However, individual roles within a species were highly variable. This highlights the risks of basing estimates of a species' position in a network on few observed individuals, and of assuming that all individuals behave in the same way as the species as a whole.

How does sampling methodology shape the Zackenberg network?

Descriptions of species' roles based on visitation and pollen-load data were broadly similar, but far from identical. Absolute degree, ranked degree, and interaction strength were all significantly and positively correlated between network representations, even though the correlation was stronger for degree than for interaction strength. These differences were largely explained by the greater number of interactions per individual insect that are revealed by pollen loads – where the pollen an insect carries reflects the visits made over recent days or weeks. Sets of interaction partners could be quite different between the two network realisations, but these differences could largely be explained by accounting for differences in the number of links detectable per individual insect using the two sampling approaches. Motif roles, on the other hand, were more different between the sampling methods than expected for many species. Because this measure of a species' position in the network relies upon both the focal species' interaction partners and the partners of those partners, relatively small differences in the number and set of interaction partners observed can quickly multiply to large differences in motif roles. These contrasting levels of difference, and the extent to which observed differences

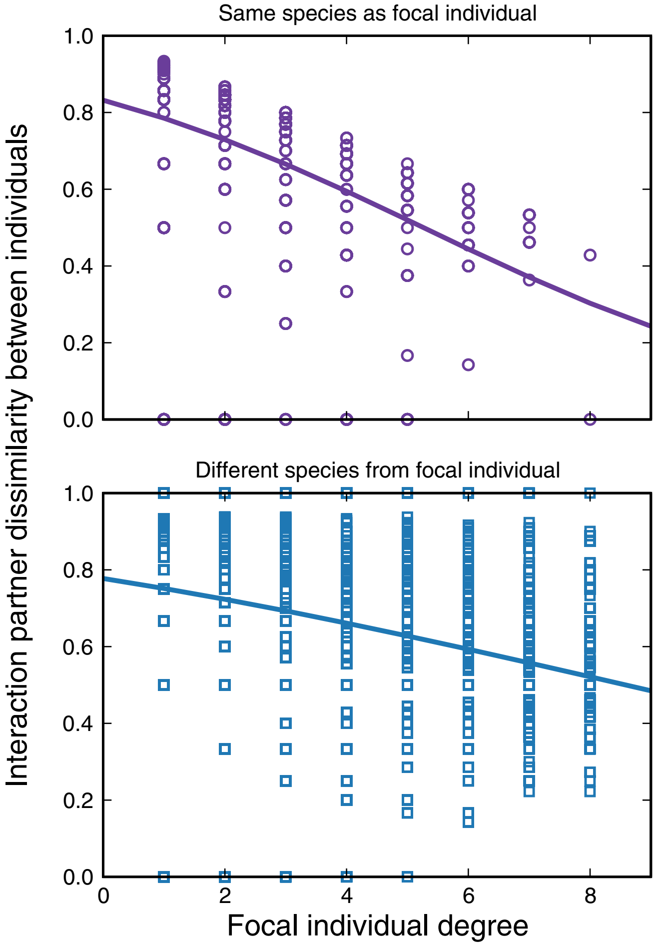

Figure 6. The interaction partners of a focal individual and any other individual insect tended to converge as the focal individual's degree increased, but this convergence was twice as fast when compared to another individual of the same species (top).

can be attributed to different amounts of information given by visitation and pollen-load data, provides a clear takeaway message: neither of the sampling methods alone is likely to provide the full story on a taxon's role in a pollination network.

On the one hand, species that are identified as generalists by visitation data are typically also generalists according to pollen-load data (and vice versa). Likewise, an interaction that is strong in one type of observed network is also generally strong in the other. However, as Fig. 2C shows, either carriers of large amounts of pollen or frequent flower visitors can be overlooked. These missing (strong) interactions mean that species' observed degrees or sets of interaction partners will not tell the whole story, regardless of the sampling strategy used. Moreover, the meaning of these missing (and observed) interactions depends on whether we consider the plant's or insect's perspective on the interaction.

Previous studies in bee-dominated, warm temperate systems have also found that both visitation and pollen-load sampling missed some interactions (Bosch et al. 2009, Alarcón 2010). Bosch et al. (2009) suggested that many observed visits that did not result in pollen transport will correspond to small insects visiting flowers with large corollas where they simply bypass the anthers. Alarcón (2010), on the other hand, reported that > 25% of the insects sampled did not carry pollen from the plant they were captured upon, suggesting that insects visiting plants without carrying pollen may be common. Indeed, Alarcón (2010) found that plants' and insects' degrees were lower in the pollen-load network than the visitation network, whereas Bosch et al. (2009) found the opposite. While we found that mean degrees were higher in the pollen-load network, consistent with Bosch et al. (2009), this pattern differed with the level of detail examined. At the species level, > 50% of taxa showed statistically similar degrees in both network representations. These findings may be partly attributable to the fact that the Zackenberg pollinator fauna is dominated by flies, which are small and relatively smooth and therefore likely collect fewer pollen grains per visit (Stavert et al. 2016). It is possible that more individuals are required in such systems to capture most of the interactions per species. Together with the substantial variation in the Zackenberg pollination between years (Cirtwill et al. 2018b), this possibility makes us hesitant to assume that interactions included in the flower–visitor network but absent from the pollen-load network necessarily represent insects 'cheating', as suggested by Alarcón (2010). While individual flies may rarely carry pollen from some plants, visits which are rare on a per-individual basis may be common at a community level if these insect species are abundant, or interactions which are rare in one year may be common in others (Bosch et al. 2009). In addition, our study system is much more generalised than either Bosch et al. (2009) or Alarcón (2010). Flowering tends to be both brief and variable in high-Arctic plants (Høye and Forchhammer 2008, Kankaanpää et al. 2018, Schmidt et al. 2023), and insects with long active periods (for which a single plant is unlikely to flower for the whole active season) are known to be more generalist in this system (Olesen et al. 2008). As these long-active insects are likely to be encountered throughout the flowering season, including at times when some of their plant partners are not flowering, visitation and pollen-load sampling may thus provide similar pictures of generality when integrated over the season. Pollen-load data may thus be most valuable in systems that are thought to contain mainly specialists, where the extra level of per-individual detail can confirm or deny this hypothesis.

Apart from identifying species' roles within a network, it is important to consider which ecological processes best match each type of sampling. Pollen-load data are a closer proxy for pollination than are visitation data, as pollen loads reflect insects which could deliver pollen to a conspecific plant individual (Willmer 2011). Visitation sampling, which detected many interactions not reflected in the pollen-load network, may over-estimate the number of true pollinators of a plant. Note that, from a plant's perspective, it matters little whether any conspecific pollen an insect carries was collected on a visit to the corresponding plant or through secondary pollen acquisition: when an insect might pick up pollen of a plant species *a* by visiting plant species *b* if another insect previously deposited pollen from plant *a* on plant *b*. The insect carrying conspecific pollen is a potential pollinator regardless of the proximate source of this pollen unless secondary pollen acquisition is strongly associated with much older and less-viable pollen, which to our knowledge is not the case. Pollen-load data, however, are also not a foolproof guide to pollination service. Insects differ greatly between and within taxa on the amount of pollen they deposit per visit (King et al. 2013, Stavert et al. 2016, Cirtwill et al. 2022), such that an insect that carries abundant pollen may still be a poor pollinator if that pollen is carried in a location that does not contact stigmas or is groomed off and/or consumed or stored, or if it mainly deposits self pollen on a self-incompatible stigma (Morris et al. 1995, King et al. 2013).

Incorporating information on pollen deposition and fruit set can further change our perception of species' roles in a community. For example, if a plant is visited by many insects but most fail to deposit conspecific pollen, then that plant may be understood as a specialist associate of those insects that do deposit conspecific pollen despite its variety of visitors (Alarcón 2010, Ballantyne et al. 2015). In one study of a very low-diversity, bee-dominated temperate system, Ballantyne et al. (2015) found that incorporating information on the pollen deposited during a single visit increased the measured specialisation of both plants and insects. Like Alarcón (2010) and unlike Bosch et al. (2009), many flower visits did not result in pollen deposition. This seems to be related to foraging behaviour, with pollen foragers depositing more pollen than nectar foragers (Ballantyne et al. 2015, 2017). Similarly, pollen deposition on flowers increased with the amount of time spent on the flower (Bernauer et al. 2022). If this finding holds true across systems, it is possible that other adaptations which increase the time spent in a flower (e.g. basking or mating in flowers) may also increase a pollinator's effectiveness. However, the opposite may also be the case if shorter visits lead to less self-pollen deposition and more cross pollination between plants (e.g. ants promoting outcrossing by scaring off pollinators when they visit flowers; Villamil et al. 2022). However, several studies of fruit set emphasize the importance of pollinator abundance (i.e. visitation frequency) and highlight the potential for visitor diversity to contribute to fruit set (Eeraerts et al. 2020, Martins et al. 2015, Bernauer et al. 2022). Indeed, in one case visitors depositing different amounts of pollen per visit nevertheless yielded similar fruit and seed set, thus the number of visitors counted (Park et al. 2016). We may then conclude that while the collection and deposition of pollen by flower visitors is an essential component of pollination, visitation frequency remains a vital parameter to fully understand pollinator importance (Ballantyne et al. 2015, 2017).

Visitation data may be particularly valuable when the aim is to fully capture insects' resource use. The reward for visiting a flower is generally food, either nectar or pollen, but may also include other benefits such as heat or mating opportunities (Simpson and Neff 1981). Obtaining some of these non-food rewards may not lead to pollen being deposited on insects' bodies; similarly, insects may obtain nectar without providing pollen transport due to morphological mismatch or specific behaviours (like nectar theft or robbing; Inouye 1980). In general, therefore, visitation data provide a more inclusive view of the plants used by insects than do pollen-load data, though it must be remembered that not all of these interactions will be mutually beneficial to insect and plant (Alarcón 2010). That said, comparing the interactions recorded in visitation and pollen-load data may reveal non-mutualistic interactions that give insects some benefit while plants are negatively affected (as with nectar robbing) or experience little effect (e.g. from an insect basking on petals).

Taken together, our results indicate that visitation and pollen-load data give similar insights into specialisation but far from identical descriptions of how species fit into ecological networks. While summary statistics such as degree may be similar, regardless of the approach, higher-dimensional descriptions of a species' role such as the list of interaction partners or motif roles are more susceptible to random variation due to sampling. For motifs and other measures that incorporate information on indirect interactions or broader network structure as well as a focal species' direct partners, these small differences can combine to give significantly different observed roles. Moreover, both sampling strategies tend to neglect intraspecific variation that can reflect the rewards obtained by plants and insects, and both are ultimately only proxies as it is not feasible to track the outcome of any particular visit or fate of any particular pollen grain across a whole community. To combat these deficiencies, it is best to combine multiple sampling approaches wherever feasible (ideally including some measure of pollen deposition by different insect species, the level of selfing by different plants, etc.). Where only one type of sampling is possible, researchers should bear in mind the strong possibility that they are working with only a partial view of the system, and exercise caution when addressing the details of network structure and functioning.

How do individual roles relate to species?

One of the major strengths of pollen-load data is that they provide data at the level of individual insects (though not individual plants). This greater resolution allows us to consider how individual roles relate to those of species. Specifically, we tested whether individual-level roles matched the overall role of the species and whether individuals had consistent roles within a species. Briefly, individuals generally had similar roles to their species role, but roles were quite variable for individuals within a species. These results are consistent with earlier work showing substantial intraspecific variability, especially for species with high abundance and/or long active periods (Tur et al. 2014). This means that while species identity does predict how individuals fit into their communities, we cannot use species-level data to estimate what any particular individual may do (Heinrich 1979).

Fitness consequences to flowers from differing roles

The consequences of the mismatch between species and individual roles depends on the taxonomic perspective we consider. For plants, where outcrossing relies on the same individual insect visiting multiple individuals of a plant species, understanding individual roles is especially important. Low specificity (generalism) in pollinators implies the potential for frequent switching between plants and, therefore, lower-quality pollen transport. Assuming that co-flowering plant species receive pollen from the same part of the body of a shared pollinator, a generalist pollinator could deposit pollen from many plant species; in empirical studies, heterospecific pollen may constitute up to 70% of the pollen load (Arceo-Gómez and Ashman 2011). Heterospecific pollen deposition may decrease plant fitness and reproduction through several mechanisms, including the clogging of stigmas, allelopathic inhibition of pollen tube growth, and takeover of ovules (Morales and Traveset 2008), resulting in decreases in plant reproductive success (Ashman and Arceo-Gómez 2013). What is more, pollen is constantly lost between visits along the visitation sequence, further lowering the efficacy of pollination (Bateman 1947). Where generalist pollinators are made up of more-specialised individuals, however, there is less risk of heterospecific pollen deposition and pollen loss. This individual-level specialisation (flower constancy) has been shown in bumblebees (Heinrich 1979, Somme et al. 2015) and is also consistent with the lower individual-level than species-level degrees in our dataset (though we found that more-generalist species also had more-generalist individuals). However, researchers should also note that visitation rates may be lower than expected if only some individual pollinators visit a focal plant. Understanding individual roles of insects can, therefore, give a much better indication of the pollination service that each taxon is likely to provide.

Fundamental versus realised niche of insects shown by species' and individuals' roles

From an insect's perspective, individual and species roles are both relevant to population survival, as both individuals and the species as a whole must obtain sufficient resources to survive and reproduce. Here, the interaction partners of an individual and a species can be thought of as representing somewhat different phenomena. At the species level, the overall set of interaction partners observed over time will be akin to the fundamental niche, reflecting the range of species that can be interacted with. Of this wider set, any individual at a given time and place will typically encounter a more limited range of interaction partners. This can be seen as the smaller realised niche of the individual, i.e. of the set of partners with which it does interact.

The individual-level realised niche will be shaped by resource (flower) availability, but also a number of other factors. For example, resource use by an individual may reflect individual-level preferences (Latty and Trueblood 2020), limitations on individual memories (Chittka et al. 1999), habituation, or learning (Leadbeater and Chittka 2007). Taking all of the above into account, realised interactions will also be constrained by the need to balance different nutritional needs. Interactions with a potential resource species will therefore depend on the individual's fundamental niche (i.e. the set of species it can interact with), its environment (the set of available resources), and its personal history (learning, preferences, and the set of resources previously visited).

Although both visitation and pollen-load data used in this study were collected over the whole active season, pollen-load and visitation data sampled during shorter term periods may also provide different views of a species' or individual's niche. Pollen often remains on an insect's body for some time after the relevant flower was visited, meaning that pollen-load data reflect an insect's interactions over a longer time period than a single flower-visitor survey. When constructing networks based on a limited sampling period (especially 'snapshot' networks which may reflect a single day), visitation data are then more reflective of an insect's realised niche at a particular phenological stage, abiotic conditions, etc. Though the residence time of pollen on insects varies widely depending on insect morphology, behaviour, etc., pollen-load data from a short-term sample nevertheless provide a better guide to the insect's fundamental niche, as they reflect visits made under a wider variety of conditions than a brief visitation survey. Where it is unfeasible to survey a site over a whole active season, or where precise phenological information is not important, we therefore suggest that pollen-load data may be a more reliable description of species' roles.

Combining different data types

Given the differences in interactions detected by visitation and pollen-load data, the two approaches are best seen as complementary rather than alternative (Bosch et al. 2009). The question then becomes how to combine these different data. Qualitatively, this is straightforward: binary interactions are included if detected using either visitation or pollen-load data as in Bosch et al. (2009). Combining quantitative data from different sources is more difficult as it is generally not known how many pollen grains are gained or lost per visit. In theory it would be possible to extrapolate a number of visits represented by each pollen load using the number of pollen grains of plant i acquired during a typical visit by insect j, but in practice the number of plant–insect combinations to be tested and the difficulty of sampling the pollen obtained during a single visit introduces major uncertainty in how many visits contributed to a given pollen load. Conservatively, one can count one visit per plant species represented in the pollen load (Cirtwill et al. 2022), perhaps after applying a threshold to reduce the likelihood of false positives due to insects collecting previously deposited heterospecific pollen (Bosch et al. 2009). However, this approach discards the quantitative information provided by the pollen load; even allowing for variation in the amount of pollen released per flower across plant species, the observation that an insect carries more grains of pollen from one plant than another is biologically relevant. One possible way to combine the quantitative information provided by visitation and pollen-load data is by using both data types to estimate pollinator (or plant) importances in a similar way as single-visit pollen deposition and visitation frequency are used to define pollinator importances in Ne'eman et al. (2010), King et al. (2013) and Ballantyne et al. (2015). This can be achieved by defining the strength of an interaction as a function of the proportion of visits made to each plant and the proportion of that plant's pollen found across all insects (Timberlake et al. unpubl., Villa-Galaviz et al. 2023). Note that, as this index was developed in the context of crop pollination, it aims to estimate conspecific pollen transport rather than insect diets. In practice, this is reflected in the fact that visits which do not result in pollen being carried do not contribute to a species' importance score. Where it is important to include flower visits which may benefit an insect without pollen transport (e.g. where small insects are known to obtain nectar from large corollas as in Bosch et al. 2009), the index could likely be modified by summing or averaging, rather than multiplying, importances based on visitation and pollen-load data.

Conclusions

Describing the structure of plant–pollinator networks is essential in order to detect impacts of habitat and climate change on pollination. This endeavour assumes that network structure reflects ecosystem functioning, but our dissection of the plant–pollinator networks of Zackenberg reveals that our perception of the architecture of the network depends on the approach by – and level to which – we choose to describe it (Willmer 2011, Cirtwill et al. 2022). While species-level specialisation was similar when estimated based on visitation or pollen-load data, more-detailed descriptions of species roles differed between network representations. Similarly, individual roles could be quite variable within a species, meaning that the species-level role may be a poor predictor of what any particular individual will do. These mismatches emphasize the importance of 1) adopting a dual perspective on bipartite networks (and acknowledging how our perception of the network will be moulded by the relative effort invested in each approach) and 2) incorporating information on individual variation in interactions. Including as much information as possible can guard against differences in the apparent structure of a pollination network that may be simply artefacts of the sampling technique chosen.

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Author contributions

Alyssa R. Cirtwill: Conceptualization (equal); Formal analysis (lead); Methodology (equal); Writing – original draft (lead); Writing – review and editing (equal). **Helena Wirta**: Conceptualization (supporting); Data curation (lead); Writing – original draft (equal); Writing – review and editing (equal). **Riikka Kaartinen**: Data curation (supporting); Resources (supporting); Writing – review and editing (supporting). **Gavin Ballantyne**: Data curation (supporting); Resources (supporting); Writing – review and editing (supporting). **Graham N. Stone**: Data curation (supporting); Resources (supporting); Writing – review and editing (supporting). **Helen Cunnold**: Data curation (supporting); Resources (supporting); Writing – review and editing (supporting). **Mikko Tiusanen**: Data curation (supporting); Resources (supporting); Writing – review and editing (supporting). **Tomas Roslin:** Conceptualization (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.jwstqjqh1 (Cirtwill et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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