Generalized mutualisms promote range expansion in both plant and ant partners

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PN and MEF conceptualized the study, performed the analyses and wrote the first draft of the manuscript. BG, EPE and AKS contributed the data used in the study and contributed to designing

the analysis and revising the manuscript. All authors have approved the submission of this manuscript and declare that there are no conflicts of interest.

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All data and code used in this manuscript are openly available at https://github.com/The-Frederickson-Lab/ant-legume-range

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Abstract

Mutualism improves organismal fitness, but strong dependence on another species can also limit a species' ability to thrive in a new range if its partner is absent. We assembled a large, global dataset on mutualistic traits and species ranges to investigate how multiple plant-animal and plant-microbe mutualisms affect the spread of legumes and ants to novel ranges. We found that generalized mutualisms increase the likelihood that a species establishes and thrives beyond its native range, whereas specialized mutualisms either do not affect or reduce non-native spread. This pattern held in both legumes and ants, indicating that specificity between mutualistic partners is a key determinant of ecological success in a new habitat. Our global analysis shows that mutualism plays an important, if often overlooked, role in plant and insect invasions.

Introduction

Life did not take over the globe by combat, but by networking. – Margulis & Sagan (1986)

When a species arrives in a new range, its ecological success in the novel habitat is determined by biotic and abiotic factors (Paquette and Hargreaves 2021). Past studies have investigated how climate, life history, and antagonistic species interactions (e.g., enemy release, Meijer *et al.* 2016) influence range expansions and biological invasions. Fewer studies investigate how positive interactions such as mutualisms shape range dynamics (Shaw *et al.* 2021; Moles *et al.* 2022; Fowler *et al.* 2023). Here, we ask: how does mutualism contribute to the global spread of legumes and ants?

How mutualism affects the eco-evolutionary success of participating species is the subject of debate. Mutualism increases fitness or population size by helping organisms overcome resource limitation, cope with stressors, or avoid or escape enemies. Thus, mutualism might increase the niche breadth or geographic range of species (Bruno *et al.* 2003; Afkhami *et al.* 2014a; Batstone *et al.* 2018), buffer against environmental change (Lau & Lennon 2012), or even create the kind of ecological opportunity that leads to adaptive radiation (Weber & Agrawal 2014; Zeng & Wiens 2021). However, mutualism may also make populations more vulnerable to environmental change and result in local or global co-extinctions (Brodie *et al.* 2014). If one species is highly specialized on another, it may struggle to persist under new environmental conditions or in a new range if its mutualistic partner becomes scarce, even if there are no direct negative effects of the new environment on the focal species (Brodie *et al.* 2014, Kiers *et al.* 2015, Benning & Moeller 2021). Moreover, mutualisms are expected to break down because of the threat of 'cheating' or exploitation (Porter & Simms 2014; Jones *et al.* 2015, but see Frederickson 2017) and widespread context-dependency (Chamberlain *et al.* 2014). Such ecological or evolutionary fragility might

prevent mutualists from thriving in new habitats or environments (Kiers *et al.* 2010), especially if mutualisms are most beneficial under the historical abiotic or biotic conditions in which the interaction evolved (Batstone *et al.* 2020).

Recent work has found evidence for both views: some studies have found that mutualism facilitates niche and range expansion (Afkhami *et al.* 2014a), while other studies have found the opposite (Duffy & Johnson 2017; Simonsen *et al.* 2017; Benning & Moeller 2021). One key determinant of the direction of effects appears to be the degree of specialization of the mutualism (Batstone *et al.* 2018; Harrison *et al.* 2018; Parshuram *et al.* 2023). Typically, the more generalized an interaction, the more likely a species is to encounter a compatible mutualist in its new range. If finding compatible partners in the new range is likely, and benefits derived from mutualism ameliorate abiotic or biotic stressors, mutualism can promote range expansion by allowing hosts to survive in otherwise uninhabitable ranges (Afkhami *et al.* 2014a). In contrast, if compatible partners are scarce and the species requires specific mutualistic partners, being mutualistic may hinder range expansion (Duffy & Johnson 2017; Simonsen *et al.* 2017; Harrison *et al.* 2018). Thus, specialization may constrain a mutualistic species' ecological success outside its native range (Harrison *et al.* 2018).

These ideas can be extended to the study of how species introduced to new habitats by anthropogenic activity come to colonize them successfully—i.e., to invasion biology. Indeed, there is growing evidence that successful plant invaders have generalized interactions with pollinators, seed dispersers, and arbuscular mycorrhizal fungi (Richardson *et al.* 2000; Albrecht *et al.* 2014; García *et al.* 2014; Menzel *et al.* 2017). Furthermore, mutualism is predicted to cause "invasional meltdown" (Simberloff & von Holle 1999), whereby positive feedback between mutualistic co-invaders amplifies their spread or impacts (O'Dowd *et al.* 2003; Prior *et al.* 2014).

We investigated mutualism's effects on introduced range size in ants and legumes. We chose these taxa because many ants and legumes are highly invasive species; these two families alone constitute 11% of the taxa on the IUCN's list of the World's 100 Worst Invasive Alien Species ("GISD" 2022). Substantial prior research has explored ecological factors that influence ant and legume invasions separately (e.g., Bradshaw *et al.* 2008; Wong *et al.* 2023), but no study has systematically evaluated the contribution of many mutualism types to the global spread of ants or legumes.

We investigated how ant-plant and plant-microbe mutualisms affect ant and legume range expansions. Mutualistic ants provide protection against enemies or seed dispersal services to many legumes, which reward ants with extrafloral nectar (EFN), nest sites in the form of live plant cavities (domatia), or lipid-rich appendages on seeds (elaiosomes). Most, but not all, legumes also engage in nutritional mutualisms with nitrogen-fixing rhizobia and phosphorus-provisioning mycorrhizae. These mutualisms span a continuum from highly generalized interactions such as seed dispersal by ants (myrmecochory) and ant-plant protection mutualisms mediated by EFNs, to highly specialized symbioses between ants and domatia-bearing plants (myrmecophytes), with variable partner specificity within legume-rhizobium and legume-mycorrhiza mutualisms. We compiled global range and trait datasets to test how mutualisms affect the invasive spread of legumes and ants in what is, to our knowledge, the largest comprehensive assessment to-date of mutualism and range size.

Materials and methods

Legume range data. We obtained range size data from a previous global analysis of legume geographic distributions (Simonsen *et al.* 2017). This dataset includes range data for over 3500 legume species and was originally compiled from records in the International Legume Database

& Information Service (ILDIS, www.ildis.org). ILDIS lists which countries, states, or provinces each legume species occurs in, and whether it is native or introduced in each politically defined region. Summing the areas of each region where a legume occurs over-estimates range size because a species may occupy only a small portion of a politically defined spatial polygon. Therefore, we followed previous studies (Simonsen *et al.* 2017; Harrison *et al.* 2018; Parshuram *et al.* 2023) and analyzed the number of non-contiguous introduced ranges for each species, rather than total introduced range area.

Legume mutualistic traits. We obtained data on legume associations with rhizobia from Simonsen *et al.* (2017) who compiled it from Werner *et al.* (2014); this study scored over 5000 legume species as 'symbiotic' or not, based on whether the legume forms nodules with rhizobia. We obtained data on interactions with mycorrhizae from an extensively curated dataset on the mycorrhizal associations of 14,870 plant species (Soudzilovskaia *et al.* 2020). We obtained data on the presence of EFNs from a curated, and frequently updated global list of plant species with EFNs (www.extrafloralnectaries.org) (Weber *et al.* 2015). Fabaceae has more EFN-producing plant species than any other plant family (Weber *et al.* 2015). We used data on which legumes have ant domatia from Chomicki and Renner (2015). Because these published lists of EFN- and domatia-bearing plants contain most records of EFN- and domatia- bearing plants known to science, we assumed that domatia and EFNs are absent from legumes not listed in Chomicki and Renner (2015), and www.extrafloralnectaries.org respectively. However, it is possible that this approach mis-classifies some legume species that are not well-studied. To control for this effect, we included the number of publications for each legume species available through CrossRef as a covariate. In contrast, for the legume-rhizobium and legume-mycorrhiza mutualisms, if there was no data for a legume species in Simonsen *et al.* (2017) or Soudzilovskaia *et al.* (2020), respectively,

we omitted the species from further analysis, since our data on these mutualisms was not exhaustive. We harmonized species names across datasets and used the R package *taxize* (Chamberlain & Szöcs 2013) to verify accurate species names and synonyms. The final dataset consisted of all legume species for which we had range size data and some mutualistic trait data.

Ant range data. We obtained data on the native and introduced range sizes of ants from the Global Ant Biodiversity Informatics (GABI) Project (Guénard *et al.* 2017). To calculate the total area of the native and introduced range for each species, we summed the areas of the spatial polygons making up an ant species' native or introduced range. This approach over-estimates ant range size, so again we calculated the number of non-contiguous introduced ranges for each ant species by determining whether all pairs of spatial polygons making up its introduced range share a border using the *st_disjoint* function in the *sp* package in R (Pebesma *et al.* 2023) and converting the resulting matrix into a graph using the *igraph* package (Nepusz *et al.* 2023). We counted the independent subgraphs in the graph to determine the number of non-contiguous introduced ranges.

Ant mutualistic traits. We obtained data on which ant species visit EFNs, nest in domatia, and disperse elaiosome-bearing seeds from Kaur *et al.* (2019) where the authors text-mined the abstracts of nearly 90,000 published articles about ants to algorithmically score which ant species do or do not visit EFNs, nest in domatia, or disperse seeds. For seed dispersal, they validated the text-mining results by comparing to a global list of seed-dispersing ants assembled and curated by a myrmecochory expert (Dr. Crisanto Gomez). We treated these ant traits (visits EFNs, nests in domatia, disperses seeds) as binary, categorial variables.

Data analysis. All analyses were conducted in R version 4.2.0 (R Core Team 2022). For legume and ant introductions, we fit two models each: a generalized linear mixed model with a binomial error distribution for whether (1) or not (0) a species has been successfully introduced outside its

native range, and a linear mixed model with a Gaussian error distribution of the log-transformed number of introduced ranges for species with at least one non-native range in the dataset (i.e., the second model excluded species that have not established outside their native range). For legume range size, we had two datasets that we modelled separately: one had trait data on the presence or absence of EFNs, domatia, and nodules for 3977 legume species, and the other had trait data on the presence or absence of AM and EM fungi for 723 legume species. For the larger dataset, we included the main effects of EFNs, domatia, and nodules and all possible interactions as predictors but simplified models by removing non-significant interactions. For the mycorrhizal dataset, we did not have sufficient degrees of freedom to model all five mutualistic traits and their interactions, so we fit a model with AM fungi, EM fungi, and their interaction as predictors, and then omitted the non-significant interaction and re-fit. Using the smaller mycorrhizal dataset, we also fit models with a count of the number of mutualisms each legume species engages in as a continuous variable (range: 0-4, as no legume has EFNs, domatia, nodules, AM, and EM; see SI). In all legume models, we included several other predictors available from Simonsen *et al.* (2017)'s dataset, specifically plant life history (annual or perennial), plant habit (woody or herbaceous), the number (range 0-9) of distinct human uses and the absolute latitude of the centroid of each legume's native range. We also included counts of number of publications available for each legume species, determined using the *cr_works* function in the *rcrossref* package (Chamberlain *et al.* 2020) as a predictor. For ant range size, we fit models with EFN visitation, residing in domatia, and seed dispersal as predictors. We calculated the absolute latitude of the centroid of each ant's native range and included it as a covariate in all ant models. There is no equivalent in the ant range dataset to the 'number of human uses' variable in the legume range dataset, but we used available information on the mode of ant introduction to classify introduced ants as "intercepted" (i.e., at customs),

188 "indoor introduced," or "exotic (naturalized)" as per Wong *et al.* (2023), and tested whether
189 mutualistic traits affected the probability that an ant would be introduced indoors, intercepted by
190 customs, or become naturalized in its introduced range. We used the *lmer* and *glmer* functions to
191 fit models (package *lme4*; Bates 2010) and then ran Type III Wald chi-square tests to assess
192 statistical significance using the *Anova* function from the *car* package (Fox *et al.* 2015). In both
193 legume and ant models, we accounted for the phylogenetic non-independence of species in our
194 dataset (Felsenstein 1985) by including tribe as a random effect in the mixed models. We also fit
195 phylogenetic generalized least squares (PGLS) models (methods in SI), although they have lower
196 statistical power because they exclude species for which we have trait and range data but no
197 phylogenetic information.

198 **Results**

199 *Legumes.* In total, the legume range dataset included 3977 species, of which 3581 associate with
200 nitrogen-fixing bacteria, 280 have extrafloral nectaries, and 24 have domatia. The smaller dataset
201 on legumes with mycorrhizal fungi included 572 with arbuscular mycorrhizal (AM) fungi, 38 with
202 ectomycorrhizal (EM) fungi, 80 with both AM and EM fungi (690 total taxa with mycorrhizae),
203 and 33 without mycorrhizal fungi.

204 The presence of EFNs, but not domatia, nodules, or either type of mycorrhizae,
205 significantly increased the likelihood of a legume successfully establishing in at least one non-
206 native range (Figure 1, Table 1). Legumes with EFNs have also colonized significantly more
207 introduced ranges than legumes without EFNs (Figure 1, Table 1). Although having domatia did
208 not affect whether a legume species is introduced to at least one new range, domatia did
209 significantly reduce the number of introduced ranges (although there were only 7 introduced
210 legumes with domatia; Figure 1, Table 1). None of the belowground mutualisms significantly

211 predicted introduction success or the number of introduced ranges (Figure 1, Table 1), although
212 we observed the same trend reported by Simonsen *et al.* (2017), in which legumes that associate
213 with rhizobia colonized fewer introduced ranges than non-nodulating legumes. The PGLS model
214 also found a significant positive effect of EFNs, but no other mutualisms, on legume introductions
215 (details in SI). Thus, overall, EFNs had consistently large, positive effects on legume introductions,
216 domatia had weaker negative to neutral effects, and mycorrhizal fungi and nodules had no
217 significant effects. Nonetheless, there was a significant, positive effect of engaging in more
218 mutualisms on legume introduction success, and a marginally significant ($p = 0.07$) positive effect
219 of engaging in more mutualisms on the number of introduced ranges (Figure S1, Table S1).
220 Nodulation and AM fungi were the most widespread mutualisms in the legume dataset (additional
221 details in SI) and this result suggests they may increase introduction success when combined with
222 other mutualistic traits, but we did not fit a model testing all five mutualistic traits (EFNs, domatia,
223 nodules, and AM and EM fungi) and all their possible interactions because of the small size of the
224 legume-mycorrhizae dataset.

225 As in Simonsen *et al.* (2017), legumes with more human uses were both more likely to be
226 introduced and established in more introduced ranges (Table 1), and annuals were significantly
227 more likely to be introduced than perennials, although only in the model of EFN, domatia, and
228 nodulation effects (Table 1). Native range area had inconsistent effects across models; legumes
229 with larger native range areas were more likely to be introduced in the model of EFN, domatia,
230 and nodulation effects (Table 1), but in the smaller mycorrhizal dataset, models predicted that
231 introduced legumes with larger native range areas have spread to fewer introduced ranges (Table
232 1). Woody legumes were significantly more likely to be introduced but spread to fewer introduced
233 ranges than herbaceous legumes in both the model of EFN, domatia, and nodulation effects, and

234 in the smaller mycorrhizal dataset (Table 1). The absolute midpoint latitude of a legume's native
235 range never significantly predicted its introduction success or number of introduced ranges,
236 meaning there was no difference among tropical, sub-tropical, and temperate legumes in non-
237 native spread. The number of studies on each species, a proxy for how well-studied a species is,
238 also never significantly predicted introduction success or introduced range size in legumes.

239 Mutualistic traits generally had non-significant effects on the total native range area of
240 legumes, except having both domatia and EFNs strongly decreased native range area (Figure S2,
241 Table S2). However, only four legume species in the dataset have domatia and EFNs (three ant-
242 acacias and *Humboldtia laurifolia*). Covariate effects on native range size are described in the SI.

243 *Ants.* In total, we had range and trait data for 3023 species, of which 115 visit EFNs, 297 disperse
244 seeds, and 58 nest in domatia. Ant species that visit EFNs were more likely to be introduced and
245 have spread to more introduced ranges than other ants (Figure 2, Table 2). Seed-dispersing ant
246 species were also more likely to be introduced but have not spread to more introduced ranges than
247 ants that do not disperse seeds (Figure 2, Table 2). In contrast, nesting in domatia had no significant
248 effect on introduction success or number of introduced ranges (Figure 2, Table 2). Ants with larger
249 native range areas were more likely to be introduced but have not invaded more ranges (Table 2).
250 The midpoint latitude of an ant's native range was significantly negatively associated with both
251 introduction success and the number of introduced ranges (Table 2), meaning that tropical ants
252 have had greater non-native spread than temperate ant species. The PGLS model also found
253 significant, positive effects of visiting EFNs and dispersing seeds, but not nesting in domatia, on
254 the number of introduced ranges (details in SI).

255 Mutualistic traits never had significant interaction effects on introduction success or
256 introduced range area in the mixed models, so the final models fit main effects of mutualistic traits

257 only (Table 2). In other words, mutualisms had additive effects on ant introductions, and not sub-
258 additive or synergistic effects. There was also a significantly positive effect of the number of
259 mutualisms on ant introduction success and number of introduced ranges (Figure S3, Table S3).

260 Unlike in legumes, mutualisms significantly predicted ant native range sizes. Ants that visit
261 EFNs or disperse seeds had significantly larger native range areas than species that do not
262 participate in these mutualisms (Figure S4, Table S4, and see SI for covariates).

263 Ants that visit EFNs were significantly more likely to establish indoors, but no more likely
264 to be naturalized outdoors or intercepted at customs than other ants (Figure 3, Table S5). Nesting
265 in domatia had no significant effects on customs interception, indoor establishment, or
266 naturalization (Figure 3, Table S5). Ants that disperse seeds were significantly more likely to be
267 intercepted at customs, but significantly less likely to establish indoors, and equally likely to be
268 naturalized as other ants (Figure 3, Table S5).

269 **Discussion**

270 Several mutualisms affected introduction success and invasive spread, with generalized
271 mutualisms facilitating range expansion. Notably, the very generalized mutualism between EFN-
272 bearing legumes and EFN-visiting ants increased the likelihood of being introduced to new ranges,
273 as well as the number of introduced ranges, in both partners. Dispersing seeds, another generalized
274 mutualism, was also associated with increased invasiveness in ants. In contrast, associating with
275 rhizobia or mycorrhizal fungi did not significantly affect the non-native spread of legumes, and
276 residing in domatia had no significant effect on ant invasions. Finally, producing domatia
277 constrained non-native spread in legumes. These results suggest that generalized mutualisms

278 improve the likelihood of successful colonization of new ranges, with specialized mutualisms
279 having no, or opposite, effects.

280 There is debate about how mutualisms impact ecological success. On the one hand,
281 associating with a mutualist may enable a species to better tolerate abiotic or biotic stressors in a
282 new range (Afkhami *et al.* 2014b; Batstone *et al.* 2018). On the other hand, specialization on a
283 mutualistic partner may reduce a species' ability to colonize ranges where its partner is absent
284 (Simonsen *et al.* 2017; Harrison *et al.* 2018b; Benning & Moeller 2019; but see Birnbaum *et al.*
285 2012). Our study suggests that both scenarios occur, although there was stronger evidence for the
286 former. Very generalized mutualisms may allow species to associate with previously unseen
287 mutualistic partners and colonize new ranges (Richardson *et al.* 2000).

288 Our study is the first to find that the mutualism between EFN-bearing plants and EFN-
289 visiting ants has reciprocally positive effects on range expansions in both partners observable at
290 the macroecological scale. In all models, legumes with EFNs were better invaders, as were ants
291 that visited EFNs. The mutualism between EFN-visiting ants and EFN-bearing plants is usually
292 generalized in both plant and ant partners (Heil & McKey 2003; Marazzi *et al.* 2013; but see Heil
293 *et al.* 2010). EFN-visiting ants tend to be cosmopolitan, and EFN-producing legume species may
294 have higher ecological success because they recruit local ant species, some of which may serve as
295 bodyguards against herbivores in new ranges, even without sharing evolutionary history. This is
296 evidenced by records of native ant species visiting the EFNs of invasive plant species (Eichhorn
297 *et al.* 2011; Johnson *et al.* 2019). Our results also suggest that ant species that visit EFNs are more
298 successful at colonizing new habitats. Extrafloral nectar from native plant species may serve as a
299 valuable food resource for newly introduced ant species (as recorded by Ness & Bronstein 2004;
300 Lach *et al.* 2009; Savage *et al.* 2009; Riginos *et al.* 2015) even when the species have not interacted

before. There are also many reports of invasive ants visiting EFNs on invasive plants (Lach *et al.* 2010; Eichhorn *et al.* 2011; Gippet *et al.* 2018), even when they come from different regions, suggesting that little or no coevolution is required for a new interaction to be established. In contrast, the mutualism between domatia-nesting ants and domatia-bearing plants is quite specialized in both ant and plant partners (Chomicki and Renner 2015; but see Chanam *et al.* 2014; Volp *et al.* 2022), likely explaining why domatia reduced invasive spread in legumes, while nesting in domatia had no effect in ant introductions.

Much as ants visit EFNs on unfamiliar plants, seed-dispersing ants often pick up elaiosome-bearing seeds from invasive plant species even if they have not encountered them before (Passos & Oliveira 2003; Rowles & O'Dowd 2009; Stuble *et al.* 2010; Rodriguez-Cabal *et al.* 2012; Devenish *et al.* 2019; Anjos *et al.* 2020) and as expected, seed-dispersing ants had larger native and introduced range sizes than ants that do not pick up seeds. While seed-dispersing ants often interact with many plant species, so long as their seeds have elaiosomes, this interaction may be less generalized from the plant perspective, with only a few ant species being effective seed dispersers (Manzaneda & Rey 2009; Ness *et al.* 2009). Thus, while ants may benefit from "dispersing" seeds in their new range, the same cannot be assumed for introduced myrmecochorous plants (Warren *et al.* 2010). However, we were limited by the availability of trait data to testing the effects of the mutualism between seed-dispersing ants and myrmecochorous plants only in ants, not in legumes.

In legumes, associating with rhizobia had no significant negative effects on introduction success. A previous study using the same dataset (Simonsen *et al.* 2017) found that legumes that form nodules with rhizobia have spread to fewer new ranges than non-nodulating legumes, and we found a non-significant trend in the same direction, although our model structures were different.

Our analysis included more mutualistic traits than Simonsen *et al.* (2017), and we had limited statistical power to test for all the possible interactions between mutualistic traits and covariates. In Simonsen *et al.* (2017), however, the higher non-native spread of non-symbiotic legumes was only observed only among species that had a low number of human uses. The ability to nodulate and hence fix nitrogen is a useful trait for humans (e.g., in forage or rotation crops), thus humans may deliberately introduce symbiotic legumes and overcome the establishment barrier caused by lack of rhizobial partners. In a follow-up study to Simonsen *et al.* (2017), Harrison *et al.* (2018) found that even within nodulating legumes, species that associate with more rhizobial strains have larger introduced ranges than those that interact with fewer strains, substantiating the trend of generalized mutualisms increasing range expansion that we observe across mutualism types, but within a single kind of association. Furthermore, Parshuram *et al.* (2023) recently found that specialization in legume-rhizobium mutualisms constrains range expansions only in polyploid, and not in diploid legumes. Thus, variation among nodulating legumes in their specificity on rhizobia and interactions between mutualism and other traits probably explain why nodulation alone did not predict legume introduction success or invasive spread in our analysis.

Interacting with AM fungi had a non-significant positive effect on the successful introduction of legumes, while interacting with EM fungi had a non-significant negative effect. The overwhelming majority of plant species are mycorrhizal (Brundrett 2009; Maherali *et al.* 2016) and thus our dataset contained only 33 legume species that did not partner with mycorrhizal fungi, meaning that we had low statistical power to detect effects of mycorrhizae on legume range expansions. Although we did not observe any significant effects of AM or EM fungi on legume introductions, the limiting effect of EM fungi on range expansions has been studied extensively in pines (Nuñez *et al.* 2009; Hayward *et al.* 2015; Policelli *et al.* 2019), which famously could not be

347 successfully cultivated in the southern hemisphere until they were inoculated with soil from their
348 native range containing suitable EM fungi (Richardson 2000).

349 In both legumes and ants, we found that participating in more mutualisms increased the
350 likelihood of successful introduction and spread in the new range. This result suggests that the
351 positive effects of generalized mutualisms counteract any negative effects of specialized
352 mutualisms when a species colonizes a new range and that, overall, mutualism promotes, rather
353 than hinders, range expansion. Recent studies have also shown that AM fungi and rhizobia act
354 synergistically in their interactions with legumes, promoting plant growth when together more than
355 expected from the growth-promotion effects of rhizobia or AM fungi alone (Larimer *et al.* 2014;
356 Afkhami & Stinchcombe 2016; Afkhami *et al.* 2021). In legumes, the most common mutualisms
357 are with rhizobia and AM fungi, and the synergistic effects of these mutualisms may drive the
358 increase in colonization success we observe for legumes that participate in more types of
359 mutualisms. Multiple mutualist effects (Afkhami *et al.* 2014) may provide more insights into the
360 mechanisms of how multiple mutualistic partners influence each other and their shared host, but
361 most current studies focus on only one kind of mutualism in isolation, especially at large
362 biogeographic or macroevolutionary scales (Chamberlain & Rudgers 2012; Godschalx *et al.* 2015;
363 Dutton *et al.* 2016; Afkhami *et al.* 2021; Laurich *et al.* 2022).

364 In legumes, mutualism had little effect on native range size, suggesting that different eco-
365 evolutionary processes are involved in determining the native and introduced ranges of legumes
366 (Sexton *et al.* 2009). The only strong effect of mutualism on legume native range size was the
367 negative interaction between EFNs and domatia, in which legumes with both traits had
368 significantly smaller native ranges than other legumes. This type of highly specialized ant-plant
369 mutualism, in which plants both feed and house their ant symbionts, is rare, and occurred in only

370 four legumes in our dataset. In contrast, in ants, mutualism had strong effects on both native and
371 introduced ranges. Because the trait data for ants were generated by text-mining scholarly literature
372 (Kaur *et al.* 2019), one explanation for this pattern is that mutualisms are more likely to be studied
373 in widespread ant species and remain severely under-reported in ant species with small ranges.
374 However, the text-mined trait dataset of Kaur *et al.* (2019) classified an ant species as a non-
375 mutualist only if the species had received at least some study in the scholarly literature (i.e., they
376 did not categorize unstudied ants, which might have smaller ranges on average, as non-mutualists).
377 Furthermore, native range size is likely overestimated in our dataset (for both legumes and ants),
378 because it is calculated from the summed areas of all politically defined spatial polygons where a
379 species has historically occurred, regardless of how much of the polygon the species inhabits. We
380 have no reason to suspect that native range size is overestimated more in mutualists than non-
381 mutualists, but the native range results should nonetheless be interpreted with caution. This issue
382 does not affect our analyses of introduction success or the number of introduced ranges, although
383 both native and introduced ranges may still be under-estimated because of limited data on species
384 occurrences, especially in the Global South.

385 Our results also suggest that human activity is an important determinant of legume and ant
386 invasion success when viewed through a mutualism lens too. For legumes, the number of human
387 uses contributed significantly to the likelihood of being introduced and the number of introduced
388 ranges. Agriculture can be considered a mutualism between plants and humans (Boucher 1985;
389 Spengler 2020; Angourakis *et al.* 2022) and the dispersal of cultivated species to new ranges is a
390 consequence of this interaction. Reciprocally positive interactions between humans and legumes
391 have clearly accelerated the introduction of legumes to new ranges.

Humans have also contributed to the non-native spread of ant species around the globe (Gippet *et al.* 2019; Gippet & Bertelsmeier 2021; Lach 2021). EFN-visiting ant species were more likely to establish indoors, possibly because of the abundance of sugary, nectar-like foods present in human settlements, because they were co-introduced with ornamental plants in indoor locations like greenhouses, or because they are more often tropical in origin (Luo *et al.* 2022) and thus thrive in warmer indoor environments. In contrast, seed-dispersing ants often originate from and invade mid-latitude regions, and they were more likely to be intercepted and less likely to be introduced indoors. The Mediterranean or temperate climates where myrmecochory is most common (Lengyel *et al.* 2010) may also be regions with strong customs surveillance of novel insect pests.

Mutualism is not generally considered a driver of macroecological patterns, but our results suggest that the benefits derived from generalized mutualisms increase ant and legume introductions globally. Indeed, mutualisms between introduced species may mediate the rapid spread of both partners, potentially accelerating biodiversity loss and other ecosystem changes, causing "invasional meltdown" (Simberloff & von Holle 1999; Traveset & Richardson 2014). Our global analysis suggests that the positive feedback that occurs between partners in mutualisms often amplifies the non-native spread of ants and legumes, but only when interactions are generalized.

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Acknowledgements

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Figures

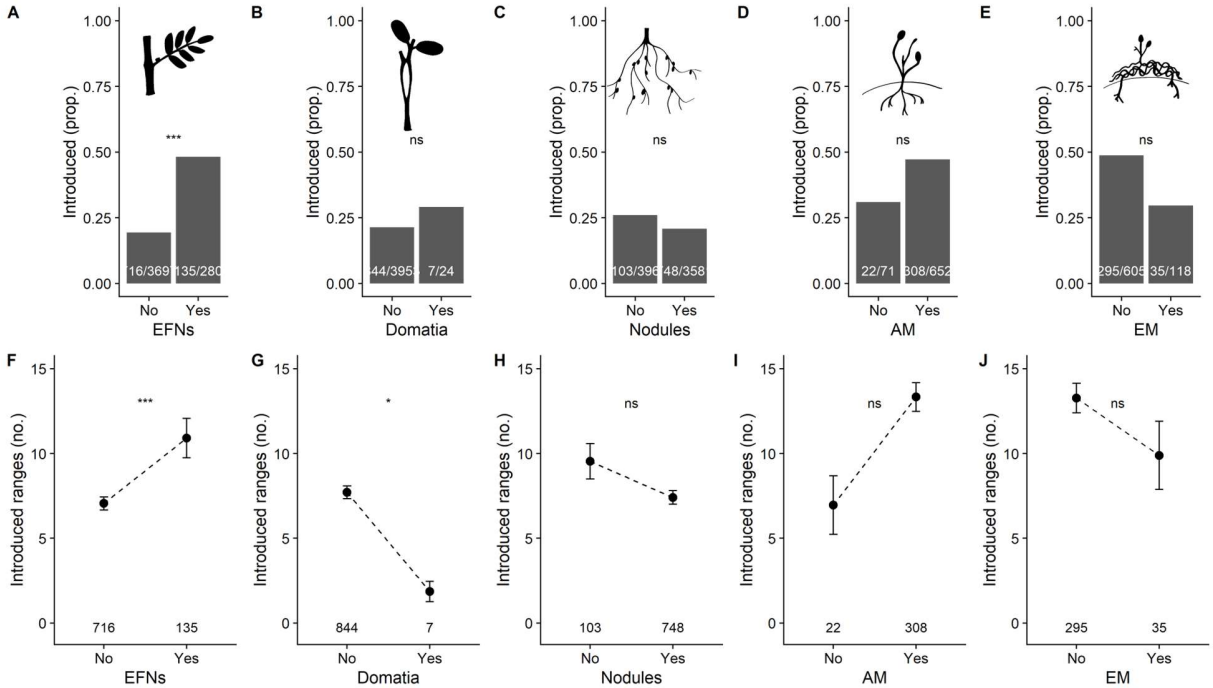

Figure 1. Relationship between the presence or absence of EFNs (A, F), domatia (B, G), nodules (C, H), arbuscular mycorrhizae (D, I), or ectomycorrhizae (E, J) and the proportion of introduced species (top) or number of introduced ranges (bottom, mean ± 1SE). Above the x-axis is the proportion of introduced taxa/total taxa (top) or number of introduced species (bottom) in each category. Significant effects indicated by *** for $p \leq 0.001$, ** for $p \leq 0.01$, and * for $p \leq 0.05$. See Table 1 for complete results of statistical models.

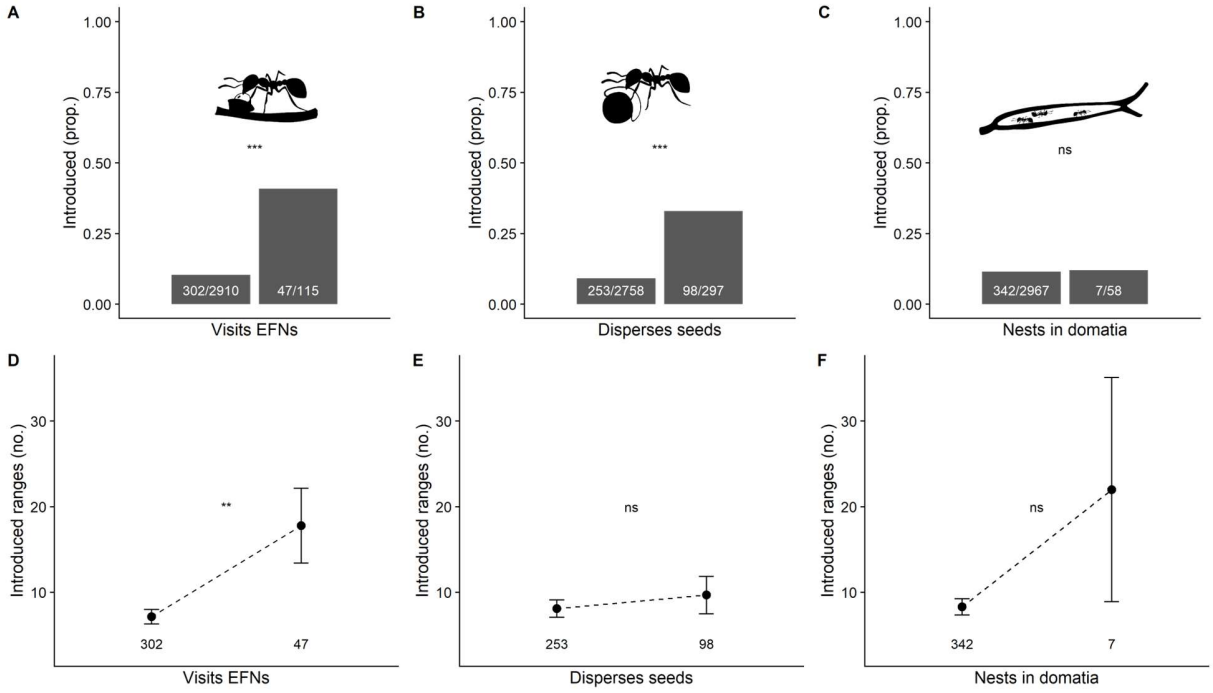

Figure 2. Relationship between ants visiting EFNs (A, D), dispersing seeds (B, E), and nesting in domatia (C, F) and the proportion of introduced species (top) or introduced range area (bottom, mean ± 1SE). Above the x-axis is the proportion of introduced taxa/total taxa (top) or number of introduced species (bottom) in each category. Significant effects indicated by *** for $p \leq 0.001$, ** for $p \leq 0.01$, and * for $p \leq 0.05$. See Table 2 for complete results of statistical models.

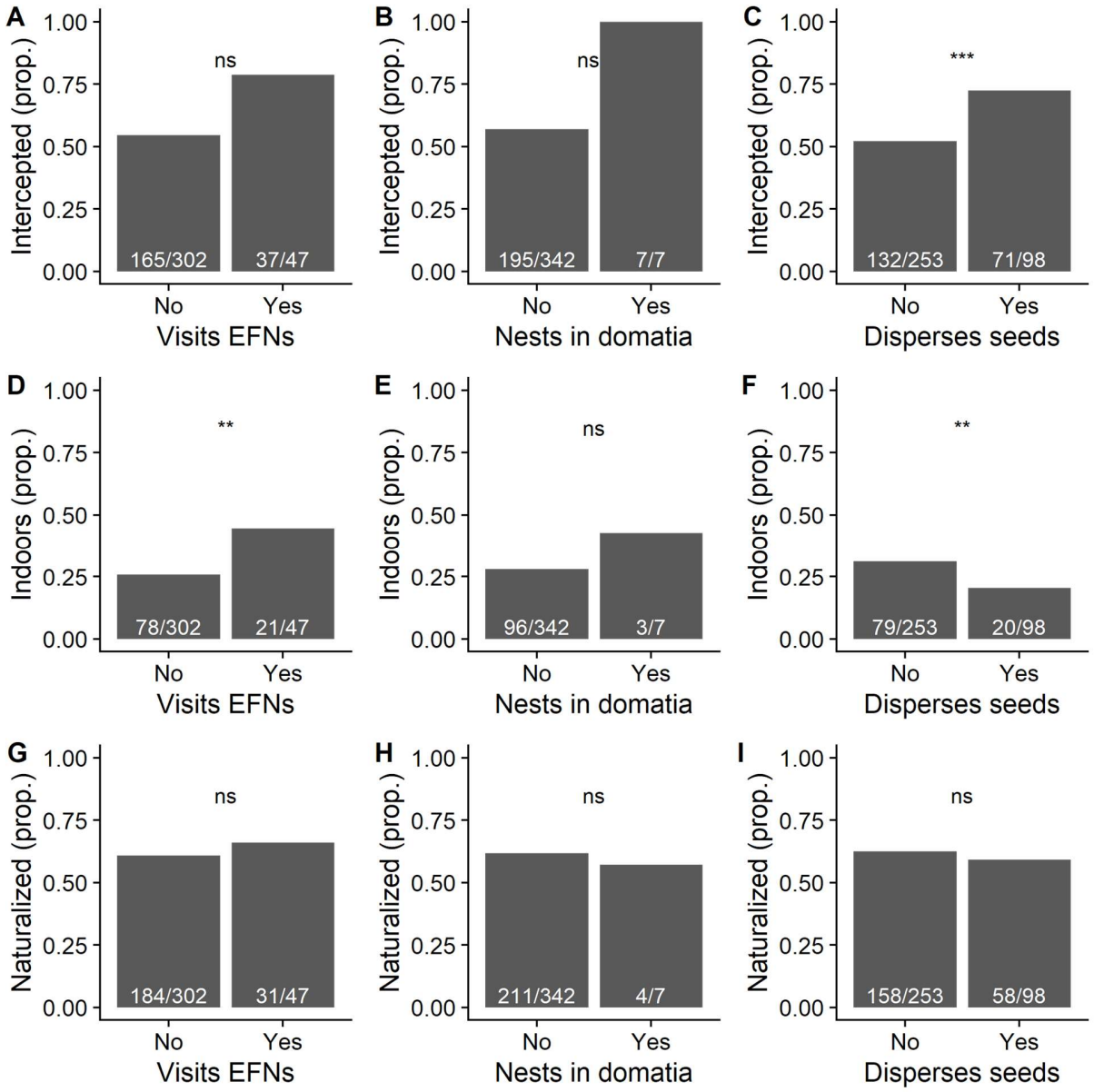

Figure 3. Relationship between ants visiting EFNs, dispersing seeds, and nesting in domatia and whether an ant species is intercepted at customs (top), establishes indoors (middle), or have become naturalized outdoors (bottom) in non-native ranges. Numbers above the x-axis indicate the number of intercepted/indoor/naturalized taxa/total introduced taxa. Significant effects indicated by *** for $p \leq 0.001$, ** for $p \leq 0.01$, and * for $p \leq 0.05$. See Table S6 for complete results of statistical models.

678 **Table 1.** Model results for the effects of A. EFNs, domatia, and nodules and B. AM and EM fungi
679 on whether legumes are successfully introduced to any novel range (left columns), and if
680 successfully introduced, how many introduced ranges they spread to (right columns). Interactions
681 among mutualistic traits were never significant and omitted from final models. Significant effects
682 *italicized* and indicated by *** for $p \leq 0.001$, ** for $p \leq 0.01$, and * for $p \leq 0.05$

A.	**Successful introduction? (Binomial GLMM)**		**Number of introduced ranges (Gaussian LMM)**	
Fixed effects	**Estimate**	**SE**	**Estimate**	**SE**
Intercept	*-3.544****	*0.296*	*0.850****	*0.163*
EFNs?	*1.254****	*0.195*	*0.342****	*0.099*
Domatia?	0.431	0.642	*-0.986**	*0.384*
Nodules?	0.399	0.238	-0.208	0.136
Total native area	*0.186***	*0.057*	-0.051	0.037
Annual?	*0.670****	*0.186*	0.010	0.120
Woody?	*0.784****	*0.162*	*-0.218**	*0.100*
Latitude	0.091	0.069	-0.064	0.042
Number of human uses	*1.002****	*0.049*	*0.320****	*0.016*
Publication count	0.064	0.048	0.022	0.032
Random effect	**Variance**		**Variance**	
Tribe	0.511		0.040	

683

B.	**Successful introduction? (Binomial GLMM)**		**Number of introduced ranges (Gaussian LMM)**	
Fixed effects	**Estimate**	**SE**	**Estimate**	**SE**
Intercept	*-2.465****	*0.535*	*0.816****	*0.266*
AM?	-0.164	0.391	0.227	0.224

EM?	-0.226	0.377	-0.023	0.218
Total native area	0.240	0.145	*-0.178***	*0.064*
Annual?	0.699	0.512	0.193	0.235
Woody?	*0.911**	*0.360*	*-0.367**	*0.165*
Latitude	0.201	0.151	-0.116	0.070
Number of human uses	*0.951****	*0.087*	*0.315****	*0.025*
Publication count	0.197	0.130	0.030	0.055
Random effect	**Variance**		**Variance**	
Tribe	0.779		0.096	

684

685 **Table 2.** Model results for the effects of visiting EFNs, dispersing seeds, and nesting in domatia
686 on whether ants are successfully introduced to any novel range (left columns), and if successfully
687 introduced, their introduced range area (right columns). Interactions among mutualistic traits were
688 never significant and omitted from final models. Significant effects *italicized* and indicated by ***
689 for $p \leq 0.001$, ** for $p \leq 0.01$, and * for $p \leq 0.05$.

	Successful introduction? (Binomial GLMM)		**Number of introduced ranges (Gaussian LMM)**	
Fixed effects	**Estimate**	**SE**	**Estimate**	**SE**
Intercept	*-2.958****	*0.187*	*0.827****	*0.154*
Visits EFNs?	*0.911****	*0.260*	*0.557***	*0.197*
Nests in domatia?	-0.485	0.525	0.354	0.478
Disperses seeds?	*1.294****	*0.188*	0.104	0.162
Total native area	*0.401****	*0.037*	0.081	0.062
Latitude	*-0.262****	*0.063*	*-0.375****	*0.065*
Random effect	**Variance**		**Variance**	
Tribe	0.676		0.415	

690