

# ECOGRAPHY

## Research article

### Climate and ant diversity explain the global distribution of ant-plant mutualisms

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Biotic interactions play an important role in shaping species geographic distributions and diversity patterns. However, the role of mutualistic interactions in shaping global plant diversity patterns remains poorly understood, particularly with respect to interactions with invertebrates. It is unclear how the nature of different mutualisms interacts with abiotic drivers and affects the distribution of mutualistic organisms. Here, we present a global-scale biogeographic analysis of three distinct ant-plant mutualisms, differentiating between plants bearing domatia, extrafloral nectaries (EFNs), and elaiosomes, based on comprehensive geographic distributions of ~ 19 000 flowering plants and ~ 13 000 ant species. Domatia and extrafloral nectaries involve indirect plant defences provided by ants, while elaiosomes attract ants to disperse seeds. Our results reveal distinct biogeographic patterns of different ant-plant mutualisms, with domatium- and EFN-bearing plant diversity decreasing sharply from the equator towards the poles, while elaiosome-bearing plants prevail at mid-latitudes. Present climate, especially mean annual temperature and precipitation, emerge as the strongest predictors of ant-associated plant diversity. In hot and moist regions, typically the tropics, the representation of EFN-bearing plants increases with the proportion of potential ant partners while domatium-bearing plants show no correlation with ants. In dry regions, plants with elaiosomes are strongly linked to interacting ant seed dispersers. Our results suggest that ants in combination with climate drive the spatial variation of plants bearing domatia, extrafloral nectaries, and elaiosomes, highlighting the importance of mutualistic interactions for understanding plant biogeography.

Keywords: biotic interactions, domatia, elaiosomes, extrafloral nectaries, global biogeography



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## Introduction

Mutualisms are fundamental for understanding the origin and maintenance of biodiversity (Bronstein et al. 2006, Lomolino et al. 2017). Interacting species have evolved various traits that serve key functions in mutualistic interactions. Geographic variation of interacting species and related traits can provide insights into the drivers governing spatial patterns of biodiversity and species responses to future change (Wisz et al. 2013, Violle et al. 2014). It is especially true when considering the influences of biotic interactions on the distribution of interacting species at local spatial scales (Dalsgaard et al. 2009). However, a growing body of research suggests that biotic drivers can influence broad-scale patterns of mutualistic species and related traits (Kissling and Schleuning 2015), such as seed dispersal mutualisms (Onstein et al. 2020, Sinnott-Armstrong et al. 2021) and plant-mycorrhizal fungi mutualisms (Delavaux et al. 2019). Despite increasing evidence on spatial variation in diversity explained by biotic interactions, the relative importance of biotic and abiotic drivers on species diversity for plant-invertebrate mutualisms remains largely unquantified at macroecological scales, which are critical for understanding global plant diversity patterns.

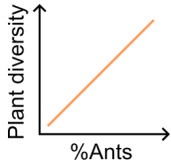
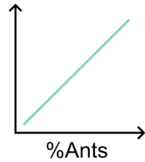
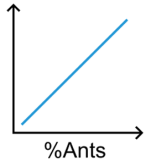
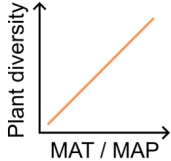


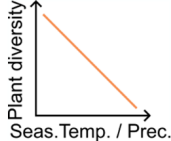
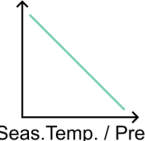
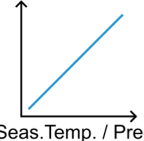
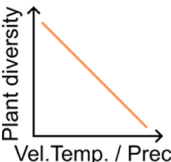
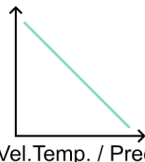
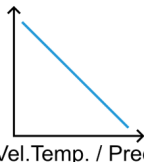
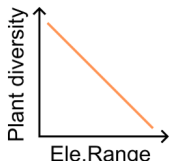
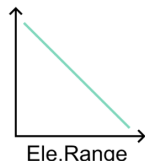
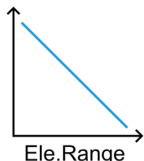
Flowering plants and ants have evolved diverse mutualistic interactions, which arose from the evolution of plant adaptive traits to ant exploitation and eventually enhanced diversification in related plant lineages (Hölldobler and Wilson 1990, Bronstein et al. 2006, Rico-Gray and Oliveira 2007, Lengyel et al. 2009, Weber and Agrawal 2014). Over 19 000 plant species rely on ants as defenders and seed dispersal vectors, with the most common plant structures being domatia, extrafloral nectaries (EFNs), and elaiosomes (Lengyel et al. 2010, Weber and Keeler 2013, Chomicki and Renner 2015). Domatia are modified plant structures such as cavities in leaves, stems, or roots that house ant colonies (Chomicki and Renner 2015). Extrafloral nectaries are plant glands that attract ants by secreting sugary nectar outside of flowers (Weber and Keeler 2013). Ants, in return, protect domatium- and EFN-bearing plants against herbivores (Rosumek et al. 2009). On the other hand, elaiosomes are nutrient-rich appendages of seeds, which reward ant mutualists that disperse seeds (myrmecochory) (Lengyel et al. 2009). Plants interacting with ants have been studied in a variety of habitats and vegetation types from local to regional scales (Pemberton 1998, Rico-Gray and Oliveira 2007). While ant-associated traits may be context-dependent, influenced by factors such as climatic conditions and herbivory stress (Palmer et al. 2008, Nogueira et al. 2020), mutualistic ant partners are suggested to shape plant communities by affecting plant fitness and reproduction (Giladi 2006, Rosumek et al. 2009). For instance, isolated islands that lack native ants have been reported to contain fewer plants with EFNs compared to mainland floras (Keeler 1985). The 'ant limitation hypothesis' postulates that ant community attributes, including ant species richness and forager abundance, may contribute to the evolutionary origin and maintenance

of ant defence mechanisms in plants (Keeler 1985, Schupp and Feener 1991). Likewise, ant activity and species richness are considered to affect myrmecochorous plant species diversity (Beattie and Culver 1981). Accordingly, ant diversity may act as a biotic driver in shaping plant diversity patterns (Table 1, H1), similar to previously observed cross-taxon congruences in diversity patterns (Kissling et al. 2007, Sandom et al. 2013).

In addition to biotic constraints, variation in water-energy dynamics, past climatic stability, habitat heterogeneity, and phylogeny may influence the spatial variation of ant-associated plants. Resource availability can constrain the maintenance of ant protection, as producing domatia and secreting nectar is costly (Heil and McKey 2003). Ant-protected plants may thus thrive in habitats and regions with high energy and water availability (Table 1, H2) (Schupp and Feener 1991, Heil and McKey 2003), although some research suggests that EFN-bearing plants may adapt in dry habitats (Leal and Peixoto 2017). Conversely, plants with elaiosomes typically occur in dry and low-nutrient soils (e.g. the Mediterranean climate in Australia and South Africa). In this case, myrmecochory is more affordable and directional in contrast to vertebrate dispersal (Giladi 2006), and thus may prevail in harsh environments. Moreover, climatic constraints can indirectly affect ant-associated plant diversity via the diversity and behaviour of ant mutualists. For example, seasonal fluctuations in resource availability, such as water and light, can negatively affect the outcomes of ant protection and the survival of ant-protected plants (Calixto et al. 2021a), potentially leading to shifts in species diversity over time. By contrast, ant-dispersed plants are likely to adapt to seasonal variations in climate, as hotspots of myrmecochory are often characterized by high seasonality in temperature and precipitation (Rico-Gray and Oliveira 2007, Leal et al. 2017). In addition to present climate conditions, past climate change may have disrupted complex biotic interactions and shaped the spatial variation of ant-associated plants (Blois et al. 2013). This may be particularly true for ant-plant mutualisms, many of which have limited dispersal abilities and small distribution ranges (Dunn et al. 2009, Sandel et al. 2011). Conversely, high environmental heterogeneity can increase niche space for plants and ants to coexist and develop interactions (Stein and Kreft 2015). Furthermore, the evolutionary history of ant-associated plants is expected to be important for their distribution. Ant-associated traits of plants show a moderate level of phylogenetic signal due to their independent evolution across multiple plant lineages (Weber and Keeler 2013, Nelsen et al. 2018). Thus, regions with shared evolutionary history are likely to have a high degree of phylogenetic relatedness, which is important to consider to fully understand the drivers of ant-associated plant diversity.

Reflecting its fundamental importance for biodiversity, a compelling body of research has accumulated on the drivers of ant-associated plant diversity at local scales. However, our understanding of the relative importance of abiotic and biotic factors at larger scales is very limited, and historically hampered by data deficiency of interacting species, particularly

Table 1. Hypotheses for the biotic and abiotic drivers of the diversity of ant-associated plants at large spatial scales. Specific predictions of how drivers affect the diversity of plants with domatia, extrafloral nectaries (EFNs), and elaiosomes are presented in orange, green, and blue lines, respectively.

Hypotheses	Explanatory variables	Domatium-bearing plants	EFN-bearing plants	Elaiosome-bearing plants
H1. Biotic interactions	Proportion of ant guild richness relative to all ant species richness (%Ants)			
H2. Water-energy dynamics	Mean annual temperature (MAT), mean annual precipitation (MAP)			
H3. Climate stability	Climate seasonality (Seas.Temp., Seas.Prec.)			
	Climate change velocity since the Last Glacial Maximum (Vel.Temp., Vel.Prec.)			
H4. Environmental heterogeneity	Elevational range (Ele.Range)			

for invertebrate groups such as ants. Here, by integrating global distribution datasets of plants and ants, as well as checklists of plants with ant-related, specialized defence and dispersal traits (Lengyel et al. 2010, Weber and Keeler 2013, Chomicki and Renner 2015, Guénard et al. 2017, Weigelt et al. 2020), we present global patterns of the three main ant-plant mutualisms, namely domatium-, EFN-, and elaiosome-bearing plants. Specifically, we assess whether the representation of ant-associated plants is associated with the proportion of species richness of potential ant partners, present climate, paleoclimate, and environmental heterogeneity. Specific hypotheses and predictions are presented in Table 1. Our study provides novel insights into the effects of biotic and abiotic factors on biodiversity in relation to three different ant-plant mutualisms.

## Material and methods

### Plant checklists and distributions

Information about flowering plant species involved in ant-plant mutualisms was sourced from comprehensive reviews on domatium-bearing plants (Chomicki and Renner 2015), extrafloral nectary (EFN)-bearing plants (Weber and Keeler

2013), and elaiosome-bearing plants (Lengyel et al. 2010), which provide information about the presence of domatia and EFNs on plants at the species level and elaiosomes at the genus level. Before extracting checklists for further analyses, we omitted duplicates and taxonomically uncertain records, and standardized all plant names following the World Checklist of Vascular Plants (WCVP, <https://powo.science.kew.org/about-wcwp>). Unmatched species were rechecked via the Taxonomic Name Resolution Service (TNRS, <https://tnrs.biendata.org>). This step led to 657 valid domatium-bearing species, 3179 valid EFN-bearing species, and 297 valid genera containing elaiosome-bearing species. In the elaiosome-bearing plant list, 217 of 297 genera were reported, with most constituent species being dispersed by ants (Lengyel et al. 2010). We therefore considered all species from 217 myrmecochorous genera as elaiosome-bearing plants, including approximately 15 189 species. To account for potential uncertainty in the ant-associated plant checklists, we conducted simulations to generate potential plant lists and compared results (Supporting information).

Native distribution information of ant-associated species was retrieved from the Global Inventory of Floras and Traits (GIFT ver. 3.0) database (Weigelt et al. 2020), which contains regional checklists of plants including 352 232 taxonomically standardized plant species across 3088 regions

worldwide. We only considered non-overlapping adjacent regions with available plant occurrences. Most regions are political units (e.g. countries or administrative units) and geographic regions (e.g. islands). We excluded oceanic islands from this analysis owing to their peculiar diversity and assembly patterns (Whittaker and Fernández-Palacios 2007). In total, our dataset contained 434 regions worldwide, including 403 mainland regions and 31 continental islands (with areas larger than 1000 km<sup>2</sup>).

### Ant guilds and distributions

To assess the effect of interacting ants on the distribution of ant-associated plants, we identified ants possibly involved in ant-plant mutualisms based on two ecological traits: diet (herbivore, omnivore, or predator) (Blanchard and Moreau 2017) and the habitat stratum occupied (arboreal, epigeic, or hypogaeic) (Lucky et al. 2013), which might represent potential selective forces on the evolution of ant-associated traits in plants (Nelsen et al. 2018). We classified ants into three guilds based on their behaviour in relation to plant interactions: 1) the guild associated with domatia, characterized by arboreal nesting and foraging, primarily occupies arboreal habitats (Marazzi et al. 2013); 2) the guild associated with extrafloral nectaries, represented by predacious ants that occupy the arboreal habitat stratum (Marazzi et al. 2013, Del-Claro et al. 2016); and 3) the ant guild that interacts with elaiosomes, which is omnivorous and mainly occupies epigeic habitats (Giladi 2006). Some genera were considered polymorphic or ambiguous because of evidence of alternative trait states or the absence of documented records, comprising 176 of 338 ant genera and about 58% of all ant species. For example, species of *Camponotus* have had highly diverse nesting preferences and were assigned a habitat stratum polymorphism. To account for the complexity and variation in the traits of diet and habitat stratum, we included polymorphic and ambiguous traits for each ant guild. For example, as species of *Camponotus* are omnivorous and polymorphic in habitat stratum, we categorized *Camponotus* to both guilds associated with EFNs and domatia. For more details on genus-level ant guild see Supporting information. Finally, we retrieved native ant species occurrences from the Global Ant Biodiversity Informatics (GABI) database (Guénard et al. 2017), which includes more than 1.9 million distributional records of more than 15 700 ant species and subspecies from comprehensive publications, digitized museum collections and specimen databases. We calculated the proportion of species richness in each ant guild relative to total ant species richness (hereafter, ant-guild-proportion) as biotic factors in our models.

### Abiotic variables

Past and present environmental factors are strong constraints acting on broad-scale diversity patterns of many taxa (Kreft and Jetz 2007, Sandel et al. 2011). Water- and energy-related variables, as well as their fluctuations, may exert direct effects on the distribution and diversity of plants as well as indirect

effects via ants (Dunn et al. 2009, Calixto et al. 2021a). We derived present climate factors from the Climatologies at high resolution for the earth's land surface areas (CHELSA ver. 1.2) dataset (Karger et al. 2017), including mean annual temperature (°C, hereafter temperature), mean annual precipitation (mm, hereafter precipitation), and precipitation seasonality (standard deviation of the monthly precipitation). The elevation range (m, the maximum elevation minus the minimum elevation of a region), as a proxy for environmental heterogeneity (Stein and Kreft 2015), was derived from the Global multi-resolution terrain elevation data at a resolution of 30 arcsecs (Danielson and Gesch 2011). Past climate stability has been documented to shape present biodiversity patterns of plants and other taxa (Sandel et al. 2011). Therefore, we also included past climate change velocity in temperature and precipitation, which were obtained as the velocity of climate change in temperature and precipitation from the Last Glacial Maximum (LGM) 21 000 y BP to the present (Hijmans et al. 2005, Braconnot et al. 2007, Sandel et al. 2011). Altitude, isothermality, and aridity were initially considered yet were not included, as they showed significant correlations (Pearson's  $r > 0.7$ ) with other variables and weaker relationships with the diversity of ants and plants. Details on abiotic variables are shown in Supporting information.

### Phylogeny

The phylogeny of ant-associated plants was obtained using the R package 'V.Phylomaker2' (www.r-project.org, Jin and Qian 2022), with the megatree GBOTB as the backbone (Smith and Brown 2018). We selected the phylogeny based on the WP database (www.worldplants.de), which was closely aligned with the taxonomy nomenclature of WCVP in our species lists. The 5379 missing species out of a total of 19 025 species were bound to the respective congener under scenario 3 of the function *phylo.maker*. We removed two EFN-bearing species that could not be taxonomically resolved and were not placed in the phylogenetic tree.

To address the potential confounding effects of phylogenetic relatedness between regions, we included phylogenetic eigenvectors as explanatory variables in our analyses, in accordance with the methodology proposed by Taylor et al. (2023). We quantified the phylogenetic beta diversity of ant-associated plants between regions using the Simpson index, which is insensitive to the variation of species richness between regions (Baselga 2010). As changes in species identity among regions can affect phylogenetic relatedness, we then calculated the standardized effect size of phylogenetic turnover (SES.Beta.Phylo) using the R package 'phyloregion' (www.r-project.org, Daru et al. 2020). This approach allowed us to measure the component of phylogenetic turnover independent of compositional turnover. To extract phylogenetic eigenvectors, we conducted a principal coordinate analysis (PCoA) on the SES.Beta.Phylo distance matrix between regions and selected the first two axes that explained over 90% of the variance in the standardized phylogenetic distances among regions. We repeated these steps for each mutualism

type. By incorporating these phylogenetic eigenvectors in our models, we were able to assess how the phylogenetic relatedness of ant-associated plant species among different regions influences their distribution patterns.

## Statistical analyses

The congruent patterns of ant and ant-associated plant species richness can be affected by various factors (Gaston 1996), such as biotic interactions and environmental conditions. Moreover, the influences of these factors on the distribution of ant-associated plants may differ due to the distinct biogeographic histories of different botanical continents. To account for potential confounding effects when quantifying the relationship between ants and ant-associated plant diversity, we calculated the standardized effect size of ant-associated plant species richness (SES.Plant). This variable measures the relative representation of ant-associated plants within each botanical continent. Specifically, we generated 1000 null communities within each botanical continent by shuffling the species identity of ant-associated plants while maintaining the total species richness of ant-associated plants within each botanical continent and the angiosperm species identity of each region. From these null communities, we obtained the mean null and SD null, and then calculated SES.Plant as (observed – mean null)/SD null. Positive values of this index indicate higher ant-associated species richness than expected by chance, while negative values indicate lower representation. We assigned botanical continents to the 434 study regions based on the centroid of each region. Before data analysis, abiotic variables were log-transformed to improve the normality of model residuals, and all variables were z-transformed to have zero mean and unit variance. All statistical analyses were conducted in R ver. 4.2.3 ([www.r-project.org](http://www.r-project.org)).

To quantify the effects of environmental and biotic drivers on the representation of ant-associated plants, we fitted linear mixed-effect models of SES.Plant using the ant-guild-proportion, elevation range, present climate (temperature, precipitation, and seasonality of temperature and precipitation), paleoclimate (past climate change velocity in temperature and precipitation), and phylogenetic eigenvectors as predictors. We included the botanical continent as a random effect because the importance of predictors may vary due to the diverse histories of the different botanical continents. To address spatial autocorrelation in model residuals that were not captured by other predictors (e.g. elaiosome-bearing plant: Moran's  $I=0.09$ ,  $p$ -value  $< 0.001$ ), we included a spatial autocovariate in the model, using the R package 'spdep' (Bivand and Piras 2015). This approach calculates the spatial weights for each observation based on the model residuals and a distance-based neighbour matrix. Spatial models performed well in dealing with our spatially autocorrelated data (e.g. elaiosome-bearing plant: Moran's  $I=0.02$ ,  $p$ -value  $=0.09$ , Supporting information). To investigate the potential effects of ant-associated plants on ant diversity, we performed additional linear mixed-effect models of the ant-guild-proportion. We included SES.Plant, elevation range, as

well as past and present climate as explanatory variables, and the botanical continent as a random effect.

To identify the direct and indirect effects of abiotic and biotic factors on plant diversity, we fitted SAR models in a piecewise structural equation modelling (SEM) framework, which is appropriate to test multivariate causal hypotheses (Lefcheck 2016). Piecewise SEM is based on directed acyclic graphs and can incorporate many model structures (e.g. spatial correlation structure) (Lefcheck 2016). We first constructed a priori theoretical SEMs that included all hypothesized pathways among plants, ants, and abiotic factors. We fitted separate SEMs for domatia, EFNs and elaiosomes as the ant-plant mutualism. Goodness-of-fit was evaluated based on Shipley's test of directed separation by comparing Fisher's C statistic to the  $\chi^2$  distribution, where an insignificant  $p$ -value ( $p$ -value  $> 0.05$ ) means no missing path exists (Lefcheck 2016). We optimized models in a stepwise manner, starting by removing the path with the lowest standardized path coefficient. The final models were determined by Fisher's C statistic and Akaike information criterion (AIC). Nagelkerke's pseudo  $R^2$  was calculated to evaluate model fit. SEMs were implemented using the 'piecewiseSEM' R package ver. 2.0.2 (Lefcheck 2016).

## Results

### Geography of ant-associated plants

The three different groups of ant-associated plants showed markedly distinct geographic patterns in species richness and proportional representation (relative proportion of interacting plants to all angiosperms per region) (Fig. 1, Supporting information). Plants with domatia and EFNs exhibited marked latitudinal gradients, with species richness and proportion peaking in tropical regions (Fig. 1). The highest diversity (domatia: 125 species in Peru; EFNs: 553 species in Venezuela) and proportion (domatia: 2.5%; EFNs: 19% of all angiosperms in Colombian regions, e.g. Guainía and Sucre) were found in tropical rainforests (Supporting information). Compared to widely distributed EFNs that showed moderate species richness in temperate regions, domatia were almost exclusively found in tropical regions. Elaiosome-bearing plant richness, in contrast, peaked in the subtropics, decreasing towards both the poles and the tropics (Fig. 1). Hot, semi-arid regions contained the highest species richness (1532 species in South Africa) and proportion (16% species in south-western Australia) of plants with elaiosomes (Supporting information). Mediterranean regions (e.g. 9% species in mainland Spain and 8.6% species in Greece) and temperate forests of the Northern Hemisphere (e.g. 648 species in Sichuan, China) were also rich in elaiosome-bearing plants (Supporting information).

### Biotic and abiotic drivers

We found that the standardized effect size of ant-associated plant richness was strongly associated with the respective

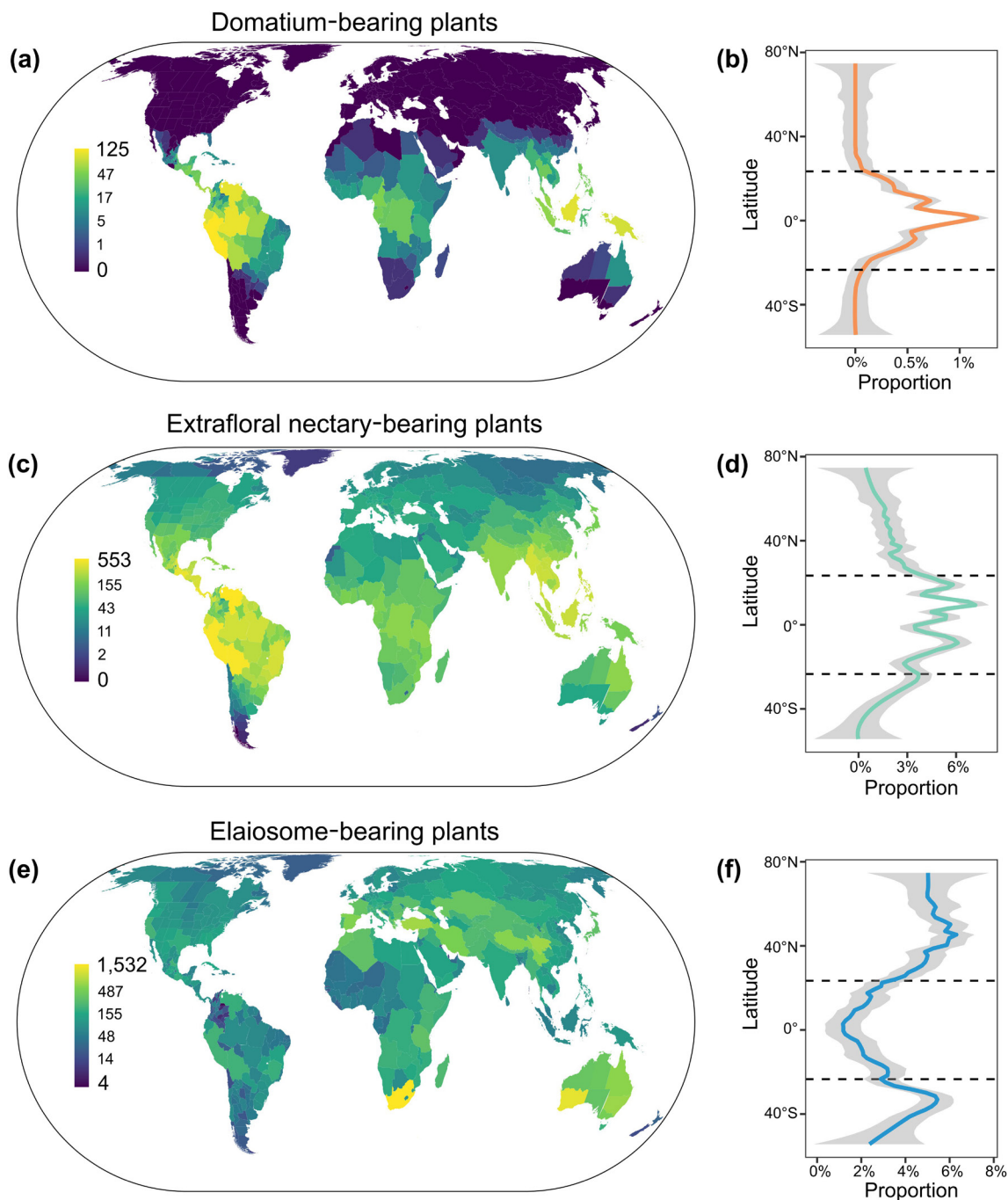


Figure 1. Global patterns of species richness and proportional representation along latitude for (a and b) domatium-bearing plants, (c and d) extrafloral nectary-bearing plants, (e and f) elaiosome-bearing plants. Species richness is indicated by the colour of regions. Proportional representation is estimated as species richness of ant-associated plants relative to angiosperm species richness and indicated along the latitudinal gradient.

ant-guild-proportion, as well as climatic, geographic, and phylogenetic factors (Fig. 2). Regions with a higher ant-guild-proportion exhibited a higher representation of EFN- and elaiosome-bearing plants. However, the prevalence of domatium-bearing plants was not associated with the domatium-related ant-guild-proportion (Fig. 2). We found that temperature and precipitation were positively related to

the representation of plants with domatia and EFNs, while negatively related to plants with elaiosomes (Fig. 2). In addition, seasonality of temperature and precipitation had negative effects on the distribution of domatium-bearing plants (Fig. 2). Compared to the present climate, past climate changes exhibited only marginal effects on the representation of ant-associated plants (Fig. 2, 3). The elevation

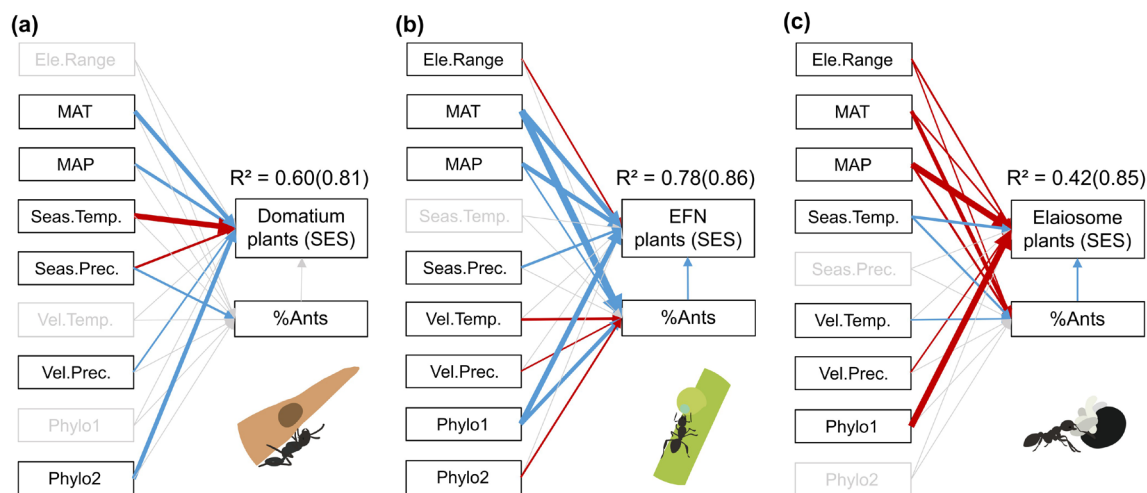


Figure 2. Structural equation models showing the effects of abiotic (climatic and geographic variables), biotic (ant-guild-proportion), and phylogenetic eigenvectors on the standardized effect size of richness patterns of (a) domatium-bearing ( $n=193$ ), (b) extrafloral nectary (EFN)-bearing ( $n=433$ ), and (c) elaiosome-bearing plants ( $n=434$ ). Boxes represent variables and arrows represent the direction of variable effects. Arrow size is proportional to the absolute value of path coefficients, and blue and red arrows represent significant ( $p < 0.05$ ) positive and negative path coefficients, respectively. Grey boxes and arrows represent insignificant ( $p > 0.05$ ) variables. The marginal  $R^2$  of the linear mixed-effect model, with conditional  $R^2$  in parenthesis, is shown. %Ants, the proportion of richness of respective ant guild relative to all ant species richness; Ele.Range, elevation range; MAT, mean annual temperature; MAP, mean annual precipitation; Seas.Temp. and Seas.Prec., seasonality in temperature and precipitation; Vel.Temp. and Vel.Prec., climate change velocity in temperature and precipitation from Last Glacial Maximum  $\sim 21000$  y BP to present; Phylo1 and Phylo2, axes of PCoA on the standardized effect size of phylogenetic turnover among regions. The spatial residual autocovariate included in the models is not shown.

range was moderately negatively linked to the prevalence of EFN- and elaiosome-bearing plants. Additionally, there was strong evidence that phylogenetic relatedness affected the representation of ant-associated plants (Fig. 2, 3). These biotic, abiotic, and phylogenetic variables together explained a substantial amount of variance, with marginal  $R^2$  ranging from 42 to 78%.

Like the effects of ants on the representation of ant-associated plants, we found that the distribution of EFN- and elaiosome-bearing plants had a significant influence on the ant-guild-proportion, respectively. However, we did not find a significant relationship between domatium-bearing plants and the domatium-related ant-guild-proportion (Supporting information). Our simulations indicated that the overall associations between ants and their interacting plants remained consistent after accounting for uncertainties in ant-associated plant checklists (Supporting information).

## Discussion

Our study revealed distinct geographic patterns of plants with domatia, extrafloral nectaries (EFNs), and elaiosomes, which were generally consistent with the evidence at smaller spatial scales. Structural equation models showed that the representation of ant-associated plants was strongly and jointly associated with the present climate, the respective ant-guild-proportion, and phylogenetic relatedness, yet no factor alone was sufficient for explaining the spatial variation of ant-associated plants. Although the effects of climate

and ant diversity may vary across different ant-plant mutualisms, our results highlight the consistent importance of both abiotic and biotic factors in shaping the diversity of ant-associated plants.

## Geography of ant-associated plants

Plants bearing domatia and EFNs showed opposing geographic patterns to those bearing elaiosomes, with species richness of domatium- and EFN-bearing plants decreasing away from the equator while elaiosome-bearing plants were most diverse at mid-latitudes. The latitudinal gradients of plants with domatia and EFNs mirror patterns of the herbivory intensity (Zvereva and Kozlov 2021), which supports previous findings that the benefits of ant-plant protective mutualisms are context-dependent and only significant when the plants are experiencing high herbivory pressure (Palmer et al. 2008, Calixto et al. 2021a). This could have driven the evolution of indirect defences via domatia and EFNs in tropical rainforests, among other biotic and environmental factors. On the contrary, the prevalence of ant-dispersed plants at mid-latitudes, where elaiosome-bearing seeds are abundant, may contribute to the observed pattern of decreasing seed size at the edge of the tropics (Moles et al. 2007), as elaiosome-bearing seeds are typically smaller than seeds dispersed by other vectors. Indeed, the presence of domatia, EFNs, and elaiosomes can covary with other traits related to reproduction, defences, and persistence, which may collectively mediate species responses to biotic and environmental factors (Bronstein et al. 2006).

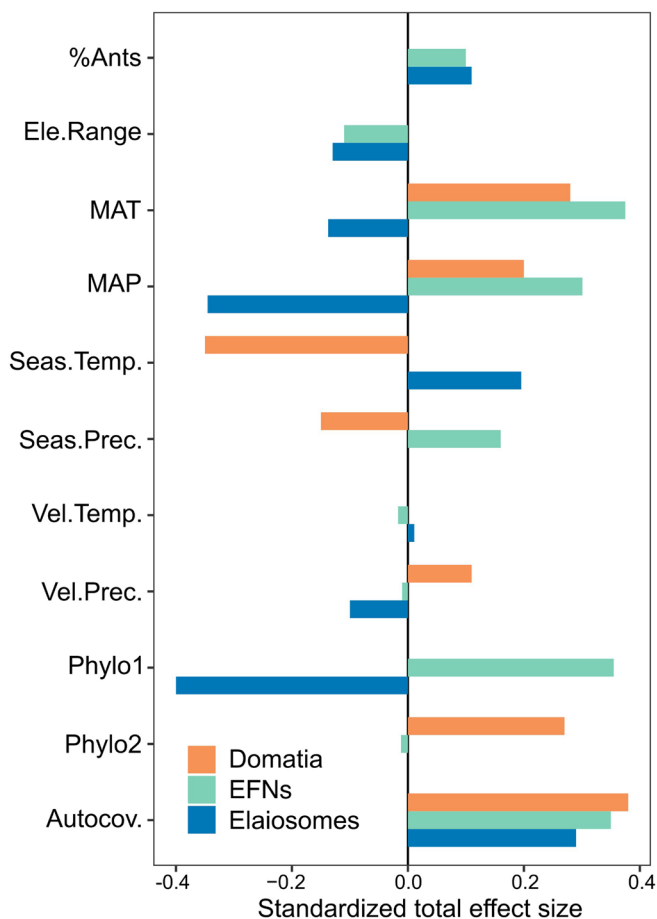


Figure 3. Effect sizes of abiotic and biotic predictors on the standardized effect size of domatium-, extrafloral nectary (EFN)-, and elaiosome-bearing species richness, calculated as the sum of direct and indirect path coefficients of structural equation models. Orange, green, and blue bars represent effects on domatium-, EFN-, and elaiosome-bearing plants. Variables follow as Fig. 2, Autocov. represents the spatial residual autocovariate.

Aside from the well-known diversity hotspots of elaiosome-bearing plants in South Africa and Australia (Rico-Gray and Oliveira 2007, Lengyel et al. 2010), the Mediterranean basin is expected to have more examples of ant-dispersed species than are currently known, as it shares a similar climate to the former regions. We found a high diversity of ant-dispersed plants in the Mediterranean basin, as well as in temperate regions of the Northern Hemisphere (e.g. the Himalayas), where so far limited attention has been given to myrmecochory. Elaiosome-bearing plants were generally scarce in the Neotropics, except for semi-arid regions such as the Cerrado and Caatinga (Leal et al. 2017). While it is likely that sampling effort influenced this pattern, the low proportion of ant dispersers in our results confirms the scarcity of plants with elaiosomes in the Neotropical rainforests. We propose that the unique evolutionary and ecological histories of each botanical continent have left profound imprints in the diversity of ant-associated plants.

## Global drivers of ant-associated plant distributions

Temperature and precipitation had a positive effect on the representation of domatia and EFNs, supporting our hypothesis H2. Particularly, the warmer and wetter habitats harbour more ant-protected plant species than expected by chance, which is consistent with previous findings (Rico-Gray and Oliveira 2007). The positive influences of temperature and precipitation may be due to their direct effect on a plant's ability to produce sugary nectar, which attracts mutualistic ants (Calixto et al. 2021a), or their indirect effect on the efficiency of ants against herbivores, which is sensitive to temperature (Tamashiro et al. 2019, Parr and Bishop 2022). Water-energy dynamics may affect the diversity of ant-protected plants not only through their direct effects on mutualisms but also indirectly via herbivory pressure, which plays an essential role in shaping mutualisms. However, it remains unclear what exact role herbivory has in mediating the relationship between plants and environmental factors. Future studies incorporating the tri-trophic interaction of ant-herbivore-plant into analyses of ant-associated plant diversity could provide a more comprehensive understanding of the mechanisms underlying these relationships.

Precipitation had a strong negative effect on elaiosome-bearing plants, while the effect of temperature was only moderate. These findings align with the high prevalence of elaiosomes in regions with harsh climates. Ants disperse and store seeds in their nests, which may contribute to persistent soil seed banks (Christian and Stanton 2004). Seeds are therefore protected from fires, desiccation, and predation of rodents in suitable habitats for germination (Hughes and Westoby 1992, Giladi 2006). Consequently, these unique benefits of myrmecochory are important for plants to persist in harsh environments characterized by relatively dry conditions, high temperature range, and low soil nutrients (Hölldobler and Wilson 1990, Giladi 2006). Furthermore, a comparison of myrmecochory prevalence between the Neotropical rainforests and semi-arid regions reinforces the finding of a negative impact of precipitation on the representation of elaiosome-bearing plants.

In addition to the impact of the present climate, the evolutionary history of ant-associated plants also exerted a strong influence on the representation of the three ant-associated plant types. This is not surprising given that ant-associated plants occur phylogenetically clustered in different lineages (e.g. EFNs in *Passiflora*, elaiosomes in *Euphorbia*), which are likely shaped by both selection and trait conservatism (Weber and Keeler 2013, Nelsen et al. 2018). The environmental preferences of ant-associated plants are therefore reflected in their phylogeny, meaning that regions with similar environmental conditions tend to be more phylogenetically related. Additionally, the elevation range showed a moderately negative effect on ant-associated plant diversity, which leads to rejecting hypothesis H4. This may be attributed to the low representation of ant-associated plants in high-altitude regions. Likewise, a negative effect of climate seasonality on myrmecophytes is consistent with their preference for



tropical forests. Past climate change influenced both plants and ants (Dunn et al. 2009, Economo et al. 2018); however, we found it to be of negligible importance on ant-associated plants. This is likely due to the divergent histories of biogeographic regions in our study, highlighting the need for a better understanding of biotic interactions under past climate change.

Our hypothesis H1 is supported by the finding that, in addition to abiotic factors and phylogeny, the corresponding ant-guild-proportion was an important factor associated with diversity patterns of EFN- and elaiosome-bearing plants. Ant community attributes, such as ant abundance (Bentley 1976), activity (Beattie and Culver 1981), and species richness (Pemberton 1998), have been proposed as important factors for local community processes of interacting plants. Our findings lend support for this hypothesis at broader spatial scales, highlighting the importance of considering biotic interactions in species distributions and diversity across spatial scales. Previous research suggests that ants promote plant fitness and reproduction, and act as a selection pressure that enhances the evolution of EFNs and elaiosomes (Giladi 2006, Rosumek et al. 2009, Nelsen et al. 2018). Our findings indicate that the mutual benefits for both partners contribute to the congruent distribution of ants and plants. While the role of ants in shaping the distribution of ant-associated plants is well established, less is known about the reciprocal influence of plants on ant distributions. Plants can offer nesting sites and essential nutrients to ants, ultimately benefiting ant colony fitness and survival (Gammans et al. 2005, Calixto et al. 2021b). Nevertheless, these benefits are often temporally dependent on the growing and seed production seasons of plants (Gutián and Garrido 2006, Calixto et al. 2021a). While there is evidence that cooperation with plants does not promote ant diversification (Nelsen et al. 2018, Kaur et al. 2019), further work is needed to better understand the role of plant sources in shaping ant distribution.

In contrast to EFN- and elaiosome-bearing plants, we found no significant relationship between domatium-bearing plants and their corresponding ant guild. One possible explanation for this is that interacting with ants has no effect on the diversification of the myrmecophytes (Chomicki and Renner 2015), leading to no correlation between the diversity of myrmecophytes and arboreal ants. Additionally, we note that the interaction between domatia and ants is highly specialized, which could result in a potential overestimation of domatium-related ant diversity. However, identifying interacting ants is challenging and has often been neglected in previous research (Kaur et al. 2019), especially for arboreal ants requiring specialized sampling methods. There may be congruence between domatia and ants, as some ants that are recorded to inhabit domatia have been found to exhibit a congruent distribution with myrmecophytes in the tropics, such as *Azteca* and *Cecropia* in the Neotropics. Further work on ant distributions and ant-plant networks holds great potential to promote our understanding of ant-plant mutualisms.

In summary, our analyses elucidated the biogeographical distributions of plants bearing domatia, EFNs, and elaiosomes, and identified the key factors driving their representation, both directly and indirectly. Climate, phylogenetic relatedness, and associated ant diversity are essential to the geography of ant-associated plants, with the effects being mediated by features of mutualistic interactions. The consideration of mutualistic interactions together with abiotic factors is critical in deciphering the factors governing the global distribution and biogeography of plants.

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## Author contributions

**Yangqing Luo:** Conceptualization (equal); Data curation (lead); Formal analysis (lead); Methodology (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Amanda Taylor:** Conceptualization (equal); Methodology (equal); Supervision (equal); Writing – review and editing (equal). **Patrick Weigelt:** Data curation (equal); Formal analysis (equal); Methodology (equal); Writing – review and editing (equal). **Benoit Guénard:** Data curation (equal); Formal analysis (equal); Methodology (equal); Writing – review and editing (equal). **Evan P. Economo:** Data curation (equal); Writing – review and editing (equal). **Arkadiusz Nowak:** Data curation (equal); Writing – review and editing (equal). **Inderjit:** Data curation (equal); Writing – review and editing (equal). **Holger Kreft:** Conceptualization (equal); Data curation (equal); Supervision (lead); Writing – review and editing (equal).

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## Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.crjdfn39j> (Luo et al. 2023).

## Supporting information

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

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