

UC Merced

Frontiers of Biogeography

Title

Global patterns in the structure and robustness of plant-herbivore networks

Permalink

<https://escholarship.org/uc/item/7ds331mf>

Journal

Frontiers of Biogeography, 8(3)

Author

Araújo, Walter Santos de

Publication Date

2016

DOI

10.21425/F58331053

Copyright Information

Copyright 2016 by the author(s). This work is made available under the terms of a Creative Commons Attribution License, available at

<https://creativecommons.org/licenses/by/4.0/>

thesis abstract

Global patterns in the structure and robustness of plant-herbivore networks

Walter Santos de Araújo

Ecology and Evolution Post-Graduate Program, Universidade Federal de Goiás, Goiânia, GO, Brazil

Current Address: Departamento de Biologia Geral, Universidade Estadual de Montes Claros, 39401-089, Montes Claros, MG, Brazil; walterbioaraujo@yahoo.com.br

Abstract. My goal is to investigate global patterns in the structure of interaction networks of insect herbivores and their host plants. Specifically, I seek to determine whether intensification of land use and the dominance of exotic host plant species influence the structure and robustness (i.e., resistance to co-extinctions) of interaction networks of insect herbivores and host plants. I also ask whether latitude has an influence on the structure and robustness of these interactions. I compiled 90 local plant-herbivore networks distributed worldwide, spanning different taxonomic groups of plants and insects and several herbivore guilds. My results showed that intensification of land use was associated with dominance of exotic plant species and can impoverish the species richness and taxonomic diversity of insect herbivores in the networks. Moreover, land use intensification surprisingly increases network specialization by decreasing connectance and nestedness, and increases modularity; while the increase in the proportion of exotic hosts had opposite effects. These changes in the network structure may be due to the proportionately greater loss of generalist herbivores relative to specialists. Land use intensification also decreases the robustness of plant-herbivore networks, while the proportion of exotic host plant species increases, which is an intriguing result that contradicts previous studies. Controlling for anthropic effects that can act on the networks, my results show that plant-herbivore networks are structured independently of latitude, suggesting that the factors that influence the interactions between host plants and insect herbivores are latitudinally invariant.

Keywords. Exotic Species, Habitat Modification, Latitudinal Gradient, Network Robustness, Network Specialization, Plant-Herbivore Interactions, Phytophagous Insects

Introduction

Terrestrial ecosystems with some level of human modification represent almost 80% of continental and island surfaces (Ellis and Ramankutty 2008). Intensification of land use by human activities directly affects biodiversity, mainly due to loss of vegetation and species extinction of both fauna and flora (Foley et al. 2005). Furthermore, the direct modification of natural habitats facilitates colonization by exotic species, which contributes to extinction of local native species and to biotic homogenization (Tilman and Lehman 2001, Seabloom et al. 2006, Didham et al. 2007). Thus, intensification of land use and colonization by exotic

species can significantly modify the structure of natural assemblages, such as those comprised of insect herbivores and their host plants, which represent an important component of terrestrial biodiversity (Price 2002).

Previous studies have shown that intensification of land use can have both a negative impact on insect herbivore richness (e.g., Bailey et al. 2010, Öckinger et al. 2012), and a positive impact on species richness of other herbivore groups (e.g., Quinn 2004, Araújo and Espírito-Santo Filho 2012). These contrasting impacts have also been observed among studies investigating the effects of land use intensification on the structure of

ecological networks among plants, herbivores and other trophic levels (Murakami et al. 2008, Villa-Galaviz et al. 2012). Hence, there is a need for studies that synthesize these investigations to assess the consistency of the response of different groups of insect herbivores to human land use.

Towards this aim, Araújo (2015) investigated global patterns among networks of ecological interaction between insect herbivores and their host plants in the context of worldwide human-induced environmental changes. I compiled information on plant-herbivore networks from throughout the world to elucidate patterns in the structure and robustness of these interactions. To illustrate my expectations, I built a conceptual model of the expected effects of land use intensification on an important aspect of network structure: specialization (Figure 1). This model shows that intensification of land use, such as loss, fragmentation and pollution of natural habitats, can affect plant communities by reducing species richness of native plants and facilitating the colonization of exotics (Didham et al. 2007). Thus, I hypothesize that land use intensification will have both a direct negative

effect on insect herbivore assemblages, and an indirect negative effect via an increase in the dominance of exotic host plants. Because it is expected that specialist herbivores will be more susceptible to land use intensification (Karttinen and Roslin 2011), the reduction of specialists relative to generalist insects is expected to influence the structure of interactions in a given network, thereby diminishing the specialization of the network itself.

Another interesting and underexplored question about plant-herbivore networks is if the structure of these networks varies along the latitudinal gradient. Some evidence shows that the diet of tropical forest herbivores is more specialized in terms of host plant diversity than the diet of temperate forest insects (Dyer et al. 2007, Forister et al. 2015). In an ecological network context, the elevated proportion of specialized interactions can reflect directly in the network structure due to a reduction in connectance and an increase in the number of modules within network (Lewinsohn et al. 2005). These differences in the plant-insect interactions along different geographical regions lead to expectation of higher specialization of plant-herbivore net-

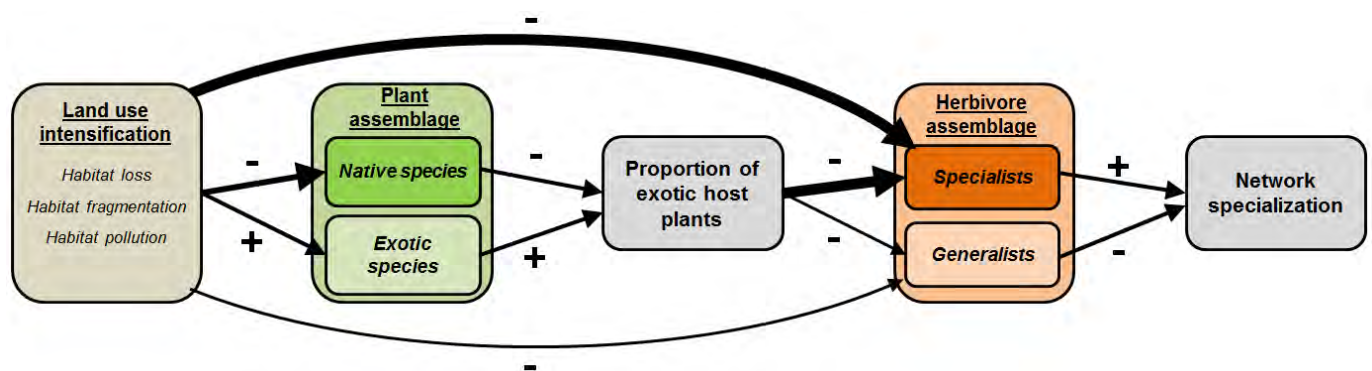


Figure 1. A conceptual model for the effects of land use intensification (LUI) on the specialization of interactions in plant-herbivore networks. First, human land use is expected to have a negative impact on the species richness of native host species, while facilitating the invasion and establishment of exotic plant species. Consequently, plant assemblages under higher levels of LUI are predicted to have a higher proportion of exotic plant species. Both LUI and the increase in the proportion of exotic host plant species would promote the loss of herbivore species at the local scale, but with greater negative impacts on the specialist herbivores than on generalists. Because of the greater reduction in the number of specialist herbivorous species, the proportion of monophagous herbivores is predicted to decrease, whereas the network connectance is predicted to increase with LUI and higher proportions of exotic host plant species. Modified of Araújo et al. (2015b).

works towards the equator, although no study has systematically investigated this.

Here, I synthesize my prior work (Araújo 2015) on three questions: (I) What are the effects of increased land use intensity and dominance of exotic plants on insect diversity in plant-insect networks? (II) What is the effect of land use intensity and exotic plant dominance on the structure and robustness of plant-herbivore networks? and (III) Does latitude have an effect on the structure and robustness of plant-insect networks.

To answer the first question, I analyzed whether land use intensity has a direct negative effect on species richness and taxonomic diversity of insect herbivores due to changes in the environmental conditions to which most of the native insect herbivores are adapted to. Additionally, I analyzed the indirect effect of increasing dominance of exotic plants, and the subsequent decreasing availability of native hosts for herbivores. Regarding the second question, because of expected differential responses by specialists and generalist herbivores, I predict positive effects of land use intensity (and exotic plant dominance) on connectance (i.e., proportion of realized interactions) and robustness (i.e., resistance to co-extinctions), and negative effects on specialization (e.g., proportion of specialist species) of plant-herbivore networks. To assess the third question regarding the role of latitude, I tested if networks of low latitudes have lower connectance and higher specialization than high latitude networks and if network robustness increases with latitude.

Methods

Compilation of plant-herbivore networks

To compile a database on plant-herbivore networks I used Scopus and Google Scholar to search for studies reporting local lists of her-

bivorous insects and their food plants using the following key-words: (plant*) and (herbivore*) and (network* or interaction* or web*) and (survey* or list*). In addition, I inspected the Interaction Web Database of the National Center for Ecological Analysis and Synthesis¹ and the literature cited by some key review papers on plant-insect interactions (e.g., Tscharrntke and Brandl 2004, Lewinsohn et al. 2005, Thebault and Fontaine 2008). Among the criteria to include a plant-herbivore network in my database are: interactions compiled in a local scale and contain at least five plant and five insect species, totaling at least 10 species. In total, I compiled 90 plant-insect herbivore networks (Figure 2) distributed over a latitudinal range of almost 90 degrees (from 37° S to 51° N). The compilation comprises a wide variety of taxonomic and functional groups of herbivorous insects, including leaf chewers, stem chewers, phloem suckers, flower head feeders, fruit flies, leaf miners and gall makers. The mean local richness of herbivores and host plants were 23.5 (± 21.3 SD) and 24.1 (± 23.1 SD), respectively. See Araújo et al. (2015a,b) for more details on data compilation.

Land use intensity and proportion of exotic plants

To assess the degree of human-induced habitat modification to which each plant-herbivore network was subjected, I developed an index of land use intensity (LUI). I defined four categories of LUI based on the descriptions of the sampling sites in the original studies: (1) pristine natural habitats (e.g., primary forests); (2) natural habitats moderately impacted by human activities (e.g., secondary forests); (3) agricultural or ruderal habitats with high diversity of plant species (e.g., agroforestry systems and abandoned pastures);

¹ www.nceas.ucsb.edu/interactionweb

and (4) agricultural or urban habitats with low diversity of plant species (e.g., active pastures and urban orchards). I used this categorization of land use as an ordinal variable ranging from 1 to 4. Based on my levels of LUI, I had 30, 25, 14, and 21 assemblages classified as levels 1, 2, 3, and 4, respectively. Moreover, for each network I classified the plant species as native or exotic according to plant databases available for the country where the network was studied. After classifying each plant

species in each network as native or exotic, I calculated the proportion of exotic plant species in each plant-herbivore network.

Measuring network structure and robustness

I used different descriptors and metrics as response variables to characterize plant-insect networks. Firstly, I used variables to describe species diversity in the second trophic level of networks, which were species richness and taxonomic diversity of insect herbivores. I

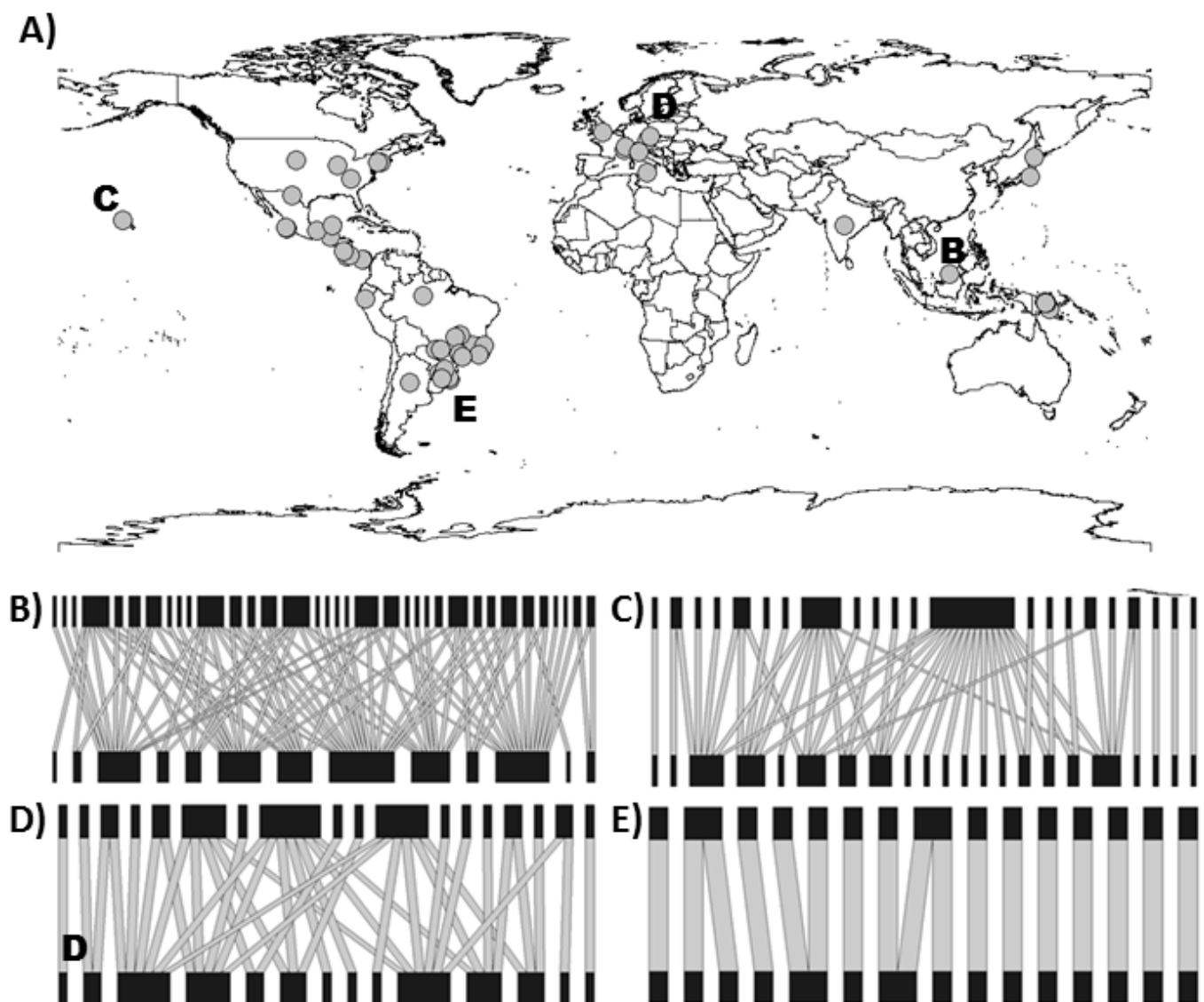


Figure 2. (A) Global distribution of the plant-herbivore networks used in the current study. Some of the networks localities are indistinguishable at this map scale. (B-E) Examples of plant-herbivore networks with different levels of land use intensity (LUI) and specialization. Herbivores are on the top and plants on the bottom of the networks. The networks are arranged in descending order of residual connectance. (B) Network with LUI level 1; (C) Network with LUI level 2; (D) Network with LUI level 3; (E) Network with LUI level 4. Modified of Araújo et al. (2015b).

used taxonomic diversity (AvTD, Clarke and Warwick 1998) due to lack of well-resolved phylogeny for most species of insect herbivores. Secondly, I used connectance (Dormann et al. 2009), proportion of monophagous herbivores, modularity (Newman's modularity measure, Newman 2004) and nestedness (NODF, Almeida-Neto et al. 2008) as structural descriptors of plant-herbivore networks. Finally, to characterize network fragility, I used a variable called *robustness* that was obtained by calculating the proportion of secondary extinction of herbivore species due to random removal (error tolerance) of plant species (Dormann et al. 2009). For more details on network measures please see Araújo et al. (2015b).

Additional variables and data analyses

To control for possible confounding effects due to great heterogeneity among the compiled networks, I considered additional variables of environmental- and sampling-related effects. The additional variables were: (1) latitude; (2) altitude; (3) sampling effort; (4) plant life form; (5) host plant richness; (6) taxonomic level of plants; (7) taxonomic level of insects; (8) taxonomic distinctness of plants and (9) taxonomic distinctness of insects. More details about definition, compilation and treatment of each variable used to control confounding effects are available in Araújo et al. (2015a,b). I examined the effects of these additional variables on LUI, proportion of exotic plants and the response variables through a visual inspection of bivariate scatter plots and Spearman's rank analysis. Only variables that showed moderate to high relationships (i.e., $r > 0.30$; $p < 0.05$) with the variables of interest were included in subsequent analyses. I adopt this criterion to identify variables important to explaining the variation observed in the response variables, and to minimize unknown effects on my explanatory variables. I then built path models to quantify the effects of LUI and the proportion of exotic host species on the response variables of the plant-

herbivore networks, while controlling for possible confounding effects. To investigate spatial and latitudinal effects on networks, I tested for the effects of the explanatory variables by adjusting a simultaneous auto-regressive model (SAR) for each response variable.

Results and Discussion

Human actions involving natural environments can lead to irreversible consequences for biodiversity, such as the disruption of ecological interactions that took thousands or millions of years to evolve (Tylianakis et al. 2010). Corroborating this, my research showed that the intensification of land use and the associated dominance of exotic plant species can impoverish networks of insect herbivores and host plants, and significantly modify the interactions between these highly diverse groups of organisms. By proposing to investigate the anthropogenic effects on the structure and fragility of plant-herbivore networks on a global scale I showed important results to clarify general patterns of impact on these interactions (Araújo 2015).

I found negative effects of LUI on species richness (and taxonomic diversity) of insect herbivores, and that these effects were mediated by an increase in the proportion of exotic host plants (Figure 3; Araújo et al. 2015a). Although I have not found a direct effect of LUI on the insect diversity, the path model showed a relative strong positive effect of LUI on proportion of exotic host plants in the networks. These results are in agreement with other studies that showed that human-modified habitats favor the occurrence of exotic species and, consequently, are poorer in native species than natural habitats (Didhan et al. 2007, Almeida-Neto et al. 2011). Investigation of network structure revealed, surprisingly, greater specialization (low connectance and nestedness and high proportion of monophages and modularity) in plant-herbivore networks located in habitats with greater LUI (Araújo et al. 2015b). It is possible that this finding is due to a proportionally greater loss of species with many interactions (i.e., generalists), which reduces the connectivity of the network (Figure 2 B-E). An alternative hypothesis is that

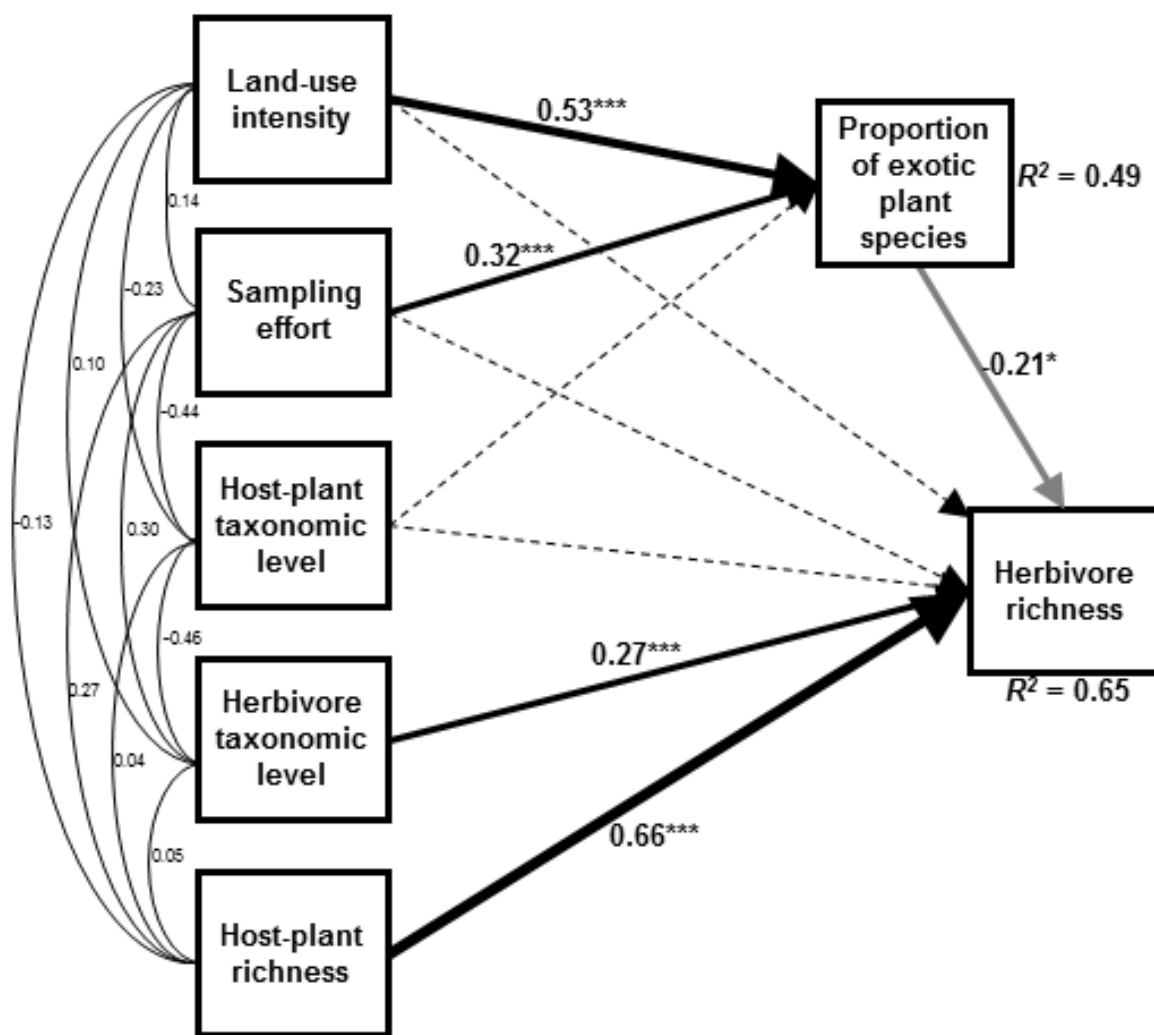


Figure 3. Path analysis for insect richness in the plant-herbivore networks explained by land use intensity, sampling effort, host plant richness, host plant taxonomic level, herbivore taxonomic level, and proportion of exotic host plants. Numbers associated with paths between variables are path coefficients presented as standardized values (scaled by the standard deviations of the variables). Black arrows represent positive effects and grey arrows represent negative effects (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). The thickness of lines and arrows is proportional to effect size. Dashed arrows $P < 0.05$ (n.s.). Modified of Araújo et al. (2015a).

the modifications caused by land use reduces the number of potential native host plant species, thereby restricting the diet of herbivores and enhancing the occurrence of local specialists (increasing the network specialization), as discussed by Araújo et al. (2015b). However, the positive effect of LUI was partially offset by a negative effect of the proportion of exotic plant species on the network specialization. My findings indicate that LUI is an important driver of network specialization, reducing the local host range for herbivore guilds already characterized as having highly specialized feeding habits. However, because the effect of LUI is offset by an opposite effect from

the proportion of exotic host species, the net overall effect will depend on the extent of replacement of native with exotic host plant species.

My analyses also showed that intensification of land use diminished network robustness (Araújo 2015). On the other hand, the increase in exotic host plant species partially offset this effect of LUI, and positively influenced network robustness. These results confirm the trend of increasing network specialization in habitats with higher LUI (and opposite effects with increasing proportion of exotic plants). Therefore, networks located in

habitats with higher LUI tend to be less robust than networks in more pristine habitats, which is a very interesting result and contrary to previous studies (Melián and Bascompte 2002, Tylianakis et al. 2007). These results can be explained by impoverishment of network connectance in more impacted habitats due to a reduction of generalist herbivores (or occurrence of local specialists, as previously discussed), which increases the probability of secondary extinctions in these networks. Moreover, by showing that LUI diminishes specialization, nestedness and robustness in the plant-herbivore networks, I also show that human-caused changes to interactions lead to abrupt structural modifications to the configuration of networks.

This work is, to my knowledge, the first to systematically quantify latitudinal effects on the structure and fragility of plant-herbivore networks on a global scale (Araújo 2015). Because of the consistent effects of LUI on plant-herbivore network structure (Araújo et al. 2015a,b), I used only networks from undisturbed habitats to investigate the effects of latitude on the specialization and robustness of plant-herbivore networks. My results revealed that plant-herbivore networks are structured independently of latitude, but that sampling effects can significantly influence estimates of network structure and fragility (Araújo 2015). These results contradict the expectation that the diet of tropical forest herbivores is more specialized than the diet of temperate forest insects (Dyer et al. 2007, Forister et al. 2015), and that there is greater specialization of plant-herbivore networks towards the equator. On the other hand, my findings corroborate previous results that showed antagonistic ecological networks do not change along latitudinal gradients (e.g.,

Morris et al. 2014). The absence of consistent structural patterns in plant-herbivore networks across latitudes suggests that the interactions between host plants and insect herbivores are structured by factors that are latitudinally invariant.

In conclusion, my findings presented herein contribute to a better understanding of the general patterns that characterize the interactions between insect herbivores and their host plants. The results uncovered that plant-herbivore networks in natural habitats are structured by factors that are latitudinally invariant, such as phylogenetic constraints, leading to a high specialization of these interactions. On the other hand, the results demonstrate that on a global scale land use intensification can modify the structure and fragility of plant-herbivore networks. However, because the effect of LUI is offset by an opposite effect by the proportion of exotic host species, the net overall effect will depend on the extent of the replacement of native with exotic host plant species. My findings have important implications for the conservation of plant-insect networks, because land use intensification and exotic species invasion can interrupt interactions between native insects and plants that have evolved over thousands to millions of years.

Acknowledgements

I want to thank my PhD supervisor, Mário Almeida-Neto, for giving me the opportunity to conduct this PhD project and for helping me throughout with design, implementation, writing and publishing. I thank all my co-authors Teja Tscharntke, Thomas Michael Lewinsohn, Leonardo Lima Bergamini and Marcos Costa Vieira for fruitful collaborations. I thank to Lucas G. Gomes for help with database compilation; to Erik Wild by English revi-

sion and to Jan Beck for manuscript suggestions. My PhD project was supported by CAPES Grant.

References

- Almeida-Neto, M., Guimaraes, P., Guimaraes, P.R., Loyola, R.D. & Ulrich, W. (2008) A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos*, 117, 1227–1239.
- Araújo, W.S., Tschamtkke, T. & Almeida-Neto, M. (2015a) Global effects of land use intensity on the impoverishment of insect herbivore assemblages. *Biodiversity and Conservation*, 24, 271–285.
- Araújo, W.S., Vieira, M.C., Lewinsohn, T.M. & Almeida-Neto, M. (2015b) Contrasting effects of land use intensity and exotic host plants on the specialization of interactions in plant-herbivore networks. *PLoS ONE* 10:e0115606.
- Araújo, W.S. (2015) Global patterns in the structure and fragility of plant-herbivore networks. PhD Thesis, Universidade Federal de Goiás. Available at: <https://repositorio.bc.ufg.br/tede/handle/tede/4737>
- Araújo, W.S. & Espírito-Santo, Filho, K. (2012) Edge effect benefits galling insects in the Brazilian Amazon. *Biodiversity and Conservation*, 21, 2991–2997.
- Bailey, D., Schmidt-Entling, M.H., Eberhart, P., Herrmann, J.D., Hofer, G., Kormann, U. & Herzog, F. (2010) Effects of habitat amount and isolation on biodiversity in fragmented traditional orchards. *Journal of Applied Ecology*, 47, 1003–1013.
- Clarke, K.R. & Warwick, R.M. (1998) A taxonomic distinctness index and its statistical properties. *Journal of Applied Ecology*, 35, 523–53.
- Didham, R.K., Tylianakis, J.M., Gemmill, N.J., Rand, T.A. & Ewers, M. (2007) Interactive effects of habitat modification and species invasion on native species decline. *Trends in Ecology and Evolution*, 22, 489–496.
- Dormann, C.F., Fründ, J., Blüthgen, N. & Gruber, B. (2009) Indices, graphs and null models: analyzing bipartite ecological networks. *The Open Ecology Journal*, 2, 7–24.
- Dyer, L. A., Singer, M.S., Lill, J.T., et al. (2007) Host specificity of Lepidoptera in tropical and temperate forests. *Nature*, 448, 696–699.
- Ellis, E.C. & Ramankutty, N. (2008) Putting people in the map: anthropogenic biomes of the world. *Frontiers in Ecology and Environment*, 6, 439–447.
- Foley, J.A., DeFries, R., Asner, G.P., et al. (2005) Global consequences of land use. *Science*, 309, 570–574.
- Forister, M.L., Dyer, L.A., Singer, M.S., Stireman III, J.O. & Lill, J.T. (2012) Revisiting the evolution of ecological specialization, with emphasis on insect-plant interactions. *Ecology*, 93, 981–991.
- Kaartinen, R. & Roslin, T. (2011) Shrinking by numbers: landscape context affects the species composition but not the quantitative structure of local food webs. *Journal of Animal Ecology*, 80, 622–631.
- Lewinsohn, T.M., Novotny, V. & Basset, Y. (2005) Insects on plants: diversity of herbivore assemblages revisited. *Annual Review of Ecology, Evolution, and Systematics*, 36, 597–620.
- Melián, C.J. & Bascompte, J. (2002) Food web structure and habitat loss. *Ecology Letters*, 5, 37–46.
- Morris, R. J., Gripenberg, S., Lewis, O. & Roslin, T. (2014) Antagonistic interaction networks are structured independently of latitude and host guild. *Ecology Letters*, 17, 340–349.
- Murakami, M., Hirao, T. & Kasei, A. (2008) Effects of habitat configuration on host-parasitoid food web structure. *Ecological Research*, 23, 1039–1049.
- Newman, M.E.J. (2004) Analysis of weighted networks. *Physical Review E*, 70, 056131.
- Öckinger, E., Lindborg, R., Sjödin, N.E. & Bommarco, R. (2012) Landscape matrix modifies richness of plants and insects in grassland fragments. *Ecography*, 35, 259–267.
- Price, P. (2002) Resource-driven terrestrial interaction webs. *Ecological Research*, 17, 241–247.
- Quinn, M.A. (2004) Influence of habitat fragmentation and crop system on Columbia basin shrubsteppe communities. *Ecological Applications*, 14, 1634–1655.
- Seabloom, E.W., Willia, J.W., Slayback, D., Stoms, D.M., Viers, J.H., Dobson, A.P. (2006) Human impacts, plant invasion, and imperiled plant species in California. *Ecological Applications*, 16, 1338–1350.
- Thebault, E. & Fontaine, C. (2008) Does asymmetric specialization differ between mutualistic and trophic networks? *Oikos*, 117, 555–563.
- Tilman, D. & Lehman, C. (2001) Human-caused environmental change: impacts on plant diversity and evolution. *Proceedings of the National Academy of Sciences*, 10, 5433–5440.
- Tschamtkke, T. & Brandl, R. (2004) Plant-insect interactions in fragmented landscapes. *Annual Review of Entomology*, 49, 405–430.
- Tylianakis, J.M., Tschamtkke, T. & Lewis, O.T. (2007) Habitat modification alters the structure of tropical host-parasitoid food webs. *Nature*, 445, 202–205.
- Tylianakis, J.M., Laliberté, E., Nielsen, A. & Bascompte, J. (2010) Conservation of species interaction networks. *Biological Conservation*, 143, 2270–2279.
- Villa-Galaviz, E., Boege, K. & del-Val, E. (2012) Resilience in plant-herbivore networks during secondary succession. *PLoS ONE* 7: e33009.

Submitted: 30 May 2016

First decision: 22 July 2016

Accepted: 07 October 2016

Edited by Jan Beck