

Ant-plant specialisation depends on network type, but not disturbance, elevation, or latitude.

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Abstract

The ecological factors driving specialisation in species interaction networks along environmental gradients at large spatial scales are poorly understood. Although such drivers can have synergistic impacts, previous work has mainly assessed effects of network type and the abiotic environment separately. We conducted a meta-analysis of existing network data to assess the interactive effects and relative importance of these drivers of specialisation in ant-plant networks at global scales. We collated 74 ant plant networks from 1979–2023, categorised into four network types: plants that provide ants nesting sites (myrmecophytes); plants that provide only food sources (myrmecophiles); plants for which ants disperse seeds (myrmecochories); plants on which ants forage only (foraging). We explored how network specialisation varies between interaction types with elevation, latitude, and anthropogenic disturbance. We used a standard measure of network specialisation ($H2'$), tested whether standardising this against network null models influenced results ($H2'$ z-score), and measured phylogenetic network specialisation (dsi^*). We found that $H2'$ was strongly affected by habitat disturbance, elevation and interaction type in a manner congruent with previous work. However, these effects disappeared once $H2'$ was standardised ($H2'$ z-score). The disappearance of these effects indicates that previous results may relate to variation in network structure rather than specialisation. This is supported by the existence of correlations between network species richness/weighted connectance and $H2'$. Phylogenetic network specialisation (dsi^*) was greater for myrmecophytes than for other three network types. This probably relates to closer co-evolution between partners in myrmecophytic network. Phylogenetic network specialisation did not vary significantly with elevation, latitude or anthropogenic disturbance. Our results demonstrate that ant-plant network types, in this case relating to strength of mutualistic interaction, is the main driver of network specialisation, and that previously reported impacts of latitude, elevation and anthropogenic habitat disturbance are likely to have been mediated via correlations with network size.

Introduction

The factors driving global scale patterns in ecological community structure are becoming increasingly well-known, with elevation, latitude and anthropogenic disturbances playing major roles (Nash et al In press; Romero et al 2020). However, because all organisms within an ecosystem are closely interconnected, variation in the distribution of a particular species in relation to the environment can also affect the species with which it interacts (Forister et al., 2012). In particular, a mechanistic understanding of how human activities alter the structure of ecological networks would be timely. This is because our world is facing accelerated anthropogenic changes, such as global warming, which causes species to move to higher latitudes and elevations (Franco et al., 2006; Memmott et al., 2007), and habitat disturbance, resulting in global diversity declines (Newbold et al., 2015). This variation in community structure is reflected in the structure of interaction networks, with consequences for multiple vital ecosystem services such as pest control (Macfadyen et al., 2011), fish stock production (Moi et al. 2022) and pollination (Burkle & Alarcón, 2011). Furthermore, current network structure predicts ongoing robustness to future natural and human-induced perturbations (Morton et al., 2022).

One of the most fundamental parameters used to quantify variation in network structure is ecological network specialisation (Dormann et al., 2008; Bascompte et al., 2003). The interaction between two groups can range from specialized, where a species interacts with a small subset of available partners and is more vulnerable to change and extinction, to generalized, where a species is less discriminate and interacts with a wide range of partners and is therefore predicted to be more resilient to change (Futuyma & Moreno., 1988). Most studies of network specialisation fall into one of two broad categories: (i) Those that compare different network types, such as different guilds, taxa, or trophic levels without accounting for environmental variation (Blüthgen et al., 2007; Cagnolo & Tavella, 2015; Guimarães et al., 2007), and (ii) Those that examine specialisation in a specific network type across environmental gradients, for example in relation to anthropogenic habitat disturbances or latitude (Schleuning et al., 2012; Gorostiaque et al., 2023; Olesen & Jordano 2003; Luna et al., 2022). Studies from the former category generally reach consistent conclusions, for example, that pollinator networks are more specialized than seed dispersal networks (Blüthgen et al., 2007). However, in the latter category results are often inconsistent between studies, sometimes depending on network size, taxonomic scope and/or geographical range of networks employed. For example, some plant-pollinator systems are more specialized in the tropics (Gorostiaque et al., 2023), while others have been found to be more specialized in temperate regions (Schleuning 2012). The specialisation of plant pollinators on plant species has been

reported to increase with elevation on islands (Olesen & Jordano, 2003), while a recent global analysis concluded that latitude and elevation did not play a role in explaining the degree of pollinator specialisation (Luna et al., 2022). As different network types can interact with environmental gradients in a complex way, the simultaneous evaluation of by drivers of specialisation is currently needed.

The application of different methods across different studies for measuring network specialisation, some of which may be confounded by other aspects of network structure (e.g. network size, network connectance), means that global-scale patterns in specialisation remain unclear (Pellissier et al., 2018). The classical method for measuring specialisation at the network level, the H_2' index, is based on the deviation from the expected probability distribution of interaction frequencies between species (Blüthgen et al., 2006). However, networks of different sizes, involving different numbers of species and links, can vary in the observed value of H_2' regardless of specialisation (Blüthgen et al., 2008). One way to overcome this shortcoming is to compare observed values of H_2' to the distribution resulting from repeated randomisation of the original network (Dormann et al., 2009). This approach can generate a standardised effect size that is less affected by other aspects of network structure (H_2' z-score; Ulrich et al., 2009). Specialisation can also be affected by availability of partner species, in particular those that are closely phylogenetically related (Segar et al., 2020). The distance specialisation index (dsi^*) allows incorporation of phylogenetic relationships and species abundances when quantifying specialisation (Jorge et al., 2014; 2017). However, the degree to which phylogenetic relatedness of resources determines consumer specialisation in networks at large spatial scales is currently unknown. Such phylogenetic signals in the interactions between species within the network are likely the result of reciprocal coevolution or long-term adaptation of consumer species to traits of resource species (Guimaraes et al., 2007). For example, common milkweed (*Asclepias syriaca*) produces chemical defensive compounds that only a small number of closely related herbivorous beetle can tolerate (Rasmann & Agrawal, 2011). A specialist may interact with a suite of closely related resource species because these are more likely to have the traits to which the consumer has adapted (Rasmann & Agrawal, 2011). Hence there is a need to explore how specialisation changed over the gradient of latitude and elevation, and the presence of disturbance, as well as how phylogenetic relatedness of the consumer or host influences these patterns.

Interactions between ants and plants provide a suitable system for exploring changes in network specialisation along environmental gradients. Ant-plant interactions are widespread and involve discrete interaction types with varying degrees of specialisation (Ness & Lach, 2010) that are easily categorised. Furthermore, ant-plant systems are well-studied, making a data collation and meta-analytical approach tenable. Finally, there are well-resolved phylogenies for both groups, allowing exploration of degree of phylogenetic specialisation in networks. Ant-plant interactions range from obligate symbiotic mutualisms such as those between myrmecophytic plants and their long-term ant partners, to non-symbiotic facultative interactions such as myrmecophily and myrmecochory (Heil & McKey, 2003), to less specific interactions in which ants opportunistically forage on plants (Rico-Gray & Oliveira, 2007). We define the myrmecophytic interactions as those in which domatia are formed on plants to provide shelter for ants. Myrmecophilic interactions, are those in which extrafloral nectaries and fruiting bodies are produced by plants as a food source for ants, but plants do not provide domatia as nest sites. Note that some domatia bearing plants also provide extrafloral nectar and food bodies, but we nonetheless classify these as myrmecophytes. Myrmecochorous interactions are those in which ants help plants disperse seeds in exchange for food (Heil & McKey, 2003). Finally, plants can provide a space for foraging and patrolling without any apparent evolved mutualism, which we define here as “foraging” interactions (Rico-Gray & Oliveira, 2007).

Although the specialisation drivers in local ant-plant networks have been studied extensively (Juárez-Juárez et al., 2023) commonality of patterns at global scales remains unclear. Myrmecophytic interactions tend to be more specialised than other kinds of ant-plant interactions, such as myrmecophily, seed dispersal (Blüthgen et al., 2007), and frugivory (Guimaraes et al., 2007), presumably driven by tighter co-evolution due to the greater intimacy of the interaction (Pires & Guimaraes, 2013). These myrmecophytic networks become less specialised with increasing elevation (Plowman et al., 2017) and anthropogenic disturbance (Emer et al., 2013), probably due to loss of partner species. However, they appear to be robust to forest fragmentation (Passmore, 2012). Yet, it is currently unknown how specialisation of myrmecophytic networks varies with

latitude. Interestingly, myrmecophilic networks show levels of specialisation similar to ant-lepidopteran networks (Cagnolo & Tavella, 2015), perhaps because ants are provided with carbohydrate-rich liquid food by plants and lepidopteran larvae respectively in these cases. Interactions in which ant workers forage on plants, but are not involved in mutualisms, are expected to show lower specialisation than other interaction types, although this has not been directly studied. The specialisation of such foraging networks does not change along a 20° range in latitude (Dáttilo & Vasconcelos 2019), although specialisation is reduced following anthropogenic forest disturbance (Corro et al., 2019). Hence, whether different types of interaction between these two ecologically important groups show common responses to latitude, elevation and anthropogenic disturbance remains unclear.

We collated globally distributed network data and used a meta-analytical approach to determine how the specialisation of ant-plant networks varies with interaction type (myrmecophytic, myrmecophilic, myrmecochorous, and foraging), anthropogenic disturbance, latitude, and elevation at global scales, including interactive effects between these predictors. We predicted that myrmecophytic interactions would be the most specialised as these involve tight co-evolutionary adaptations between partners, followed by myrmecophilic, myrmecochorous, and foraging. We also predicted that ant-plant specialisation will decrease with increasing latitude, elevation, and anthropogenic disturbance due to the scarcity of resources in these areas (Brown, 2014).

Methods

Data collection

We followed PRISMA protocol in defining our research questions, conducting data collection, and also in reporting our results using a standardised approach (O’Dea et al., 2021). This was done to minimise potential biased associated with meta-analyses. We include a check list in which our studies followed the PRISMA protocol in our supplementary data (appendix 1) Our meta-analytical approach involved quantification of network patterns through collation of original data, and calculation of network metric using those data, rather than through collation of effect sizes from previous studies (Xing & Fayle, 2021). This manuscript is part of the LifeWebs project, a collaborative effort that aims to use a meta-analytic approach to investigate how interaction networks respond to global-scale environmental gradients (www.lifewebs.net). We collated existing ant-plant interaction networks by searching for publications on the Web of Science (WoS) online database. These published datasets were supplemented by direct requests to authors of papers in which the data had not been published, and furthermore through requests to data authors identified through snowballing (see below). We excluded datasets in which the links between ant and plant species were not available (i.e. where we were unable to build a bipartite network). The use of a single search engine may have led to some studies being missed but allowed us to focus on high quality network in a systematic manner. Data collection activities were carried out throughout 2021, with no date limits imposed. We searched the Web of Science database using the keywords "ant-plant interaction" and then refine this search using the additional keywords, "extrafloral nectaries" (EFN) OR "food bodies" (FB), OR "myrmecophily", OR "Co-occurrence", OR "ant-plant foraging," OR "myrmecochory". We only selected networks that consisted of at least three plant species and at least three ant species. We excluded networks that consisted of only presence/absence data, as analyses on binary data are more sensitive to sampling effort (Miranda et al., 2019), which varied between studies in our collated data. We also excluded networks collated from museum collections because these were not quantitative and often lacked geographical data. Lastly, we excluded studies that pooled ant-plant data across a whole region or country, for example, *Macaranga* spp. and *Crematogaster* spp. in Southeast Asia (Fiala et al., 1999). Where necessary, we contacted authors to provide metadata. In some cases, additional more recent data (post-2021) were contributed to the network as a result. In addition, we conducted a snowball search by identifying relevant references in all collated data papers. Our decision tree for including/excluding network is presented in Figure 1. It has to be noted that our studies has some geographical limitation as there are not many studies in Africa fulfil our criteria.

Our protocol resulted in a total of 74 ant-plant interaction networks. These included 18 myrmecophytic, 17 myrmecophilic, 14 myrmecochorous, and 25 foraging networks. The networks spanned an absolute latitudinal

range of 1.8° to 49° and an elevational range from 4 m to 2800 m above sea level (asl) with 41 networks in undisturbed areas, and 33 networks in disturbed areas (Figure 2 & 3). In some cases, the network data were not published with the corresponding paper and the author did not respond to our request. Hence these networks were excluded. However, since these occurrences were a minority (10 / 74) we believe our collated networks represent a substantial proportion of those available.

We classified the networks into four types: (i) *myrmecophytic* : networks where plants provide nesting space (domatia) for ants; (ii) *myrmecophilic* : networks where plants offer food to ants (extrafloral nectaries (EFN) and food bodies (FB) but without domatia); (iii) *myrmecochorous* : networks involving ant dispersal of plant seeds, or ant consumption of fruits; (iv) *foraging* : networks in which interactions between ants and plants were recorded, with ants being found foraging on plants, but without utilising any plant-provided resources. Latitude, elevation, and presence/absence of anthropogenic disturbance were recorded as metadata for each network. If elevation was not included in the article or provided by the author, we determined this from the geographic coordinates in the study site description using google earth (elevation determined in this way for 9 of 74 networks). If the elevational range across multiple sites within a study was less than 300 meters, we combined these sites into a single network and used the mean elevation value (14 of 74 networks resulted from such merging). Where sites within a study were > 300 m apart in terms of elevation we retained the data as multiple separate networks (10 of 74 networks). In these cases, study identity was retained as a random factor in all models, to account for greater similarity in sampling effort and methodology within studies than between studies. Each network was classified as being in either anthropogenically disturbed (gardens, recently cut secondary forests or production forests) or undisturbed (primary forests or nature reserves), based on the original study description. We combined different kinds of disturbed habitats into one category because sample sizes for finer grained categories were not large enough for statistical analyses. Finally, we updated the species names of plants using *taxize* in R with the gbif database (<https://www.gbif.org/>), accessed January 2022. We manually fixed typos when names were classified as “fuzzy” according to *taxize* and rechecked the updated plant names on the WFO database (<http://www.worldfloraonline.org/>) when names were classified as “doubtful”. Meanwhile, ant taxonomic names were checked manually using the AntWeb (<https://www.antweb.org/>) and AntWiki databases (<https://www.antwiki.org/>), accessed July 2022. We mapped the network sampling locations using QGIS 3.16.15 to visualize the distribution of our sites. We also chose the network with the median species richness from each interaction type to visualize the differences in structure across each network type. These networks were plotted using the *plotweb* function in the *bipartite* package.

Calculation of network specialisation indices

Network specialisation was first calculated using the H_2' index (Blüthgen et al., 2007) in the *bipartite* package (all analyses were carried out in R 4.2.3; R Development Core Team; <http://www.R-project.org>). This measures the degree to which each species interacts with a restricted group of partner species, given the species pool of partners available. We chose this index as it gives an overall measure of specialisation of all species in the network, across upper and lower network levels. The H_2' index is calculated based on the deviation of the observed number of interactions per species from the expected number of interactions, given the marginal total abundances of each species (Bluthgen et al., 2007). However, since each network had a different structure in terms of size, species abundance, and sampling effort, which might affect H_2' independently of species specialisation *per se*, we also generated 1000 null models for each network, recalculated H_2' for each, and calculated a standardised effect size (H_2' z-score) to assess deviation from random expectation. We used the *vaznull* randomisation algorithm that maintains network connectance and total number of individuals (Ulrich et al., 2009) which is relatively conservative (Dorman et al., 2009). H_2' and H_2' z-score were calculated for all selected networks using the *networklevel* function of the *bipartite* package (Dormann et al., 2008). For the calculation of H_2' and H_2' z-score, we used all 74 interaction networks (see above).

We then tested whether networks were specialised in terms of resource phylogenetic relatedness, while accounting for resource abundance (Jorge et al., 2017), using the *dsi** index in the *dizzy* package. Note that here “resource” indicates either ants or plants. This index is scaled by the null expectation of random re-

source use (in a similar manner to the H_2' standardised effect size calculations detailed above) and weighted by resource abundance. Plant abundance was calculated as the sum of occupied and unoccupied plant individuals for each plant species. For ants, only those found occurring on the plants were considered. This was because all networks were standardised through plant sampling, and hence no data were available on ant occurrences not associated with plants. Analyses were conducted both in terms of ant specialisation on plants (i.e., concerning plant partner phylogenetic relatedness; dsi^* ants) and plant specialisation on ants (i.e. concerning ant partner phylogenetic relatedness; dsi^* plants). For the former, we calculated dsi^* only for networks comprising three or more plant families, and for the latter, we used networks with three or more ant genera. We calculated the phylogenetic distance of plants as resources using the *PhyloMaker* package at species-level resolution. For ants, we downloaded sequence data from GenBank for all the ant genera from Moreau et al. (2006). We selected the 53 ant genera represented in our own networks and re-aligned the DNA matrices using MAFFT version 7 (Katoh and Standley, 2003) with maximum likelihood estimation (ML) using RAxML 8.2.9 (Stamatakis, 2014). Supplementary material provides further details on the construction of the phylogenetic ant tree at genus level (appendix 2) and Genbank accession numbers for all sequences used (appendix 3). We used the 64 networks for which resource (i.e plant) abundance was available to calculate dsi^* (13 myrmecophytic, 14 myrmecophilic, 13 myrmecochorous, and 24 foraging).

Modelling network metrics in relation to environmental gradients

We performed four separate analyses using H_2' , H_2' z-score, dsi^* ants, and dsi^* plants as response variables, the environmental predictors as fixed effects (latitude, elevation, and anthropogenic disturbance), and study identity as a random effect (full model in supplementary, appendix 4 & 5). Linear mixed effects models (*lmer* function in the *lme4* package) were used to predict changes in H_2' and H_2' z-score, fitted using maximal log-likelihood (REML = F) in order to compare models with different fixed effects. Generalized linear mixed effects models with beta error distribution (*glmmTMB* function in the *glmmTMB* package) were used to predict dsi^* ants, and dsi^* plants, as dsi^* varies between 0 and 1. Model selection was based on the corrected Akaike Information Criterion (AICc), calculated for the complete set of models using the *dredge* function in the *MuMIn* package. The global model included all main predictor variables and first order interactions between network type and each of the other three predictors. The model with the lowest AICc score was selected. For categorical predictor variables in the final model, to understand which factor levels differed significantly, we inspected test statistics and p-values for pairwise contrasts between levels, using the *relevel* function where necessary to explore all pairwise comparisons. Note that family level type 1 error rate is retained at 0.05 for these comparisons, so no further correction for multiple testing is required. This was also done for interactions involving categorical predictors. Lastly, because only foraging networks were present above 1500 m a.s.l. (Figure 3), we removed these four outliers in terms of predictor variables, and repeated our full analyses to explore whether these data were driving any of the patterns we observed. We found that the model from all response variable stayed the same but with higher AICc (see supplementary, appendix 6 & 7). Hence, for the remainder of the paper, we present the analysis of the full dataset.

Results

The final model for H_2' included an interaction between elevation and interaction type, and main effects of disturbance, elevation and interaction type (*lmer*; AICc = -34.5, $n = 74$, $\log\text{Lik} = 30.3$; Table 1; Figure 5a; Figure 6a). Undisturbed areas had higher network specialisation than disturbed areas ($P = 0.001$). Overall, myrmecophytic networks were more specialised (higher H_2' score) than other interaction types ($P < 0.001$). However, given the significant interaction between the effects of interaction type and elevation ($P < 0.001$), we interpret this result with caution. Pairwise comparisons showed that the relationship between elevation and specialisation (H_2') differed between myrmecophytic networks and both myrmecochorous and foraging networks ($P < 0.001$) but not with myrmecophilic networks ($P = 0.130$). All other pairwise comparisons were non-significant ($P > 0.05$). Myrmecophytic networks showed the greatest specialisation at lower elevations, with rapid decreases in specialisation with increasing elevation. Myrmecophilic networks showed a less pronounced decline in specialisation with elevation, while specialisation of myrmecochorous and foraging networks remained low at all elevations. Latitude was not included in the final model for H_2' (Figure 5e).

Intriguingly, when H_2' scores were standardised by comparison with a null model (z-score), the final model included no main effects or interaction terms (lmer; AICc = 528.8, $n = 74$, logLik = -261.2; Table 1; Figure 5b; Figure 6b, f). That is, none of the predictors from the unstandardised H_2' model was included in the standardised model.

Accounting for phylogeny of partners, the best model for ant specialisation on plants (dsi*ants) included only network type (glmm; AICc = -70.7, $n = 64$, logLik = 42.1; Table 1; Figure 5c). Myrmecophytic networks were more specialised than the other three network types ($P < 0.001$) and myrmecophilic networks showed greater specialisation than foraging networks ($P < 0.001$). All other pairwise comparisons between network types were non-significant ($P > 0.05$). Main effects of latitude, elevation and disturbance were not present in the final model (Figure 6c, g), nor were any interaction terms. The final model for plant specialisation on ants (dsi*plants) also included only network type (glmm; AICc = -46.3, $n = 64$, logLik = 29.9; Table 1; Figure 4d). Myrmecophytic networks were more specialised than myrmecophilic ($P < 0.001$), myrmecochoric ($P < 0.001$) or foraging networks ($P < 0.001$). All other pairwise comparisons were non-significant ($P > 0.05$). Main effects of latitude, elevation and disturbance were not present in the final model, nor were any interaction terms (Figure 5d, h). 1.

Discussion

Here, using a data collation and meta-analytical approach, we demonstrate that network type is the most important driver of ant-plant network interaction specificity. Unstandardised H_2' specialisation results recapitulate previous studies, showing reduced specialisation with elevation for myrmecophytes, higher specialisation of myrmecophytes than other network types at lower elevation, and decreased specificity in response to disturbance. However, all effects were lost when H_2' was standardised by comparison with null network models. This may have been due to confounding effects of matrix size and connectance on uncorrected H_2' . Both ants and plants were significantly more phylogenetically specialised in myrmecophytic networks than in other network types, although there was no significant effects of elevation, latitude, or disturbance. This is the most comprehensive analysis of global scale ant-plant network structure to date, and the first to employ null models to standardise network metrics and to explore phylogenetic specialisation.

More physically intimate network that involve greater commitment to exchange of goods and services (in the case of mutualisms), are predicted to evolve to become more specific (González-Teuber & Heil, 2015). We found this expected effect when assessing specificity independent of phylogeny and uncorrected by null modelling (H_2'), with myrmecophytic networks at lower elevations showing higher specificity than for other network types. Unexpectedly, this effect was not present when H_2' standardised effect sizes were used as the response variable. This indicates that the results for unstandardised H_2' may have been driven by other aspects of network structure, and not by specificity *per se*. post-hoc analyses show that both total network species richness, and weighted connectance are strongly negatively correlated with H_2' (see supplementary, appendix 8), but are only weakly related to H_2' z-scores (appendix 8). This might be because networks with higher connectance are those in which links are found evenly across species in the network, and hence have lower specificity. However, the differences in results when standardising H_2' suggest that, at least in terms of network specificity, this evenness of links is to be expected on the basis of network structure alone. Hence it is vital to compare observed network metrics to distributions expected under random network assembly to avoid biases due to confounding aspects of network structure. This approach has not always been implemented in previous studies.

However, in terms of network phylogenetic specialisation, using the dsi* metric, which is already standardised against null models, we found that myrmecophytic networks were more specialised than other network types. This was the case both in terms of ant specialisation on plants and plant specialisation on ants. Each ant species interacted with a more phylogenetically clustered group of plant species than would be expected at random, and vice versa. This potentially indicates long-term coevolution between myrmecophytic plants and their ant partners, characterised by exchange of multiple goods and services. Plants can provide specialised morphological structures (e.g., domatia) that promote partner choice and thus allow direction of benefits to more beneficial mutualistic partners (Heil & McKey 2003). Myrmecophytic plants also sometimes provide

FB and EFN for their ant partners. Ants can provide herbivore protection, competitor trimming, nutrients (Mayer et al., 2013), and CO₂ for photosynthesis (Treseder et al., 1995). Such complex behaviours and morphologies are likely to be phylogenetically conserved, resulting in the observed high levels of network phylogenetic specificity in myrmecophytic networks. This is consistent with previous (non-phylogenetic) work showing that myrmecophytic networks are characterized by strong compartmentalization (Fonseca & Ganade, 1996).

The other network types (myrmecophilic, myrmecochorous and foraging) showed lower levels of phylogenetic specialisation than myrmecophilic networks. This is likely due to the lack of evolution of specialized morphological structures relating to the ant-plant interaction. Although EFNs predominantly attract ants for protection, they can also attract other defensive arthropods including parasitoids, wasps, spiders, mites, bugs, and predatory beetles (Heil, 2015). It is also possible that plants produce EFNs to reduce ant consumption of flower nectar and so to maximise visitations of other pollinators on flowers (Wagner & Kay, 2002). However, myrmecophilic networks showed higher specialisation than foraging networks in terms of ant specialisation on plants. This may be because ants can benefit greatly from EFNs, which contain monosaccharides and disaccharides, and amino acids that are an important energy source (Marazzi et al., 2013) and even alter the predatory behavior of some ants (Wilder & Eubanks, 2010). Indeed, some plants can even coerce their EFN-feeding ant partners through “addiction” based on enzyme inhibition, preventing the ants from feeding on other food sources (Heil et al., 2014; Houadria et al., 2023). Myrmecochorous ants tended to be generalists, being attracted to the non-specific food offered by the plants in the elaiosome (Levine et al., 2019). Although Anjos et al. (2018) showed that ants attracted to elaiosomes (a small lipid-rich structure used by ants as a food source) are more specialized than ants attracted to fruit pulp, our data combined both network types to increase statistical power, and so we were unable to explore this. Lastly, foraging networks exhibit a lower specialisation, presumably in part because this was the only network type that did not necessarily involve a mutualism between the partners. Species involved in these networks are highly adaptable and tend to exploit a wide range of resources within their environment.

Although unstandardised specialisation (H_2') showed similar relationships with elevation and habitat disturbance to previous studies, these relationships were not present for analysis of standardised H_2' or for phylogenetic network specialisation (dsi^*). The interaction between network type and elevation was due specifically to differences between responses of myrmecophytic networks and myrmecochoric and foraging networks. The former showed a strong reduction in specificity (H_2') with elevation, while the latter two showed uniform low specialisation across all elevations. This pattern is consistent with the lack of herbivores at higher elevations and hence the reduced need for plant protection by ants (Moraes & Vasconcelos, 2009). For example, *Myristica subulata*, a myrmecophytic plant that is abundant across a range of elevations, benefits less from myrmecophytic networks at higher elevations, and shows lower specificity towards its ant partner (Plowman et al., 2017). Previous work has showed that more intimate networks, such as myrmecophytic networks, can be more susceptible to disturbance (Emer et al., 2013; Fayle et al. 2017), while less intimate networks might not be significantly affected by disturbance in island regions (Klimes 2017) but may experience greater impact in mainland or continental contexts (Corro et al., 2019). However, we found no difference in response to disturbance between network types (no significant interaction between the predictors), although we did find an overall decreased specialisation (H_2') in response to anthropogenic habitat disturbance. Our failure to replicate any of these results with either standardised H_2' or with measures of phylogenetic network structure (dsi^*) raises the possibility that results from previous studies are artefacts, again driven by variation in other network properties. For example, mean network species richness in undisturbed networks was 61.7, compared to that in disturbed networks of 33.9, and network species richness is negatively correlated with H_2' (supplementary, appendix 8). However, combining networks that have been collected using different methods, and with differing sampling efforts is likely to introduce considerable noise into response variables, even when these are standardised against null models and so we feel that our results do not necessarily preclude the existence of such patterns.

Taken together, our results show that ant-plant network specificity is not strongly affected by latitude, elevation or anthropogenic habitat disturbance, but that rather the mode of interaction between the partners

is most important. Mutualistic networks involving myrmecophytic plants are highly phylogenetically specialised, due to their long term coevolutionary interaction. Although our meta-analysis recapitulates previous results in terms of relationships between unstandardised H_2' and elevation and disturbance, these results are not present when H_2' is standardised against null models, or where phylogenetic specialisation is assessed. This demonstrates the importance of standardising metrics of network structure against null expectations. Overall, we show that strength and intimacy of mutualistic interactions drives patterns of network specialisation at global scales, even across gradients of elevation, latitude and anthropogenic land-use change, all of which have minimal impacts on network structure.

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Data accessibility

Data and R code available on Dryad Digital Repository: (<https://datadryad.org/stash/share/VLKpk3JE1oLjrEknVRXHBIY7>)

Tables

Table 1. Summary statistics of the best five models chosen through ‘dredge’ function for each of the four response variables sorted from the lowest AICc (Int: Intercept, Dst: Disturbance, Elv: Elevation, ltt: Latitude, Typ: Network type).

Global model: lmer(H2 ~ Type + Latitude + Elevation + Disturbance + Type:Elevation + Type:Disturbance + Type:Latitude + (1 | ID), data = ho, REML = F)

Cnd (Int)

0.6760

0.6914

0.5653

0.5831

0.5699

0.6470

Global model: lmer(H2.Zscore ~ Type + Latitude + Elevation + Disturbance + Type:Elevation + Type:Disturbance + Type:Latitude + (1 | ID), data = ho, REML = F)

Cnd (Int)

4.683

5.994

3.562

5.098

4.962

6.425

Global model: $\text{glmmTMB}(\text{DSI.Ants} \sim \text{Type} + \text{Latitude} + \text{Elevation} + \text{Disturbance} + \text{Type:Elevation} + \text{Type:Disturbance})$

Cnd (Int)

1.759

1.724

2.281

1.748

1.773

1.712

Global model: $\text{glmmTMB}(\text{DSI.Plants} \sim \text{Type} + \text{Latitude} + \text{Elevation} + \text{Disturbance} + \text{Type:Elevation} + \text{Type:Disturbance})$

Cnd (Int)

1.3550

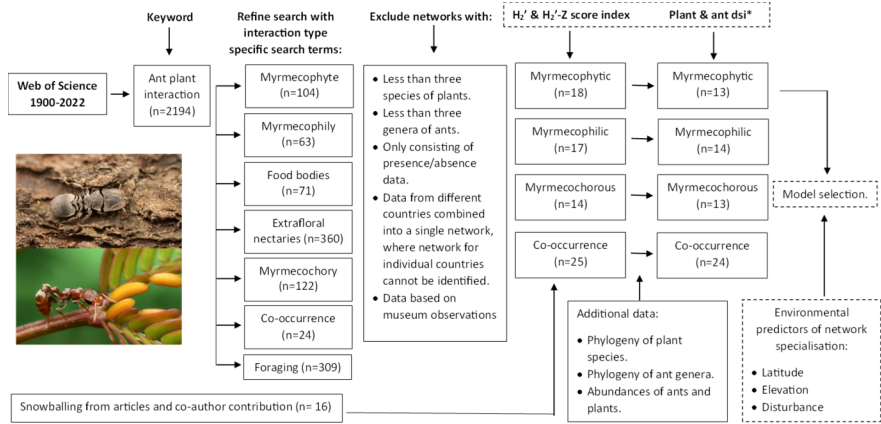
1.3580

0.8224

0.6224

1.4170

1.1310



Figures

Figure 1. The decision trees of which networks data included and excluded from calculation.



Figure 2. The geographical distribution of the four kinds of ant-plant networks used in this study.

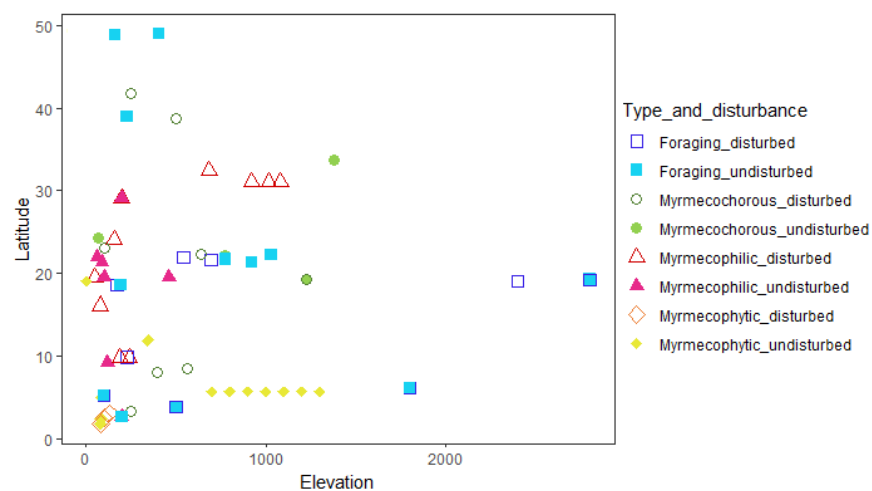


Figure 3. The distribution of ant-plant networks within the elevation-latitude parameter space, in relation to interaction type and presence of anthropogenic disturbance.

Figure 5. The effect of network types and disturbance on specialisation of ant-plant interactions as measured using four different specialisation indices. (a) H_2' network specialisation. (b) Standardised effects size of deviation of observed H_2' from that generated using a null model (H_2' z-score). (c) Degree of ant specialisation on plants in terms of plant partner phylogenetic relatedness (dsi*ants). (d) Degree of plant specialisation on ants in terms of ant partner phylogenetic relatedness (dsi*plants). Different letters indicate significant differences in specificity between network types or levels of disturbance, although note that for panel (a) there is also a significant interaction involving interaction type (See Fig 4a), and so the main effect should be interpreted with caution.

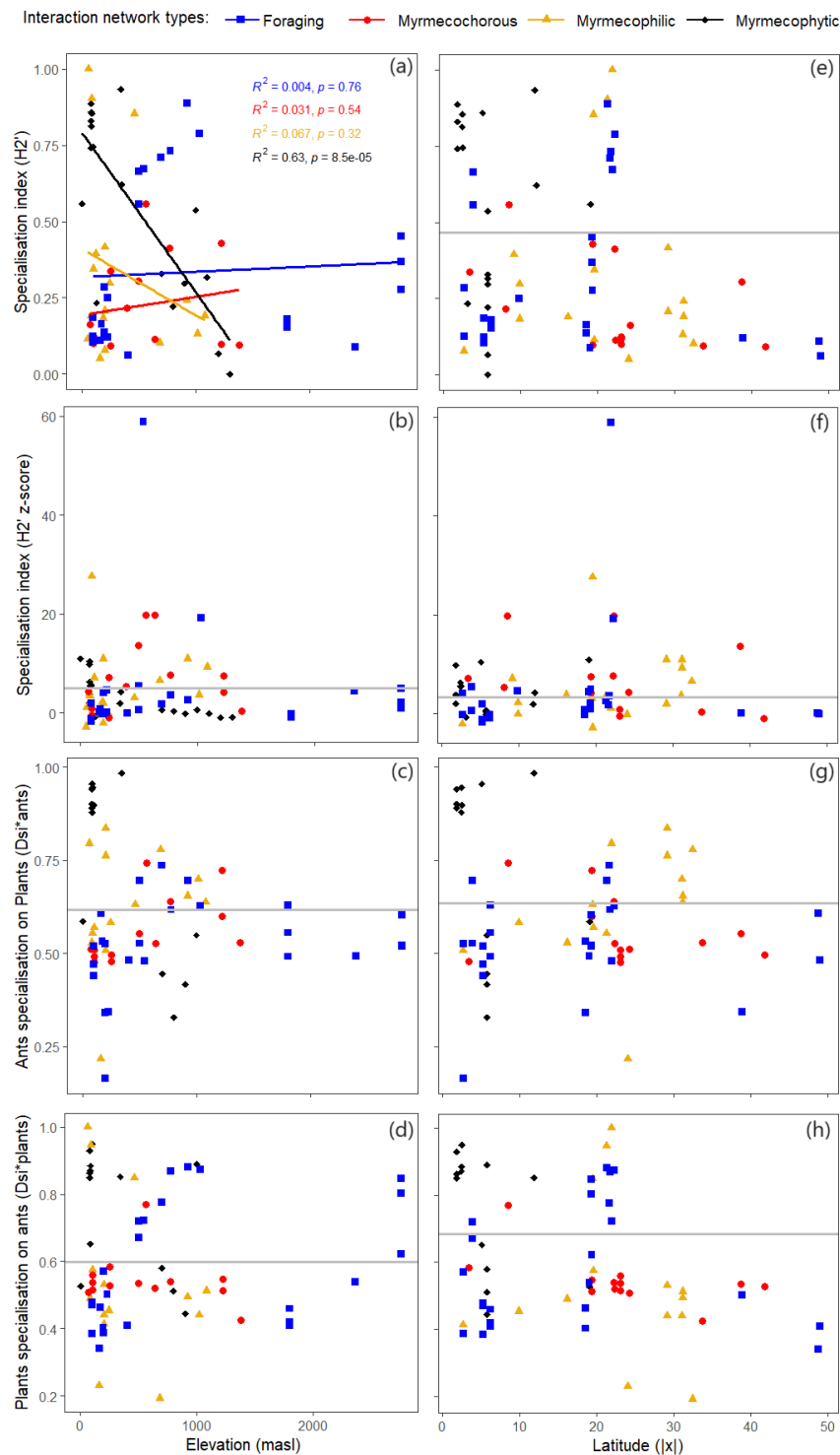


Figure 6. The relations between latitude and elevation and specialisation of ant-plant networks as measured using four different specialisation indices. The fitted line in panel (a) denotes a significant interaction between network type and elevation on network specificity as measured by H_2' and different letters indicate significant

differences in specificity between interaction types that interact with elevation.