Ant predation on herbivores through a multitrophic lens: how effects of ants on plant herbivore defense and natural enemies vary along temperature gradients.

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Figures: 4/ 4 max.

Abstract

Ants are keystone predators in terrestrial trophic cascades. Addressing ants' roles in multitrophic interactions across regional gradients is important for understanding mechanisms behind range limits of species. We present four hypotheses of trophic dynamics occurring when ants are rare: 1. There is a shift in predator communities, 2. Plants decrease investments in ant attraction and increase production of secondary metabolites, 3. Lower herbivory at high elevations allow plants to tolerate herbivory, and 4. Distribution of ant-plants can be limited to the distribution of ant abundance. Conducting experiments on multitrophic effects of ants across elevational gradients, and incorporating these results to ecological niche modeling (ENM) will improve our knowledge of the impacts of global change on ants, trophic interactions, and biodiversity.

Keywords

Ants, multitrophic interactions, plant defenses, herbivore, natural enemies, species distribution range, elevation.

Introduction

Multitrophic interactions affect a variety of ecosystem parameters, from primary productivity to population dynamics [1*, 2]. Among the best studied top-down drivers of multitrophic interactions in terrestrial ecosystems are ants involved in facultative or obligate relationships with plants [3*,4]. Recent meta-analysis on ant-plant interactions found that for 64 species of plants across a broad latitudinal range, attracting ants always resulted in a positive effect on plants [5]. However, there is geographic variation in effect sizes: plant-ant interactions are

stronger in tropical regions and have been associated with higher temperatures at a global scale [5, 6]. Because of this potential for ants to act as plant defenders, determinants of plant distributions, and transformers of entire ecosystems, it is compelling to consider how multitrophic interactions are different in ecosystems where ants are far less abundant [7**].

Here we discuss tropical elevational gradients as useful gradients for studying the interdependence between ants and plants. We first ask which mechanisms restrict or enable a species' distribution range, we then discuss benefits of studies along elevational gradients, and we propose a general model of biotic effects on diversity that integrates four mechanistic hypotheses: 1. In the absence of ants, predator communities shift and other natural enemies fill the functional role provided by ants as indirect plant defenses [8*]. 2. Plants compensate for the lack of ants by allocating fewer resources to ant attraction and more resources towards production of secondary metabolites [9*]. 3. The reduced herbivore pressure at high elevations can have relatively small impacts on plants, thus facilitating a reduction in plant defenses [10*]. 4. The distribution of ant-plants at high elevations and temperate latitudes can be limited by the lack of ants [11*]. Ancillary to this conceptual model is the notion that multitrophic interactions should be incorporated in ecological niche models. Thus niche models for species involved in multitrophic interactions should include predictions on how different defense mechanisms, including ants, plant secondary metabolites, and other important drivers of trophic interactions, vary in strength across elevations.

Do trophic interactions affect species distributions?

For any species the interplay between abiotic factors and biotic interactions may limit their distribution. For any particular ecosystem, an important research goal is to

determine which organisms are primarily constrained by physiology and which are more affected by the presence of competitors, enemies or mutualists. Biotic effects can be important determinants of distributions for a wide array of taxa; for example, pathogens were responsible for 38% of seedling mortality in an experiment examining why trees from tropical dry forests are not present in rain forests [12]. Herbivory was also a factor determining the difference in plant composition between Peruvian Amazon clay and white sand soils [13**]. At most spatial scales, plant distributions and assemblages are clearly influenced by abiotic factors and environmental filtering, but strong patterns from small scale herbivore exclusions suggest that herbivores could determine plant assemblages at larger scales [14].

The effects of biotic interactions on species distributions are not limited to local scales [15**]. There is a wealth of multitrophic interactions studies across broad gradients, but few studies combine species distribution modeling with biotic interactions. As a result, ecologists have omitted biotic interactions as important factors that determine species distributions. Excluding biotic interactions limits the predictive power of distribution models and obscures the important effects that changes in species interactions can have on extinctions or on the altered species distributions that are predicted to occur in response to global change [16, 17].

Ecological studies along tropical elevational gradients

Multiple environmental factors change along any elevational gradient. As elevation increases, temperature decreases, precipitation can change substantially, net primary productivity (NPP) tends to decrease, and species richness usually shows hump-shaped patterns with peaks at low to medium elevations [18]. Steep mountains, such as the Andes, are characterized by particularly strong temperature gradients that are barriers to

physiological adaptations, resulting in limited distribution ranges of plant and animal species [19]. In addition, tropical and temperate mountains are different because there is minimal overlap between the climate of tropical mountain tops and valleys. Moreover, such differences in climate force lineages of organisms to have narrow temperature tolerance, thus dispersal and gene flow across mountain passes is lower for tropical organisms than for temperate ones ([20**], see also [21]).

At a local scale, exclusion of ant-predators has resulted in changes of plant communities at a Costa Rican lowland rainforest [14]. Unfortunately, extrapolating such studies to landscape scales is not easy since trophic interactions may vary in space and time [22]. Documenting geographic variation in the strength of top-down or bottom-up effects, along with measuring competitive exclusion at landscape scales, will allow ecologists to incorporate these trophic interactions into species distribution models. Elevational gradients are ideal for this approach because of the rapid changes in top-down and bottom-up forces across relatively small spatial scales. Fine scale elevation studies of herbivores have allowed us to document current shifts on species distributions as a response to climate change [23, 24]. In addition, predictions of future species distributions are linked to the tight interactions between specialized consumers and resources. Understanding the consequences of global change must include co-extinction risks associated with these biotic interactions [18, 25].

It is well documented that ant species richness in the tropics peaks at relatively low elevations, then declines and approaches nearly zero at ca. 2000m [7**]. The sharp decrease of ant richness above 2000m has been attributed to the lower energy availability at these elevations [26], and to a low tolerance of social insects to cooler and excessively humid conditions [27]. This decrease in ant richness and density translates into a decline of an important predator guild – recruiting foragers [26, 28]. However it is unclear how

will montane ecosystems fare if the distribution range of ants shifts upward.

Ants are not as abundant in temperate regions as they are in the tropics, and are rare at high elevations, yet some ant-plants have ranges that extend to locations without ants. We hypothesize that plasticity and adaptation for plants and herbivores in habitats with and without ants will depend on the nature of their relationship and on pressure by herbivores [29, 30]. And upward range expansion with ants may benefit ant-plants but be detrimental to herbivores that have not coevolved with ants as keystone predators[19**].

Conceptual model

Variation in multitrophic relationships involving ants across elevational gradients is likely to affect species distributions of plants, herbivores, and enemies [18]. We present a conceptual model comprised of four hypotheses, each of which includes a different mechanism by which ants can modify plant, herbivore, or enemy distributions.

1. In the absence of ants, other predators, which are not equally affected by temperature decreases, should thrive and fill the functional role provided by ants -Figure 1.

The main two mechanisms by which ant absence may shape assemblages of other predators are release from (1) competitive exclusion and (2) intraguild predation by ants. Ants are often involved in strong intraguild interactions, affecting other predator groups such as spiders, ladybird beetles and birds [31-32]. Predation studies using clay caterpillars across a tropical gradient revealed that bird predation became relatively more important at elevations at which ants are rare [8*]. Multiple experimental studies have revealed strong intraguild interactions between ants and spiders resulting in exclusion of either group depending on the predator community composition [e.g. 31, 33]. In the case of ant abundance increasing at montane elevations, due to climate change, they would

interfere with predators that thrive in the absence of ants. For example, coffee plants (*Coffea arabica*, Rubiaceae) in Mexico are defended by ants whenever they have ant-plants in their vicinity and by other predators in their absence [32].

2. Plants compensate for the absence of ants by allocating fewer resources to ant attraction and more resources towards production of secondary metabolites - Figure 2.

There are two potential trade-offs between ant defense and chemical defense in plants. The first is an evolutionary trade-off, for which selection favors investment in either ant attractants or increased secondary metabolites, the second is due to plasticity within a plant species – when investment is high in ant rewards, fewer resources are available for other plant defenses. Both trade-offs rely on the assumption that resource allocation into ant attractants versus direct defense are linked. For example, studies of plants with extra floral nectaries (EFN) at high elevations demonstrated that plants allocate resources to defense differently when ants are absent. In *Bixa orellana* (Bixaceae), sepal nectaries promote ant-protection against seed predators at their lowland range but do not exist in plants at high elevations, where ants are absent [34]. Similarly, *Inga* (Fabaceae) species in Panama reduce the production of nectar and increase the production of phenolics at high elevations [9*]. Similar plasticity has been observed in other tropical woody plants such as *Piper* (Piperaceae) and *Acacia* (Fabaceae). Both genera exhibit evolutionary trade-offs and plasticity within a plant species: When plants host ants and invest in rewards to their guards, they show reduced secondary metabolites [35-36].

If these trade-offs are generally important and ants are significant predators, one would predict that the decline of ants at higher elevations would be correlated with an elevational gradient where plant secondary metabolites increase at higher elevations, as

observed on *Inga* [9*]. However, empirical data for changes in chemical defense across elevational gradients are still scarce. The lack of consistent, carefully collected empirical data on plant defenses across replicated elevational gradients represents a major gap in our understanding of ant defense versus direct defense against herbivores and will be a fecund area for future research.

3. Plants tolerate herbivores, and overall herbivory decreases at the higher elevations that lack ants - Figure 3.

Plant tolerance, defined as plants' ability to sustain physiological stress without hitting an ecological threshold, is feasible only if at elevations where top-down forces are low, herbivore populations are low. Elevational gradients in herbivory are likewise not well documented, but again theory predicts that such gradients could exist. First, plant species richness is generally lower at higher elevations, and this is associated with lower herbivore abundance and diversity [37]. Second, damaging levels of herbivory are less common due to the lower net primary productivity and stronger constraints on ectothermic herbivores through unfavorable weather.

Lower and more stochastic herbivory in space and time at high elevations may force plants into tolerance as there are less predictable patterns of attack [38]. Also, lower diversity of plants at higher elevations can facilitate less intense interspecific competition, allowing a plant species to tolerate greater levels of herbivory without negative effects. However, higher temperatures may enable range expansions for herbivores or even a decline in predation or parasitism, due to associated increases in extreme weather events [39]. These factors could counteract plants' adaptive tolerance to herbivores and contract plants' species distribution ranges.

Vicia sepium (Fabaceae) and associated arthropods comprise a temperate-zone

system that has provided empirical support for this hypothesis – plants at higher elevations were more susceptible to attacks by herbivores. Herbivores achieved increased biomass when they were experimentally fed high elevation ecotypes of *V. sepium*, suggesting that these plants are not as well defended. However, in the field, plants thrive due to herbivore pressure being lower at such elevations [10*].

4. Plants that rely on ant protection are not found at elevations that lack ants - Figure 4.

Ants serve as plant defenders but there are significant physiological and ecological costs associated with providing nutrition or shelter for their nests [40] – these costs cannot be maintained in the absence of ants. Alternatively, ants can mediate the establishment of plants on poor soils through providing nutrients and cultivating fungal gardens inside domatia [41]. The phenotypically plastic allocation of plant resources invested in any defense (or other mutualistic benefits from ants), direct or indirect, should represent a balance between the local abiotic conditions such as temperature, precipitation and soil resources, the abundance and identity of associated herbivores, and the effectiveness and abundance of herbivore natural enemies [13**,42].

Myrmecophytes represent a clear example of how changes in multitrophic interactions across elevational gradients have impacts on species distributions. Those plants rely completely on ants for survival and are unable to extend their distribution ranges beyond that of the ants they host. For example, the relationship between *Piper immutatum* and associated *Pheidole* ants is responsible for a tightly restricted plant range – *P. immutatum* occurs only at elevations where ants are present (i.e., in the NE Andes below 1700m [11**]). This has been observed in most studies, in fact there are no records of true myrmecophytes thriving at any location without their suitable plant ants [43].

Conclusions and synthesis

The opinions presented here are a combination of predictions based on theory and empirical data. We suggest that focused studies are needed to achieve a better understanding of how ants, as predators, contribute to ecosystem processes and shape plant species distribution ranges. Testing these hypotheses requires combining traditional natural history and common garden experiments with new tools. For example, the few available studies on putative elevational gradients of secondary metabolites employed rather crude measures of uninformative classes of secondary metabolites (e.g., "phenolics"), whereas novel tools in metabolomics would allow for a full characterization of the secondary metabolome [42]. We recommend studying plant-herbivore-enemy interactions with consistent methodology across multiple elevational gradients in order to obtain reliable estimates of multitrophic interactions. The presence and prevalence of ants should always be explicitly addressed in these studies, and could even be experimentally manipulated through ant-exclusion. Finally, these experiments should be integrated into spatially explicit models that incorporate variance/covariance matrices calculated across a range of spatial scales [44]. Predictions of ENM should go beyond presence/absence and include probabilities of finding specific trophic or mutualistic interactions. Such an approach will provide significant contributions to attempts at predicting how individual species and its associated diversity will respond to global change parameters.

Cited literature

1. Dyer, L.A., Walla, T.R., Greeney, H.F., Stireman, J.O. and Hazen R.F. , *Diversity of interactions: a metric for studies of biodiversity*. Biotropica, 2010. **42**: p. 281- 289.
There is an increased interest in how diversity of ecological interactions is tightly linked to community stability and ecosystem parameters, but most measures of interaction diversity

251 *are based on unrealistic global or regional food webs; this paper provides context for*
 252 *quantitative measures of interaction diversity at ecologically relevant scales.*

253 2. Romero, G.Q., Goncalves-Souza T, Vieira C., and J. Koricheva, *Ecosystem engineering effects*
 254 *on species diversity across ecosystems: a meta-analysis.* Biological Reviews, 2014. **90**(3): p.
 255 877-890.

256 *3. Heil, M. and D. McKey, *Protective ant-plant interactions as model systems in ecological and*
 257 *evolutionary research.* Annual Review of Ecology Evolution and Systematics, 2003. **34**: p. 425-
 258 453. *A thorough and insightful review of how ants protect plants and how ant-plants are ideal*
 259 *systems for studies in evolutionary ecology and plant-animal interactions.*

260 4. Massad, T.J., Fincher, R.M., Smilanich, A.M., and L.A. Dyer. 2011. *A quantitative evaluation of*
 261 *major plant defense hypotheses, nature versus nurture, and chemistry versus ants.*
 262 *Arthropod-Plant Interactions.* **Arthropod-Plant Interactions** 5:125-139.

263 5. Chamberlain, S. and J.N. Holland. *Quantitative synthesis of context dependency in ant-plant*
 264 *protection mutualisms.* 2009. Ecology 90(9): 2384-2382.

265 6. Rodríguez-Castañeda, G., *The world and its shades of green: A meta-analysis on trophic*
 266 *cascades across temperature and precipitation gradients.* Global Ecology and Biogeography
 267 2013. **22**: p. 118-130.

268 **7. Longino, J.T., M.G. Branstetter, and R.K. Colwell, *How ants drop out: ant abundance on*
 269 *tropical mountains.* Plos One, 2014. **9**(8): p. e104030 1-9.
 270 *This is one of many papers from Longino and colleagues that provide rigorous documentation*
 271 *of the relationship between elevation, ant community diversity, and abundances; in Central*
 272 *America ant communities exhibit a peak in diversity at 800 m and high, unchanging*
 273 *abundances from the lowlands up to 1500 m. Above 1500m they find low abundances of*
 274 *ants.*

275 *8. Tvardikova, K.a.V.N., *Predation on exposed and leaf-rolling artificial caterpillars in tropical*
 276 *forests of Papua New Guinea.* Journal of Tropical Ecology, 2012. **28**(04): p. 331-341.

By experimentally exposing clay caterpillars along a complete elevational gradient the authors established that in the absence of ants, birds increase the attacks on herbivores on plants.

- *9. Koptur, S., *Alternative Defenses against Herbivores in Inga (Fabaceae, Mimosoideae) over an Elevational Gradient*. Ecology, 1985. **66**(5): p. 1639-1650.

This paper experimentally studies the production of nectar and secondary compounds in two species of Inga and shows how the plants reduce the production of EFN and increase in phenolic production in the absence of ants along a tropical elevation gradient.

- *10. Rasmann, S., A. Burl, M. Gallot-Lavallee, J. Joaquim, J. Purcell and L. Pellissier, *Differential allocation and deployment of direct and indirect defenses by Vicia sepium along elevation gradients*. Journal of Ecology, 2014. **102**: p. 930-938.

The beneficial role of ants protecting plants and queuing on EFN production is established in this study as well as a reduction of production of ant attractants and the ability to resist herbivory at high elevations thanks to a mutualistic interaction with mycorrhizae.

11. Rodríguez-Castañeda, G., R.E. Forkner, E.J. Tepe, G.L. Gentry, and L.A. Dyer, *Weighing defensive and nutritive roles of ant mutualisms across a tropical altitudinal gradient*. Biotropica, 2011. **43**(343-350).

The role of biotic interactions on range limits of a plant were studied by conducting a reciprocal transplant and ant exclusion experiment; this study demonstrated that the plant drops out at elevations without ants and that ants effectively deter herbivory.

12. Spear, E.R., P.D. Coley, and T.A. Kursar, *Do pathogens limit the distributions of tropical trees across a rainfall gradient?* Journal of ecology, 2014. **103**(1): p.165-174.

- **13. Fine, P.V.A., I. Mesones, and P.D. Coley, *Herbivores promote habitat specialization by trees in amazonian forests*. Science, 2004. **305**(5684): p. 663-665.

A must read - this simple reciprocal transplant experiment demonstrates that soil nutrients and herbivory interact to limit the distributions of tree species.

- 302 **14. Letourneau, D.K., and L.A. Dyer, *Experimental test in lowland tropical forest shows top-down*
303 *effects through four trophic levels*. Ecology, 1998. **79**(5): p. 1678-1687.
- 304 15. Wisz, M.S., J.Pottier, W. D. Kissling, L. Pellissier, J. Lenoir, C.F. Damgaard, C.F.Dormann,
305 M.C.Forchhammer, J.A.Grytnes, A.Guisan, R.K. Heikkinen, T.T. Høye, I.Kuhn, M. Luoto, L.
306 Maiorano, M. C. Nilsson, S. Normand, E. Ockinger, N.M. Schmidt, M. Termansen, A.
307 Timmermann, D.A. Wardle, P. Aastrup and J.C. Svenning, *The role of biotic interactions in*
308 *shaping distributions and realised assemblages of species: implications for species*
309 *distribution modelling*. Biological Reviews of the Cambridge Society 2013. **88**: p. 15-30.
310 *This thorough literature review clearly demonstrates that species interactions are a necessary*
311 *component of any species distribution modeling that requires good spatially and temporally*
312 *explicit data.*
- 313 16. Araujo, M.B. and M. Luoto, *The importance of biotic interactions for modelling species*
314 *distributions under climate change*. Global Ecology and Biogeography, 2007. **16**(6): p. 743-
315 753.
- 316 17. Mod, H.K., Le Roux P.C., Guisan A., Luoto M, *Biotic interactions boost spatial models of*
317 *species richness*. . Ecography, 2015. **38**(9): p. 913-921.
- 318 18. Rahbek, C., *The role of spatial scale and the perception of large-scale species-richness*
319 *patterns*. Ecology Letters, 2005. **8**(2): p. 224-239.
- 320 **19. Colwell, R.K., et al., *Global warming, elevational range shifts, and lowland biotic attrition in*
321 *the wet tropics*. Science, 2008. **322**(5899): p. 258-261.
- 322 20. Janzen, D.H., *Why mountain passes are higher in the tropics*. American Naturalist, 1967.
323 **101**(919): p. 233-249.
324 *This citation classic posits that dispersal is impeded more through passes in tropical*
325 *mountains versus passes at the same elevation at higher latitudes due to relatively lower*
326 *seasonality in temperature; subsequent studies have found support for this hypothesis.*

- 327 21. Ghalambor, C.K., et al. *Are mountain passes higher in the tropics? Janzen's hypothesis*
328 *revisited*. 2006. Integrative and Comparative Biology **46** (2006) 5-17.
- 329 22. Gripenberg, S., and T. Roslyn, *Up or down in space? Uniting the bottom-up versus top-down*
330 *paradigm and spatial ecology*. Oikos, 2007. **116**(2): p. 181-188.
- 331 23. Parmesan, C. and G. Yohe, *A globally coherent fingerprint of climate change impacts across*
332 *natural systems*. Nature, 2003. **421**(6918): p. 37-42.
- 333 24. Chen, I.C., et al., *Elevation increases in moth assemblages over 42 years on a tropical*
334 *mountain*. Proceedings of the National Academy of Sciences of the United States of America,
335 2009. **106**(5): p. 1479-1483.
- 336 25. Colwell, R.K., R.R. Dunn, and N.C. Harris. Coextinction and persistence of dependent species
337 in a changing world. Annual Review of Ecology Evolution and Systematics , 2012.**43**:183-203
- 338 26. Kaspari, M., S. O'Donnell, and J.R. Kercher, *Energy, density, and constraints to species*
339 *richness: Ant assemblages along a productivity gradient*. American Naturalist, 2000. **155**(2):
340 p. 280-293.
- 341 27. Dunn, R.R., N.J. Sanders, S.B. Menke, M.D. Weiser, M.C. Fitzpatrick, E. Laurent, J.P. Lessard, D.
342 Agosti, A. Andersen, C. Bruhl, X. Cerda, A. Ellison, B. Fisher, H. Gibb, N. Gotelli, A. Gove, B.
343 Guenard, M. Janda, M. Kaspari, J. T. Longino, J. Majer, T.P. McGlynn, S.B. Menke, C.Parr, S.
344 Philpott, M. Pfeiffer, J. Retana, A. Suarez, H. Vasconcelos, *Climatic drivers of hemispheric*
345 *asymmetry in global patterns of ant species richness*. Ecology Letters, 2009. **12**: p. 324-333.
- 346 28. O'Donnell, S., Kumar A, *Microclimatic factors associated with elevational changes in army ant*
347 *density in tropical montane forest*. Ecological Entomology, 2006. **31**(491-498).
- 348 29. Mondor, E.B.J.F.A., *Conspicuous extra-floral nectaries are inducible in Vicia faba*. Ecology
349 Letters, 2003. **6**(495-497).
- 350 30. Heil, M., B. Fiala, B. Baumann, KE Linsemair, *Temporal spatial and biotic variations in*
351 *extrafloral nectar secretion by Macaranga tanarius*. Functional Ecology, 2000. **14**: p. 749-757.

- 352 31. Sanders, D., C. Platner, *Intraguild interactions between spiders and ants and top-down*
353 *control in a grassland food web*. *Oecologia*, 2007. **150**: p. 611-624.
- 354 32. Vandermeer, J., I. Perfecto, S. Philpott, *Ecological complexity and pest control in organic*
355 *coffee production: uncovering an autonomous ecosystem service*. *Bioscience*, 2010. **60**(7): p.
356 527-537.
- 357 33. Nahas, L., M. Gonzaga, K Del-Claro, *Emergent impacts of ant and spider interactions:*
358 *Herbivory reductions in a tropical Savannah tree*. *Biotropica*, 2012. **44**(4): p. 498-505.
- 359 34. Bentley, B.L., *Extrafloral nectaries and protection by pugnacious bodyguards*. *Annual Review*
360 *of Ecology and Systematics*, 1977. **8**: p. 407-427.
- 361 35. Dyer, L.A., C.D. Dodson, J. Beihoffer, D.K. Letourneau, *Trade-offs in antiherbivore defenses in*
362 *Piper cenocladum: ant mutualists versus plant secondary metabolites*. *Journal of Chemical*
363 *Ecology*, 2001. **27**(3): p. 581-92.
- 364 36. Ward, D., T.P. Young, *Effects of large mammalian herbivores and ant symbionts on condensed*
365 *tannins of Acacia drepanolobium in Kenya*. *Journal of Chemical Ecology*, 2002. **28**(5): p. 913-
366 929.
- 367 37. Dyer, L.A. and D.K. Letourneau. 2013. Can Climate Change Trigger Massive Diversity Cascades
368 in Terrestrial Ecosystems? *Diversity* **5**:1-35.
- 369 38. Zangerl, A.R., C.E. Rutledge, *The probability of attack and patterns of constitutive and induced*
370 *defense: a test of optimal defense theory*. *American Naturalist*, 1996. **147**: p. 599-608.
- 371 39. Stireman III, J.O., L.A. Dyer, D.H. Janzen, M.S. Singer, J.T. Lill, R.J. Marquis, R.E. Ricklefs, G.L.
372 Gentry, W. Hallwachs, P.D. Coley, J.A. Barone, H.F. Greeney, H. Connahs, P. Barbosa, H.C.
373 Morais and I.R. Diniz. *Climatic unpredictability and parasitism of caterpillars: Implications of*
374 *global warming*. *Proceedings of the National Academy of Sciences of the United States of*
375 *America*, 2005. **102**(48): p. 17384-17387.
- 376 40. Rico-Gray, V. and P.S. Oliveira, *The ecology and evolution of ant-plant interactions*. 2007,
377 Chicago: University of Chicago press. 322.

41. Mayer, V.E., M.E. Fredrickson, D. McKey, R. Blatrix., *Current issues in the evolutionary ecology of ant-plant symbioses*. New Phytologist, 2014. **202**: p. 749-764.
 42. Richards, L.A., L. A. Dyer, M.L. Forister, A.M. Smilanich, C.D. Dodson, M.D. Leonard and C. S. Jeffrey. 2015. Phytochemical diversity drives tropical plant-insect community diversity. *Proceedings of the National Academy of Sciences* **112**: 10973–10978.
 43. Chomicki, G., S. Renner, *Phylogenetics and molecular clocks reveal the repeated evolution of ant-plants after the late Miocene in Africa and the early Miocene in Australasia and the Neotropics*. New Phytologist, 2015.**207**(2):411–24.
 - **44. Lamb, E.G., K.L. Mengersen, K.J. Stewart, U. Attanayake, and S.D. Siciliano, *Spatially explicit structural equation modeling*. Ecology, 2014. **95**(9): p. 2434-2442.
- This breakthrough paper incorporates coefficients from structural equation modeling to a spatial predictive context. By not only incorporating causal hypotheses among individual causes (like on a classic structural equation model), but the model specifies a series of spatial causal hypotheses about how variables affect one another at a distance.*

Figure 1. *In the absence of ants, other predators, which are not equally affected by temperature constraints, should thrive and fill the functional role provided by ants.* (a) Global distribution range niche model of a host plant and its close relationship with the global distribution of ant abundance. ● **Host plant distribution**, ● **Global distribution of ant abundance** (b) A path model that includes hypotheses about causal relationships mediated by multitrophic interactions and plant traits at the landscape scale. When keystone predators change, the elevational pattern of hostplant distribution is not affected by variation in ant abundance across elevations. ● **Elevation zone where ants are rare** (other predators, such as birds, spiders or parasitoids become dominant predators) ● **Elevation with moderate ant abundance and diversity**. ● **Elevation zone where army ants and leafcutter ants thrive.** (c) Graphical model of interactions of a plant species with herbivores and enemies in which the plant does not produce ant attractants but it still may benefit from ants at elevations where ants are common (e.g. *Coffea arabica*, ants are important predators of herbivores when there are ant-plants in the

vicinity but other predators may take over in their absence). **Orange arrows indicate the presence of ants in the trophic system.** **Black arrows indicate the absence of ants in the trophic system.** Solid arrows denote direct effects, intermittent arrows denote an indirect effect. Pointed arrows denote a positive causal effect; a bullet ended arrow indicates a negative causal effect. The width of the arrow denotes the strength of the effect.

Figure 2. *Ant-related plants compensate for the absence of mutualists by allocating fewer resources to ant attraction and more resources towards production of secondary metabolites.* (a) Global distribution range niche model of a host plant and its relationship with global distribution of ant abundance; in this case the lack of ant activity does not directly restrict the distribution of host plant but their distributions often coincide **Host plant distribution** **Global distribution of ant abundance** (b) A path model that examines associations between multitrophic interactions and plant traits at the landscape scale. **Elevation zone where ants are rare** Plants compensate for the lack of ants by diverting resources from attracting ants to production of secondary metabolites. **Elevation zone where local ant abundance peaks.** Largest reported ant colony sizes for locally abundant ants, such as those species living inside host plants, occur in this zone. Diversity and abundance of defensive secondary compounds are highly modified at this elevation. **Elevation zone where army ants and leafcutter ants thrive.** Direct defenses are modified, such as antifungal secondary metabolites that effectively deter damage from leafcutter ants. (c). Graphical model of interactions of a plant species with extrafloral nectaries that actively attracts ants when they are present (e.g., a species of *Inga* with EFNs), but intensifies the production of secondary metabolites for defense in the absence of ants. **Orange arrows indicate the presence of ants in the trophic system.** **Black arrows indicate the absence of ants in the trophic system.** Solid arrows denote direct effects, intermittent arrows denote an indirect effect. Pointed arrows denote a positive causal effect, a bullet ended arrow indicates a negative causal effect. The width of the arrow denotes the strength of the effect.

Figure 3. *Plants resist herbivores, and overall herbivory decreases at higher elevations.* (a) Global distribution range niche model of a host plant and its relationship with global distribution of ant abundance. The distribution of the host plant may, in this case, be restricted by herbivory. **Host plant distribution** **Global distribution of ant**

abundance (b) A path model that examines associations between multitrophic interactions and plant traits at the landscape scale. ● **Elevation zone where ants are rare.** Plants resist herbivores; under conditions where herbivores regularly outbreak or experience predictably favorable conditions, they may restrict the elevation range of the plant. ● **Elevation zone where local ant abundance peaks** ● **Elevation zone where army ants and leafcutter ants thrive.** (c) Graphical model of interactions of a plant species with upper trophic levels in which the plant produces ant attractants at lower elevations, but resists herbivory at elevations at which ants are rare (e.g., *Vicia sepium* Fabaceae). ● **Orange arrows indicate the presence of ants in the trophic system.** ● **Black arrows indicate the absence of ants in the trophic system.**

Figure 4. *Myrmecophytes that rely on protection through specialist partner ants are not found at elevations that lack these ants.* (a) Global distribution range niche model of a host plant and its relationship with the distribution of ants. ● **Host plant distribution.** ● **Global distribution of ant abundance** (b) A path model that examines associations between multitrophic interactions and plant traits at the landscape scale. ● **Elevation zone at which ants are rare.** No functional populations of myrmecophytes are expected at these elevations. ● **Elevation with moderate ant abundance and diversity** ● **Elevation zone at which army ants and leafcutter ants thrive.** (c) Graphical model of interactions of a plant species and upper trophic levels in which the plant hosts and feeds ants, in turn ants provide nutrients and herbivore defense for the host plant (e.g., *Piper immutatum* Piperaceae). ● **Orange arrows indicate the presence of ants in the trophic system.** ● **Black arrows indicate the absence of ants in the trophic system.** Solid arrows denote direct effects, intermittent arrows denote an indirect effect. Pointed arrows denote a positive causal effect, a bullet ended arrow indicates a negative causal effect. The width of the arrow denotes the strength of the effect.

Figure 1

Figure1bw

Figure2

Figure2bw

Figure3

Figure 4

Figure4bw