ISBN 978-82-326-4250-2 (printed version)
ISBN 978-82-326-4251-9 (electronic version)
ISSN 1503-8181

NTNU
Norwegian University of
Science and Technology

Emma-Liina Marjakangas

Doctoral theses at NTNU, 2019:327

NTNU

Doctoral Thesis

NTNU
Norwegian University of
Science and Technology
Faculty of Natural Sciences
Department of Biology

Doctoral theses at NTNU, 2019:327

Emma-Liina Marjakangas

Understanding species interactions in the tropics: dynamics within and between trophic levels

NTNU
Norwegian University of
Science and Technology

Emma-Liina Marjakangas

Understanding species interactions in the tropics: dynamics within and between trophic levels

Thesis for the degree of Philosophiae Doctor

Trondheim, November 2019

Norwegian University of Science and Technology
Faculty of Natural Sciences
Department of Biology

NTNU
Norwegian University of
Science and Technology

NTNU
Norwegian University of Science and Technology

Thesis for the degree of Philosophiae Doctor

Faculty of Natural Sciences
Department of Biology

ISBN 978-82-326-4250-2 (printed version)
ISBN 978-82-326-4251-9 (electronic version)
ISSN 1503-8181

Doctoral theses at NTNU, 2019:327

Printed by Skipnes Kommunikasjon as

“The most insidious sort of extinction, the extinction of ecological interactions”

- Janzen 1974 -

D.H. Janzen. 1974. Deflowering of Central America. Natural History 83(4): 48-53

ACKNOWLEDGEMENTS

As community ecologist, I am more than aware of how everything in the community is interconnected and how no species would survive without the others. Being part of the scientific community is no different: so many people have influenced my PhD and you all deserve a huge thank you!

It's only recently that I have learnt to fully appreciate that my supervisors have given me a lot of room to grow to be the kind of scientist that I want to be. For that, you deserve the hugest thanks! Thank you Vidar, for your calm presence at my moments of panic. Otso, for asking the difficult questions and fixing my code. Nerea, for teaching me scientific writing and being my role model of a scientist. In addition to my supervisors, I have had many amazing mentors from all around the world. Thank you Mauro, Carlos, JP, Panu and Alejandro for teaching me confidence and for your trust in my creativity.

This thesis would not have happened at all without the data collection efforts of my Brazilian collaborators. I was always warmly welcomed not only to visit your research groups but also your homes, and you patiently educated me on the tropical forests that I knew essentially nothing about at the start. To experience the Brazilian nature had been my childhood dream, and to have the excuse to travel there and the opportunity to work on conserving it is beyond anything I could ever have hoped for.

Not all my support has been located overseas. I have shared the office with fun and inspirational people. It was cold with the windows always open, but the atmosphere was warm and supporting. The CBD environment with all the great friends I have made has kept me wanting to come to work even in those darkest and most sleepy November mornings. One person in particular has kept me sane in my moments of self-doubt: Elena. You are my science sister and mentor. Thank you for the wine&venting evenings and café office days, they have inspired me more than you could imagine!

Luckily, life has not been all work during the past years. Since I started my PhD, I have travelled for 434 days, enjoying tropical weather and meeting interesting people. Travelling around the world would not have been possible without the 20+ catsitters that kept the kitties alive while I was gone. The lovely city of Trondheim has offered me exercise for both the body and the mind: my amazing football team has created much needed regular opportunities to forget all about work, and the mushroom quiz team has given me a biweekly platform for learning to answer detailed questions under time pressure. The latter will surely come in handy during the defence.

Living thousands of kilometers away from family and friends has been much easier than I originally imagined, and that is because you have all made such efforts to keep in touch. My family has always encouraged me to focus on my studies and let me be my annoying, remember-to-recycle-self. Last but not least, Antti. You have done so much: patiently reading through all my manuscripts, presentations and application letters, cheering me up when rejections felt overwhelming and taking my mind off from work when I needed it.

Each of you taught me something valuable and together all those elements have made me the scientist I am today. Kiitos kaikille!

CONTENTS

List of papers vii

Synopsis 1

- Introduction 1
- Aims 6
- Methods 7
- Main results and discussion 13
- Synthesis and perspectives 19
- Reference list 22

Papers I-IV

LIST OF PAPERS

Paper I: **Marjakangas E.**, Muñoz G., Turney S., and Lessard J.-P. A framework linking trait-based processes to the assembly of bipartite networks. Manuscript.

Paper II: **Marjakangas E.**, Ovaskainen O., Abrego N., Grøtan V., de Oliveira A.A., Prado P.I., and de Lima R.A.F. Co-occurrences of tropical trees: disentangling abiotic and biotic forces. Submitted manuscript.

Paper III: **Marjakangas E.**, Abrego N., Grøtan V., de Lima R.A.F., Bello C., Bovendorp R.S., Culot L., Hasui É., Lima F., Muylaert R.L., Niebuhr B.B., de Oliveira A.A., Pereira L.A., Prado P.I., Stevens R.D., Vancine M.H., Ribeiro M.C., Galetti M., and Ovaskainen O. Fragmented tropical forests lose mutualistic plant-animal interactions. Submitted revised manuscript.

Paper IV: **Marjakangas E.**, Genes L., Pires M.M., Fernandez F.A.S., de Lima R.A.F., de Oliveira A.A., Ovaskainen O., Pires A.S., Prado P.I., and Galetti M. 2018. Estimating interaction credit for trophic rewilding in tropical forests. Philosophical Transactions of the Royal Society B. 373(1761): 20170435. doi: 10.1098/rstb.2017.0435

Declaration of contributions

Paper I: **EM** and JL initiated the study. **EM**, GM, ST and JL all conceived the conceptual approach of the study. GM designed and ran the simulations based on discussions with all authors. ST designed the null model approach with contributions from other authors. **EM** wrote the first draft of the manuscript with contributions from other authors. All authors contributed significantly to the later versions.

Paper II: **EM** and RAFL conceived the ideas and designed methodology; RAFL collected the data; **EM** analyzed the data with contributions from OO, VG and RAFL; **EM** led the writing of the manuscript with major contribution from RAFL. All authors contributed critically to the drafts and gave final approval for publication.

Paper III: **EM**, NA and OO conceived the idea; **EM**, NA, VG, MCR, MG and OO designed the study; RAFL, CB, RSB, LC, EH, RLM, FL, BN, AO, LAP, PP, RDS, MHV, MCR and MG compiled the data; **EM** conducted analyses; **EM**, NA and OO wrote the first draft of the manuscript, and all authors contributed substantially to the final manuscript.

Paper IV: MG, LG, ASP, and FASF conceived the idea; **EM**, LG, MMP and MG designed the study; RAFL, AAO, and PIP compiled the tree data; **EM** conducted analyses with contributions from OO; **EM**, LG, and MMP wrote the first draft of the manuscript, and all authors contributed substantially to the final manuscript.

All authors above have given their consent to use their work in this thesis.

INTRODUCTION

In 1984, Jared Diamond described the 'evil quartet' of mechanisms behind species extinctions: overexploitation, introduced species, habitat degradation, and co-extinctions. Since then, the evil quartet has expanded into an evil sextet, with climate change and synergistic effects being added to the list (Brook *et al.* 2008). Indeed, biodiversity is threatened globally (IUCN 2019), the current extinction rate exceeding the background rate by a thousand-fold (Pimm *et al.* 2014).

Tropical forests are rightfully considered as biodiversity conservation hotspots as they host a large proportion of the global biodiversity and are under an imminent threat due to multiple anthropogenic pressures (Myers *et al.* 2000). In the tropics, habitat loss and degradation as well as overexploitation are major drivers of biodiversity loss (Myers *et al.* 2000; Hansen *et al.* 2013; Dirzo *et al.* 2014).

As species in local communities are organized into interconnected ecological networks, also the (local) extinctions caused by anthropogenic pressures are potentially cascading through the networks via species interactions (i.e., secondary/co-extinctions; Dunn *et al.* 2009; Valdovinos 2019). Thus, considering species individually cannot provide the full picture of environmental and anthropogenic effects on biodiversity. Furthermore, ecosystem functioning (e.g., pollination, seed dispersal, and nutrient cycles) is dependent on species interactions, simultaneously affecting the environmental conditions of the local ecosystem and the species in it (Burkle *et al.* 2013; Schleuning *et al.* 2015; Harvey *et al.* 2016). Biodiversity and ecosystem functioning are hypothesized to be causally linked (i.e., 'insurance hypothesis'; Naeem & Li 1997), potentially leading to a vicious cycle where degrading ecosystems have fewer species and individuals to provide ecosystem functions that would in turn lead to further degradation of the ecosystem (Figure 1). Species interactions tend to go extinct before the species do (Valiente-Banuet *et al.* 2015), thereby leading to negative effects on ecosystem functioning and further degradation of the ecosystem.

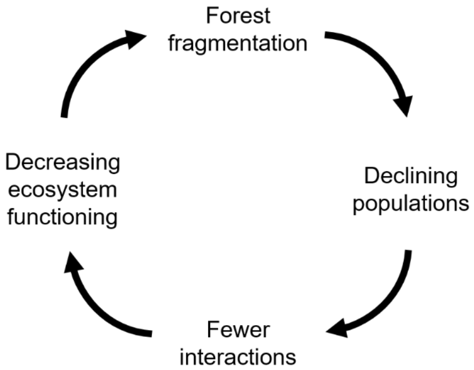


Figure 1. Schematic illustration of the causal connections among anthropogenic pressures (here, forest fragmentation), biodiversity decline, and ecosystem functioning.

For example, seed dispersal is key to forest regeneration in tropical forests, as over 70 % of the tree species depend on animal-mediated seed dispersal (e.g., Willison *et al.* 1989). Natural forest regeneration may be therefore limited when the seed disperser mutualists are removed from the local community. Markl and colleagues (2012) found that seed dispersal of trees is negatively affected by both forest fragmentation and defaunation of seed dispersing animals, potentially limiting forest regeneration in the future. Furthermore, Bello and colleagues (2015) showed with a simulation study how non-random removal of large-bodied seed dispersers may drastically decrease the carbon storage capacity of tropical forests.

Knowledge on how and why species interact with each other can provide invaluable insight into understanding the many-fold effects that the evil sextet has on biodiversity and ecosystem functioning.

Ecological networks

Ecological networks consist of interactive relationships, i.e. pairwise interaction links, between species within one trophic level or between species at different trophic levels. In general, interactions between species may be positive (e.g., mutualistic), negative (e.g., antagonistic), or neutral in terms of their effects on the interacting species. Research of ecological networks generally focuses on the interaction links between the species and on the outcomes of these links, such as the flow of energy through the trophic levels of food webs (e.g., Paine 1966; Dunne *et al.* 2002), dynamics of pollen and seed dispersal in time and space (e.g., Olesen *et al.* 2008; Emer *et al.* 2018), and spread of diseases (e.g., Muylaert *et al.* 2019). One particular form of networks, bipartite network, describes a configuration of pairwise interactions, typically between resource and consumer species, at two distinct trophic levels.

Interaction networks beyond individual pairwise interactions are relevant for both ecological and evolutionary processes. At ecological time scales, interaction networks change through disturbances and extinction-colonization processes (Leibold *et al.* 2004), whereas at evolutionary time scales, they change through (co)evolution and biogeographical processes (Guimarães *et al.* 2011). The geographic mosaic theory by Thompson (2005) postulates an ever-changing landscape of interactions that shape macroevolution. Moreover, species interactions are important for macroevolution as they affect trait evolution and lineage diversification (Harmon *et al.* 2019).

Multiple factors, including species' co-occurrences, traits and the abiotic environment, define the pairwise interactions and the structure of interaction networks as a whole (Figure 2). These factors function both within trophic levels and between them (the inner boxes in Figure 2). Furthermore, the interactions within trophic levels affect the interactions between trophic levels, as well as the other way around. For example, plant species may compete over nutrients, consequently affecting the quantity and quality of their nectar, and thus their interactions with pollinators. Alternatively, increased attraction of pollinators may lead to an overall positive interaction between two plant species (i.e., indirect facilitative interaction; Hegland *et al.* 2009). In general, species need to be in the same place at the same time (i.e., spatial and temporal co-occurrence) and their traits need to correspond in order for an interaction to take place (Figure 2). Species' traits may correspond due to coevolution (Guimarães *et al.* 2011) or due to one-sided adaptation, but separating these two mechanisms is challenging. In addition, the type and strength of interactions may vary according to the local abiotic and biotic environment, such as precipitation or presence of a shared enemy.

The configuration of pairwise interactions in a local assemblage, i.e. the structure of an interaction network, can be defined and measured in various ways. Different metrics can be calculated at multiple scales: the full network, the trophic level, and the species scale. Central network level metrics include connectance (proportion of realized interaction links in the local assemblage; Jordano 1987; Dunne *et al.* 2002), nestedness (overlap and decreasing fill in the local assemblage; Almeida-Neto *et al.* 2008), and modularity (the extent to which interactions cluster into groups; Barber 2007; Olesen *et al.* 2007).

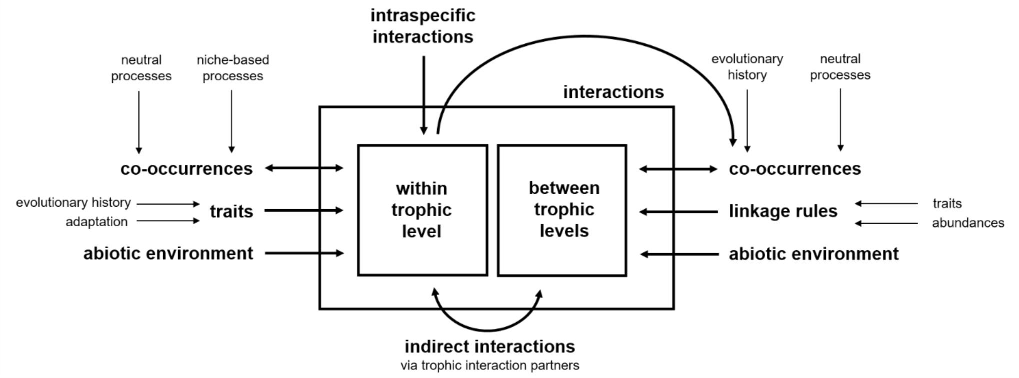


Figure 2. Flow chart of the different mechanisms affecting species' interactions within and between trophic levels. The outer box corresponds to all interactions in the local species community, whereas the inner boxes indicate the division of interactions into those within and between trophic levels. Arrows indicate the direction of the effect of the mechanisms affecting interactions within and between trophic levels (note: some effects are bidirectional). Within- and between-trophic level interactions are connected through various processes, indicated with curved arrows.

Interactions within trophic levels

The spatial and temporal co-occurrence of a species pair within a trophic level is defined by assembly processes. Assembly processes explain the local (co-)occurrence of species in a community. That is, assembly processes determine which species can disperse and establish in the local assemblage. Under neutral assembly, regionally occurring species enter the local assemblage randomly and independent of their niches (Hubbell 2001). Under niche-based assembly, species' traits are important in determining whether species can occur in the local assemblage (Cadotte & Tucker 2017). In particular, environmental filtering selects for species with traits matching the local optimum (Weiher & Keddy 1995; Cadotte & Tucker 2017). For example, in arid conditions, only plants with adaptations to low precipitation are able to establish in the assemblage. Limiting similarity, on the other hand, tends to select species with little functional overlap, i.e. minimizing trait overlap and increasing the number of local optima (MacArthur & Levins 1967). In case of limiting similarity, the underlying mechanism is interspecific competition, but without data at evolutionary time scales, only the realized, stable assemblages can be observed. The most extreme case of competition, competitive exclusion, leads to checkerboard distributions of similar species (Diamond's assembly rules; Diamond 1975). However, separating the effects of different niche-based assembly processes has proven challenging (e.g., Cadotte & Tucker 2017), thereby limiting their applicability to natural systems.

The abiotic environment may also influence pairwise interactions directly. Pairwise species interactions are suggested to shift from negative to positive along an environmental stress gradient (stress gradient hypothesis; Bertness & Callaway 1994; Castanho *et al.* 2015).

Finally, intraspecific interactions may affect interspecific interactions, most importantly through negative density dependence. When a population is regulated by negative density dependence, its growth is limited by intraspecific competition or density-dependent predation. Negative density dependence can prevent local dominance of any single species and maintain a more diverse assemblage of species. For example, seed mortality of tropical trees is negatively dependent on population density due to attraction of specialist enemies, leading to seedling survival sweet spot at intermediate distances from the parent tree (Janzen-Connell hypothesis; Janzen 1970). In this thesis, I focus on interspecific, rather than intraspecific interactions.

Interactions between trophic levels

Similarly to pairwise interactions within trophic levels, for an interaction to take place between trophic levels, species need to co-occur in space and time. For example, a species pair may be predicted to interact based on their ranges and trait matching, but this potential for an interaction is not realized due to temporal mismatch or lack of fine scale spatial co-occurrence. Co-occurrences of species at different trophic levels are determined by biogeographical factors, species' (co)evolutionary histories, and species' interactions within trophic levels (Figure 2). For example, a species pair might not co-occur due to restrictions on their ranges induced by past glaciation periods (Adams & Woodward 1989).

When two species co-occur in a local community, the probability of their interaction is defined by interaction assembly (see Figure 3 in *METHODS*). Interaction assembly refers to the linkage rules that dictate the formation of pairwise interaction links in a network. The linkage rules between a pair of species are determined based on their relative abundances in the local community or based on the degree of trait matching between them. In most cases, few trait dimensions are enough to predict majority of the interactions between species pairs and to reconstruct the network structure (Eklöf *et al.* 2013). Often pairwise interactions can be explained and predicted based on matching of functional traits among co-occurring species (Morales-Castilla *et al.* 2015; Sazatornil *et al.* 2016). Degree of constraint in trait matching may determine how likely local networks are to be rearranged after changes in species composition (Poisot *et al.* 2015). Degree of trait matching differs between hypotheses suggested in preceding literature, ranging from weak (i.e., neutral interactions) to intermediate (i.e., unidirectional forbidden links; Morales-Castilla *et al.* 2015) to strong (i.e., bidirectional morphological matching; Dehling *et al.* 2014) trait matching.

Finally, the abiotic environment is likely to affect the strength and type of interactions between trophic levels (Figure 2). Abiotic environment may fine-tune the already occurring pairwise interactions and network structure, rather than being their strongest driver.

Knowledge gaps

Data of pairwise interactions are scarce, particularly so in tropical ecosystems. In species-rich ecosystems, also statistical modelling of species' co-occurrences and pairwise interactions is difficult because of the extremely high number of potentially interacting species pairs, requiring computationally heavy calculations. Traditional modelling techniques have been inadequate to meet the challenge, but recent advances in community ecology modelling have opened new research avenues (Ovaskainen *et al.* 2017). However, also the theoretical synthesis of processes behind species interactions is scattered, largely due to the multitude of mechanisms and research fields involved.

In practice, species interactions have been mainly studied at small spatial scales and focusing on particular pairwise interactions, rather than large scale patterns and entire networks. One of the interesting current questions to be addressed is whether the results from small scale studies are scalable to larger spatial extents. Predicting responses of interaction networks to global change drivers (e.g., Valdovinos 2019) is essential in order to conserve interaction links and ecosystem functions. However, the first step towards this is to generalize responses of networks to different global change drivers at large spatial scales. To apply this knowledge to conservation and management, it is important to determine whether the local assemblages and networks are resistant to environmental changes through shifts in species composition (Tylianakis *et al.* 2010), network rearrangement (i.e. rewiring; CaraDonna *et al.* 2017; Pires 2017), and/or changes in interaction strengths between species (Saavedra *et al.* 2013).

Finally, biodiversity conservation largely focuses on individual species and habitat types and ignores the importance of interaction networks and the consequent ecosystem functions. Tylianakis and colleagues (2010) reviewed conservation aspects of interaction networks, but much more work remains to be done. For example, repeated mistakes in species introductions (e.g., cane toads in Australia) could have been avoided had focal species' interactions with other species been thoroughly studied beforehand. In general, prioritization of species' (re)introductions could be done based on their interactions with other species and their contributions to the local ecosystem functioning (Paper IV). This thesis aims to address these methodological, theoretical and conservation-related knowledge gaps.

AIMS

In this thesis, I wanted to expand the knowledge on the factors that shape interactions within and between trophic levels. The reason for this is two-fold. Firstly, I aimed to increase the basic understanding of the processes behind species interactions within and between trophic levels (Figure 2). Secondly, in order to predict responses of interaction networks to anthropogenic and other environmental pressures and to conserve them the best way possible, the underlying mechanisms affecting species interactions need to be deciphered. Thereby, I wanted to connect the obtained knowledge to potential applications for biodiversity conservation and management. This thesis focuses on several major themes that are addressed in respective chapters: linking within-trophic level assembly processes and between-trophic level interaction dynamics in a general context, evaluating assembly of species' co-occurrences within trophic levels, evaluating the effects of environmental drivers on interactions between trophic levels, and using predicted interactions between trophic levels for conservation and management prioritization. More specifically, I asked:

1. How can assembly processes within and between trophic levels be joined conceptually? What are the relative contributions of different assembly processes to resource-consumer network structure? (Paper I)
2. Which assembly processes drive the co-occurrences of tropical trees in local assemblages? How are these co-occurrences distributed across large spatial scales? (Paper II)
3. How does the abiotic environment affect the structure of tree-animal interaction networks? (Paper III)
4. How can areas and species be prioritized for species reintroductions and ecosystem function conservation? (Paper IV)

METHODS

Conceptual model of processes behind interaction network structure

In paper I, with a conceptual framework, we studied how different assembly processes within and between trophic levels influence structural properties of bipartite networks that for example tropical trees participate in. We included three building blocks that shape network structure: assembly processes at the resource trophic level (e.g., trees), assembly processes at the consumer trophic level (e.g., animals), and interaction assembly processes (Figure 3). Within the framework, we categorized the different assembly processes to be either niche-based or neutral (see *Interactions within trophic levels*). Together, these processes encompass all possible assembly processes because they are necessarily either dependent on or independent of species' niches. With niche-based processes within tropic levels we refer specifically to environmental filtering and limiting similarity. Between trophic levels, interaction assembly is also either niche-based or neutral, and defined by matching of corresponding functional traits between interacting partners (Bender *et al.* 2018) or by local relative abundances (Chacoff *et al.* 2018), respectively.

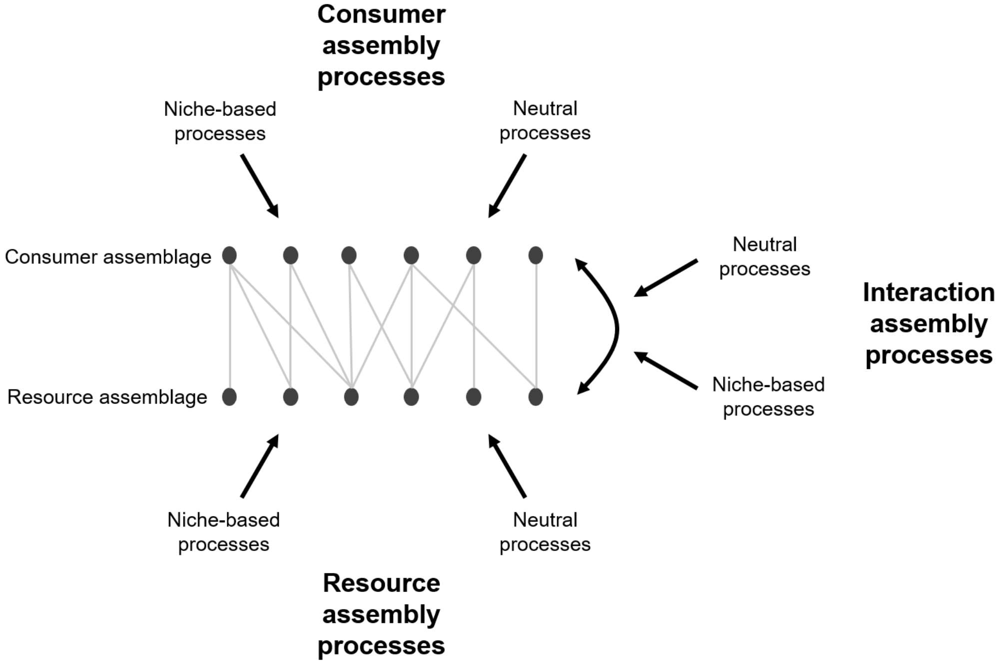


Figure 3. Processes driving bipartite network structure. Flowchart illustrates the within- and between-trophic level assembly processes affecting an interaction network. The upper row of circles represent consumer species, the lower row represents resource species, and the links represent consumer-resource interactions. Combinations of different assembly mechanisms at different trophic levels, together with interaction assembly processes, lead to varying outcomes of bipartite network structures.

To validate the conceptual model, we simulated synthetic bipartite networks under different combinations of neutral and niche-based scenarios of within-trophic level and interaction assembly processes. Resource and consumer assemblages were simulated under environmental filtering and limiting similarity scenarios to represent the effects of niche-based assembly effects within trophic levels on network structure. Niche-based interaction assembly effects were introduced through interaction probabilities defined by two distinct functional trait matching hypothesis. Then, we quantified the structures of the simulated networks. We compared the structural properties of the networks assembled under different niche-based processes to those of neutrally assembled networks. We partitioned the variation among the different components shaping bipartite network to evaluate their relative importance in defining the structure of the network under different assembly process scenarios.

To infer which assembly process drives each of the three components in the bipartite network, the trait value distribution in each simulated assemblage and trait matching between them was compared to those in the simulated regional species pool (Kraft & Ackerly 2010). Accordingly, we built stepwise trait-based null models to help identify the underlying assembly processes from observed bipartite networks.

Study system

In papers II, III and IV, we studied the drivers of within- and between-trophic level assembly processes separately. More specifically, we studied trees and their animal mutualists in various biogeographical regions in Eastern South America, including the Atlantic Forest, Caatinga, Cerrado, Pampa, and Pantanal (Figure 4). Eastern South America is characterized by a coast-inland gradient of precipitation and seasonality and a north-south gradient of temperature minimum. The study region includes forests with different vegetation types ranging from tall rainforests to open canopy savannas. The studied tree species represent different life forms (trees, treelets, palms, tree ferns and cacti) and occupy different functional spaces in terms of their life history traits. In general, tropical trees are important in maintaining the nutrient cycles, and large trees especially are highly important for ecosystem functions (Lutz *et al.* 2018). Furthermore, tropical trees support many other species through mutualistic interactions, such as pollination and frugivory. In particular, many animals depend on fruits and seeds of trees as their food resource (Fleming *et al.* 1987). These frugivores belong to various taxa, including birds, bats, and other mammals. Many birds and primates are efficient seed dispersers (Fleming & Kress 2013; Sebastián-González 2017), thereby contributing to dispersal of tree species and to regeneration of tropical forests in general. Together these trees and animals form interaction networks that have particular structures depending on the abiotic and biotic drivers at local and regional scales.

Data

For papers II, III and IV, we used empirical data of tropical species occurrences that were obtained from various data sources. Tree data were obtained from Neotropical Tree Communities database (TreeCo version 2.0; http://labtrop.ib.usp.br/doku.php?id=projetos:treeco:start). Animal data were obtained from data papers belonging to the ATLANTIC series (published in Ecology; Bovendorp *et al.* 2017; Lima *et al.* 2017; Muylaert *et al.* 2017b; Culot *et al.* 2018; Hasui *et al.* 2018). Depending on the specific question, we used different subsets of the original species occurrence data for the analyses (Table 1). Data on tree-animal interactions in papers III and IV were obtained from ATLANTIC frugivory data paper (Bello *et al.* 2017).

For modelling species occurrences and for relating network structure patterns to environmental drivers, we used environmental data from various sources based on the reported geographical coordinates of sampling sites (Olson *et al.* 2001; Hijmans *et al.* 2005; Wildlife Conservation Society & Center for International Earth Science Information Network 2005; Fischer *et al.* 2008; Ribeiro *et al.* 2009; Alvares *et al.* 2013; Soares-Filho *et al.* 2013; Chave *et al.* 2014; Fundação SOS Mata Atlântica 2014; Fick & Hijmans 2017; Ribeiro et al. in prep.). These environmental variables included data of climate, habitat fragmentation, land use, anthropogenic pressures, topography, and soil.

Predicting interspecific interactions

Data of pairwise species interactions within and between trophic levels is generally incomplete, especially in species-rich ecosystems. Therefore, we predicted and modelled species interactions within and between trophic levels in two distinct ways in papers II, III and IV: by using species co-occurrences as proxies for their interactions (Paper II) and by extrapolating observed pairwise interactions to other species pairs (Papers III and IV). For both methods, we used Hierarchical Modelling of Species Communities (HMSC) framework (Ovaskainen *et al.* 2017) as the basis for the analyses. HMSC is a joint species distribution model, and it thus models all species jointly, rather than modelling species separately and overlapping the outputs. The goal of joint species distribution models is to predict species distributions across space with the help of occurrences of other species in addition to those of the focal species. HMSC differs from many joint species distribution models due to its latent variable approach that allows decreasing the number of parameters to be estimated. Moreover, fitting models to very large datasets, such as those sampled from species-rich ecosystems, is possible.

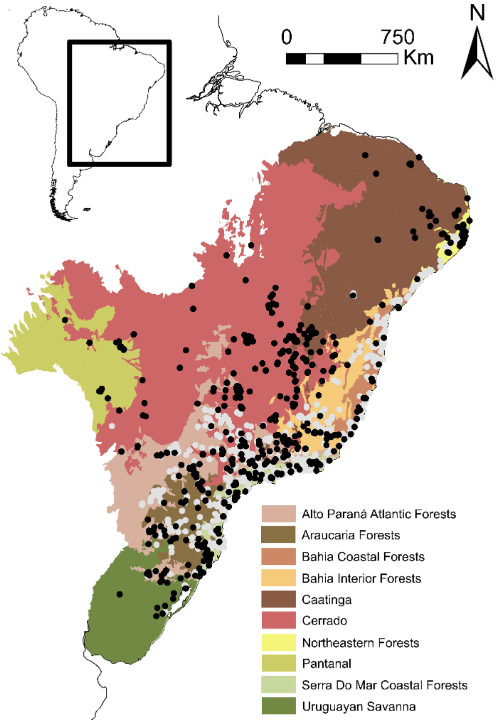


Figure 4. Spatial distribution of study regions and sampling sites in Eastern South America. Black circles indicate sampling sites of trees, light grey circles indicate sampling sites of animals, and colors delineate the studied ecoregions (Olson *et al.* 2001).

Table 1. Dimensions of data utilized in papers II, III and IV. Numbers of tree and animal species, numbers of tree and animal observations and numbers of recorded tree-animal interactions in the original data sets are reported for each paper separately. Note the different interpretation of 'observation' for different data types: for paper I using abundance (AB) data, number of observations refers to the total number of individuals recorded, whereas for papers III and IV using presence-absence (PA) data, number of observations refers to the number of individual species occurrences across sampling sites. Numbers of interactions refer to the raw interactions before extrapolation.

	Sites	**Species**		**Observations**		**Interactions**
		Tree	Animal	Tree	Animal	
II	574	1016	-	961184	-	-
III	1953	1424	407	42666	16284	3232
IV	1492	1424	211	42666	10737	2849

Within trophic level: co-occurrences as proxies for interactions

In paper II, we included latent and spatially structured latent variables in the model to account for spatial auto-correlation in the species occurrence data (Warton *et al.* 2015; Ovaskainen *et al.* 2016, 2017). Latent variables allow a representation of the species-to-species variance-covariance matrix, i.e. their pairwise co-occurrences, through latent factors and their loadings. The factor loadings indicate patterns where two species co-occur less or more often or in higher or lower abundances than expected. In paper II, we estimated co-occurrence matrices with two alternative HMSC models: 1) model without the environmental covariates to produce raw co-occurrences and 2) model with the environmental covariates to produce residual co-occurrences. Raw co-occurrences represent the overall pairwise co-occurrences among species disregarding which factors drive the co-occurrences, while residual co-occurrences can be considered as hypotheses of species interactions, since the species' shared responses to the environmental covariates are controlled for (Ovaskainen *et al.* 2017). Therefore, we utilized raw co-occurrences when inferring mechanisms behind realized species co-occurrences and residual co-occurrences when inferring the potential species interactions. Based on the raw and residual co-occurrence matrices, we calculated the proportions of positive and negative co-occurrences among all species pairs in each local sampling site across the study area. We did this to assess the spatial distribution of positive and negative co-occurrences.

Between trophic levels: extrapolating observed interactions across species pairs and study area

In papers III and IV, due to varying sampling efforts and methods, we could not estimate residual tree-animal co-occurrences between trophic levels using HMSC framework directly. Instead, we used the observed interactions by Bello *et al.* (2017) to assign all tree-animal species pairs a semi-quantitative probability of potential for an interaction. Due to low taxonomic coverage of the interaction, we extrapolated observed pairwise interactions to those species pairs that do not have data on their interaction. To fill in the data gaps, we considered potential for an interaction plausible if the animal species interacts with another tree species within the focal tree species' genus, and unlikely if the animal species has no recorded interactions with any tree species within the focal tree species' genus.

To obtain site-specific interaction probabilities for each tree-animal pair, we modelled species co-occurrences and their potential for interaction separately. That is, the predicted probability of two species interacting at a particular site is the probability that they potentially interact (independent of the site), multiplied by the probability that the two species co-occur at the particular site. We examined these co-occurrences based on the predicted communities modelled with HMSC. For each sampling site, we calculated the co-occurrence probability for each tree-animal pair as the product of their species-specific occurrence probabilities. Thereby, we could extrapolate between-trophic level interactions beyond the focal sampling sites to the entire study area.

Inferring underlying drivers of predicted interactions

In paper II, we studied the relative effects of niche-based processes, namely environmental filtering and limiting similarity, on co-occurrences of tropical tree species. We partitioned the explained variance in tree species occurrences among the environmental predictors and assessed how much of the variation was contributed to the covariates and latent variables. Furthermore, we compared the numbers of co-occurrences predicted without and with environmental variables to infer the effect of environment on the raw and residual pairwise co-occurrences, respectively. To investigate the role of limiting similarity, we studied the relationship of raw co-occurrences with pairwise trait and phylogenetic distances and tested for the correlation of the respective matrix pairs. Finally, by ordering the raw co-occurrence matrix according to the phylogenetic and trait distance dendrograms, we studied the clustering of raw positive and negative co-occurrences among the species visually.

In paper III, we studied the effect of forest fragmentation (measured as area of functionally connected forest, core-edge forest ratio and distance to nearest road) on tree-animal interaction networks. We did this by predicting tree-animal networks in 912 prediction sites across the study area. We used the extrapolated interaction probabilities to compute for each prediction site three different metrics that represent the network structure: 1) link connectance, 2) seed disperser availability (mean number of animal species with which tree species interact), and 3) proportion of interactions provided by keystone animal species. We identified keystone animal species by computing a species-specific keystone index and by selecting those species belonging to the top 5% quantile. Finally, we studied the linear relationships of each fragmentation variable and network metric pair.

Using predicted networks for conservation prioritization

In paper IV, we applied the tree-animal networks predicted in paper III to conservation prioritization. In many heavily deteriorated ecosystems, trophic rewilding, i.e. reintroducing extinct or declining species, poses the sole possibility to re-establish ecosystem functions (Galetti *et al.* 2017b). The credit of ecological interactions (i.e., interaction credit) corresponds to the number of tree-animal interactions expected to be restored if a lost or declined species is reintegrated into a given area (Genes *et al.* 2017). Quantifying interaction credit requires predicting pairwise species interactions in a local community, which is where the aforementioned tools for predicting pairwise interactions come in handy. We predicted and evaluated the outcomes of species reintroductions in terms of interaction credit by comparing expected interactions under two different scenarios: 1) a benchmark historical scenario with intact animal assemblages, and 2) the current scenario, where many sites may be defaunated relative to the historical benchmark.

MAIN RESULTS AND DISCUSSION

In paper I, we explored the conceptual framework (Figure 3) with the means of resource-consumer networks simulated under different assembly processes. The simulated networks can present many types of interactions, including mutualistic tree-animal interactions. The simulations indicated that assembly processes both within and between trophic levels contribute to the structure of bipartite interaction networks (measured as nestedness and modularity; Figure 5). Our results indicate that the interaction assembly generally plays a more important role in structuring bipartite networks than assembly of resource and consumer trophic levels. However, to a certain extent, niche-based assembly processes within trophic levels may limit the magnitude and direction of interaction assembly effects on network structure. These results highlight the importance of studying all processes (Figure 3) when aiming to understand the dynamics of ecological interactions. Partitioning the variation of network metrics into different assembly processes within and between trophic levels is an efficient way of gaining more knowledge on the relative importance of the drivers behind the studied networks.

Furthermore, to facilitate the use of the framework for observed networks, we constructed stepwise null models. The individual steps of the null models are traditionally used separately to infer assembly processes within trophic levels and sources of variation in network structure. In the first step, the trait distributions of resource, consumer, and interaction link assemblages are compared to distributions generated from random sampling of the respective regional pool to detect the relative influence of neutral and niche-based assembly processes. In the second step, the effect of niche-based assembly processes on network structure are inferred by comparing the network metric values of null and observed networks. Using the stepwise null model approach allows identifying the exact processes shaping the studied network.

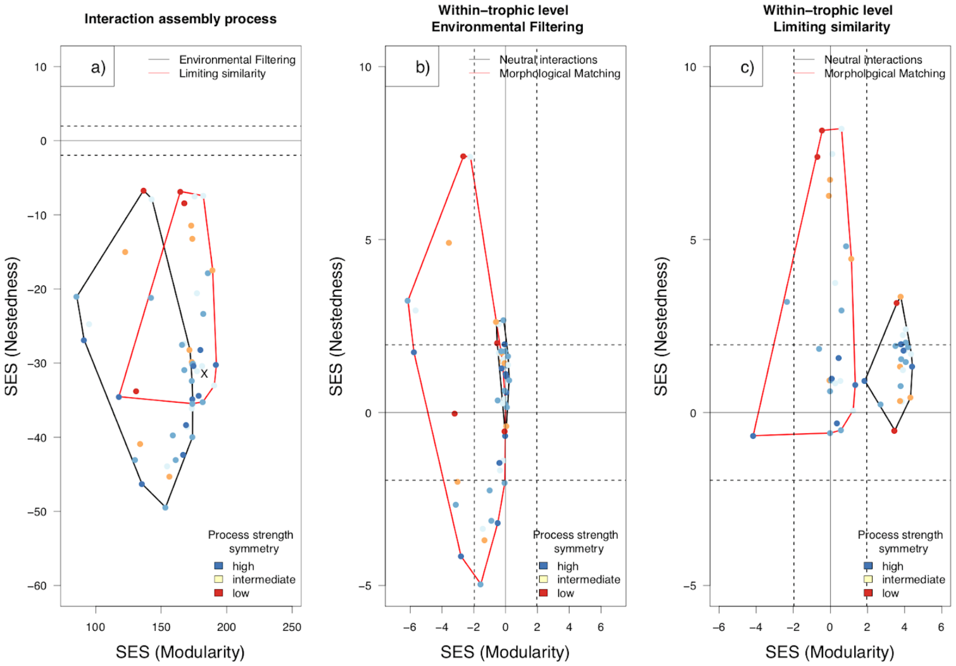


Figure 5. Standardized effect sizes (SES) of distinct assembly processes on modularity (Q) and nestedness (NODF) of simulated bipartite networks. For all panels, each point represents one assembly process combination scenario, for which the coordinates represent the average of 10 replicates of simulated networks. The color gradient of individual coordinate points represent the process strength asymmetry between trophic levels (dark red = highly asymmetric, dark blue highly symmetric). Structural properties were calculated for 500 simulated bipartite networks assembled under two hypotheses of trait matching constraints: neutral interactions and morphological matching. Networks were constructed based on simulated resource and consumer assemblages under environmental filtering or limiting similarity. The magnitude of effect was calculated as the difference from the expected network metric value of networks with pairwise interactions and species assemblages simulated under neutral assembly processes, and measured in units of standard deviations. Stippled lines denote the significance intervals (±1.96) of the effect sizes at both axis. Panel (a) illustrates the effects of interaction assembly processes on the structure of simulated networks. Points inside the convex hulls represent networks with assemblages simulated under environmental filtering conditions (circles and black lines) and limiting similarity (squares and red lines). Black X shows the effect coordinates for networks with assemblages assembled neutrally. Panels (b) and (c) illustrate the effects of within-trophic level assembly processes defining structures of networks under environmental filtering and limiting similarity, respectively. Circles inside red convex hull encompass networks with pairwise interactions defined by functional trait matching, whereas squares inside the black convex hull represent networks in which pairwise interactions were constructed based on species' relative abundances (i.e., neutral interactions).

In paper II, we studied more closely the niche-based assembly processes among tree species in Eastern South America. In particular, we studied how the co-occurrences among tree species related to environmental filtering and limiting similarity hypotheses. We found environmental filtering to be important in shaping species co-occurrences. This manifested as different proportions of positive and negative co-occurrences depending on whether environmental covariates were included in the model or not (Table 2). Furthermore, the variation in tree species occurrences was largely explained by environmental covariates, most importantly the climate. On the other hand, we found no signal of limiting similarity: strength or direction of raw co-occurrences did not depend on phylogenetic relatedness or functional similarity. The absence of limiting similarity effects on tree species co-occurrences may be explained by various factors. Firstly, competitive exclusion can take an extremely long time, leading to seemingly random patterns of species co-occurrences. Secondly, outcomes of limiting similarity may be masked because we lacked information of the spatial configuration of individual trees within sampling sites. Therefore, the co-occurrences may not reflect the fine scale avoidance of similar species as they may still co-occur within the same sampling site. Thirdly, species-saturated communities, such as tropical tree assemblages, may be characterized by convergent evolution and presence "look-a-likes" (Scheffer & van Nes 2006). The environment may be filtering groups of species that are functionally similar (Hérault 2007), thus driving functional differences among local communities at larger spatial scales.

Furthermore, in paper II, we found spatial variation in residual positive and negative co-occurrences to be distinct among ecoregions. Interestingly, these results indicate that species interactions may play a significant role in shaping the limits of ecoregions. Tree assemblages with the highest proportions of negative associations were located in the transitional zones between major biogeographical regions, such as Cerrado and Caatinga. This suggests a dispersal and/or establishment barrier between the regions, possibly founded on species interactions. Indeed, interactions among species can act as gatekeepers to new species (Fukami 2015). Thus, other species would prevent dispersal or establishment of immigrants through competitive superiority or historical priority effects (Fukami *et al.* 2005).

Table 2. Percentages of estimated raw and residual positive and negative co-occurrences at sampling site and ecoregion scales according to the models fitted to the presence-absence (PA) and abundance (AB) data.

Data	**Spatial scale**	**Co-occurrences (%)**			
		Positive		Negative	
		Raw	Residual	Raw	Residual
PA	Site	43.0	51.3	17.1	7.1
	Ecoregion	22.6	12.7	18.7	8.6
AB	Site	17.2	10.2	1.0	0.6
	Ecoregion	0.06	0.01	0.03	0.01

In paper III, we studied the environmental drivers of mutualistic interactions between fleshy-fruited trees and seed dispersing animals. We found that forest loss and fragmentation reduced quantity and quality of seed dispersal interactions between trees and animals across the study region, the Atlantic Forest (Figure 6). Network connectance and number of seed disperser partners per tree species reduced with decreasing area of functionally connected forest. The number of interactions provided by keystone frugivores was also affected by declining area of functionally connected forest. Our results highlight that fragmentation effects on seed dispersal interactions are currently mainly acting upon animal species but may have lagged and multiplicative effects on tree communities in the future (Doughty *et al.* 2016).

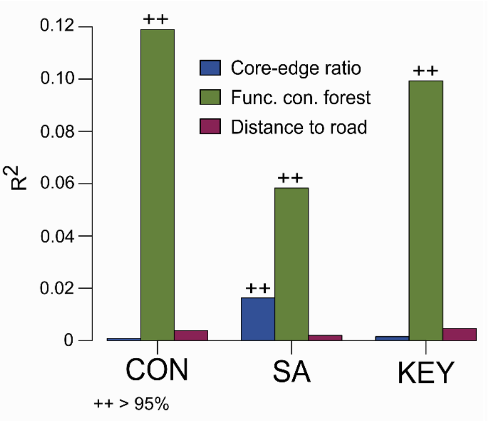


Figure 6. Effect of fragmentation-related covariates on tree-animal network metrics. Height of each bar represents the mean R^2-value over 500 linear regressions, where each network metric is considered as response variable and each fragmentation-related covariate as explanatory variable. The statistical support for fragmentation affecting interactions negatively is measured by posterior probability for the slope being positive (i.e., fragmentation reducing interactions), and is indicated by + symbol. CON = link connectance, SA = availability of animal mutualist, KEY = proportion of interactions provided by keystone animal species.

Edge effects had minor influence on tree-animal interaction networks. This result is in line with the fact that individual species have been found to show varying responses to edge effects (Oliveira *et al.* 2004; Ries *et al.* 2004), whereas the occurrence and persistence of most species generally depends positively on the area of available habitat (Bender *et al.* 1998). The Atlantic Forest is extremely fragmented with almost half of the forest cover within <100 meters from the nearest edge (Ribeiro *et al.* 2009), and thus most species that persist are necessarily at least to some extent tolerant to the edge effects (Beca *et al.* 2017).

Structural changes in the network (i.e., rewiring) could mitigate some direct and short-term effects of fragmentation on seed dispersal of trees by replacement of extinct interaction links. Our results, however, showed that the number of interactions provided both by keystone and non-keystone species were equally negatively affected by fragmentation, suggesting that the interactions provided by keystone animal species are not replaced by those provided by other species in the tree-animal network. Keystone species replacement is unlikely to take place in highly fragmented landscapes because of network clustering and the nested nature of existing interactions (Donatti *et al.* 2011). Interactions tend to be more frequent within than among subsets of species (Olesen *et al.* 2007), and therefore, the number of functionally compensatory species is limited to the species within each subset. This in turn explains the extinct interactions in the local communities under strong fragmentation effects. In paper III, the keystone animal species represented two ecologically distinct groups: old-growth forest habitat specialists, and secondary forest diet generalists that are common throughout the Atlantic Forest. These two groups are unlikely to have mutually interchangeable compensation capacity for rewiring and should therefore be considered separately in conservation and management.

In paper IV, we studied how tree-animal interactions could be restored in the highly fragmented and defaunated Atlantic Forest. We compared current and historical scenarios in terms of seed dispersing animals' ranges. We concluded that if animals were reintroduced to areas where they occurred when the Atlantic Forest was intact, many more interaction links would be realized in local communities. We quantified the credit of tree-animal interactions across the study area and found that there is a large variation in how many interactions could be gained by reintroducing animal species to the forest remnants.

More specifically, we found that reintroducing Southern Muriqui (*Brachyteles arachnoides*) and Rusty-margined guan (*Penelope superciliaris*) would be most beneficial for seed dispersal interactions (Figure 7), and both well-preserved and deteriorated regions would benefit from the reintroductions. Interaction credit hotspots were abundant in the interior regions of the Atlantic Forest (Figure 8). This region is characterized by a highly fragmented landscape resulting from the expansion of agricultural activities (Ribeiro *et al.* 2009). We also identified hotspots for species reintroductions within some regions where relatively well-preserved stretches of forest remain. These hotpots are concentrated around the largest urban areas within the Atlantic Forest, known to have low densities of many (large-sized) animal species (Galetti *et al.* 2017a). However, other factors, including captive stock size and initial threat status, should be accounted for before reintroducing individuals to the fragments. Because of these issues, common and relatively abundant species may be the most efficient way to re-establish seed dispersal and forest regeneration function in the Atlantic Forest.

Forest restoration in the Brazilian Atlantic Forest is of global importance, and recent studies have aimed at prioritizing restoration cost-effectively in the ecoregion (Strassburg *et al.* 2019). In a defaunated ecosystem, natural regeneration may be at risk (Peres *et al.* 2016). To support the forest restoration via natural regeneration, a framework to prioritize seed disperser reintroductions is essential.

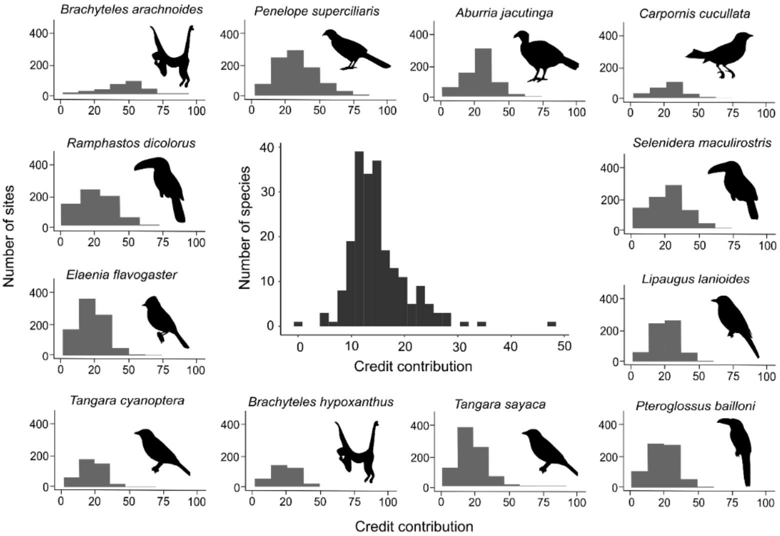


Figure 7. Distribution of animal species' contributions to the interaction credit across the Atlantic Forest. The histogram in the centre shows the distribution of the average credit contribution of each species considering all sites. Smaller histograms show the distributions of credit contribution for the 12 highest scoring species across study sites.

SYNTHESIS AND PERSPECTIVES

In this thesis, I found that species interactions within and between trophic levels are shaped by effects of 1) assembly processes on the assemblages within trophic levels, and 2) interaction assembly on the interspecific interaction links. Within trophic levels, we found that environmental and biogeographical processes drive the co-occurrences of tropical tree species. Between trophic levels, I found that anthropogenic and other environmental pressures drive bipartite tree-animal interactions. In this thesis, I have combined conceptual work and empirical data to better understand macroecological patterns and processes of pairwise species interactions and interaction networks. Predicting interactions with two different approaches has allowed me to study patterns of tropical interactions at an unprecedented spatial scale. In conclusion, understanding the different components of networks separately allows understanding the networks as a whole.

When visually comparing the spatial distributions of fragmentation effects on tree-animal interactions and interaction credit, I found that the areas with high proportions of tree-animal interactions provided by keystone animal species corresponded to the areas with low interaction credit values (Figure 8). These areas tend to have intact assemblages of both trees and animals and are therefore not in need of species reintroductions. In addition, these two maps identify well those areas that could gain a multitude of tree-animal interactions through reintroduction of seed dispersing animals: the keystone animal species are largely missing from the middle parts of the Atlantic Forest, but their interaction partners persist in the remaining forest fragments, thus leaving room for realizing interactions through species' reintroductions.

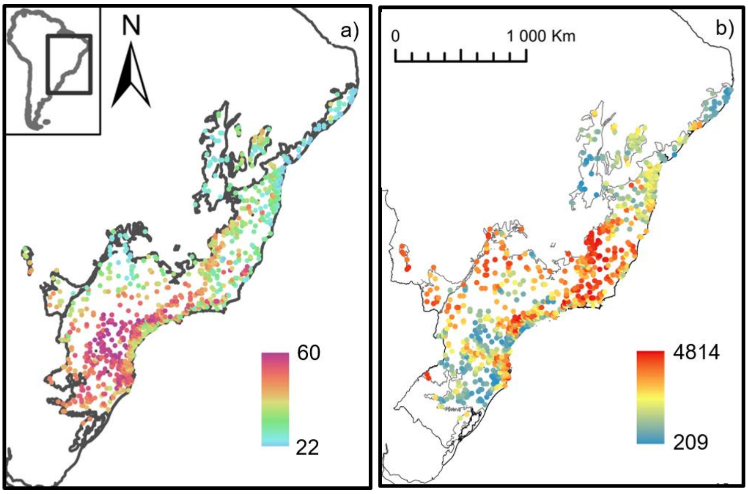


Figure 8. Spatial distribution of a) proportion of interactions provided by the keystone animal species (KEY), and b) credit of ecological interactions to be cashed through species' reintroductions across the Atlantic Forest. The values of the variables in each prediction site are illustrated by color gradients: warmest colors represent KEY and interaction credit hotspots (i.e., higher numeric values).

In general, identifying keystone species can be an efficient conservation method (Caro 2010; Cagua *et al.* 2019). However, in practice the keystone species identification is often done subjectively and leads to selection of rare species only. In paper III, I found that when accounting for their commonness, many widely distributed and common species are disproportionally important for providing ecosystem functions (here, seed dispersal). Species interactions are important in regulating most ecosystem functions (Cardinale *et al.* 2000). Thus, understanding the related mechanisms (Figure 2) is crucial in biodiversity conservation and management. Conservation science should ideally apply holistic knowledge of networks to counteract the biodiversity loss in the most efficient way.

Each of the papers in this thesis provides potential avenues for future research. Beyond paper I, the obvious next step would be to test to what extent the stepwise null models are able to detect the correct processes used in the simulations. In addition, the conceptual framework and the presented topical questions in network ecology should be explored with empirical data. Despite being computationally lighter, the used approach could also be modified to account for temporal and evolutionary dynamics in the structuring of bipartite networks. To develop the methodology in papers II, III and IV further, modelling of asymmetrical and nonstationary pairwise interactions is needed. More specifically, contributions of assemblage composition and individual interaction changes to interaction network dynamics should be quantified and modelled together (Poisot *et al.* 2015). For example, an animal may consume fruits of a tree species in a certain location, but not in another if it has more preferred resource available (Perea *et al.* 2013). However, such data is currently lacking. We also encourage future research and conservation planning to implement the interaction credit framework to other regions in need of ecosystem function restoration. Interaction credit estimates could be quantified for any ecosystem with sufficient information on species interactions and ranges. Such well-studied ecosystems exist especially in Europe and North America, both of which could also benefit from simultaneous restoration and species' reintroduction efforts (Svenning *et al.* 2016).

Understanding how the abiotic environment drives species' occurrences and co-occurrences has both conservation and methodology applications. Firstly, shifts in occurrences due to environmental factors should be accounted for in conservation prioritization as future distributions of species may not match the current ones (Miles *et al.* 2004). Secondly, presence-absence data alone may not suffice for inferring effects of environmental change on species communities as the negative population trends may be masked until species go (locally) extinct unless abundance data is obtained. Finally, when inferring species interactions from co-occurrences, environmental covariates need to be included in the model. Otherwise, estimated raw co-occurrences will largely present species' shared responses to the abiotic environment rather than actual pairwise interactions. In general, inferring interactions from co-occurrences poses problems (Morueta-Holme *et al.* 2016; Ovaskainen *et al.* 2017; Dormann *et al.* 2018; Zurell *et al.* 2018). For example, the spatial scale of observations should be accounted for, as species may co-occur within local habitat due to shared environmental requirements, but avoid each other at the finest scale due to competition over resources. Furthermore, co-occurrences may reflect indirect interactions that are difficult to discern from shared environmental requirements.

The broader future goals in network ecology include modelling multilayer networks instead of individual pairwise interactions or subsets of bipartite networks. This would mean modelling together different interaction types, such as competition, predator-prey and mutualistic interactions. Furthermore, substituting time with space is often considered problematic (Johnson & Miyanishi 2008; Damgaard 2019), which is why predictions of global change effects on communities and interaction networks should be based on comprehensive time series data and appropriate methods (Magurran 2007). This is especially important as species diversity may be stable over time, but the composition of species changes drastically (Magurran 2016). However, as time series data are scarce, also the space-for-time methods should be further developed to improve the certainty of predictions. Finally, the importance of field work cannot be stressed enough: more empirical data on species interactions along environmental gradients and with absent interactions should be sampled in order to decrease the uncertainty in the current predictions and to allow testing the conceptual frameworks that already exist.

REFERENCES

Adams, J.M. & Woodward, F.I. (1989). Patterns in tree species richness as a test of the glacial extinction hypothesis. *Nature*, 339, 699–701.

Almeida-Neto, M., Guimarães, P., Guimarães, P.R.J., Loyota, R.D. & Ulrich, W. (2008). A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos*, 117, 1227–1239.

Alvares, C.A., Stape, J.L., Sentelhas, P.C., De Moraes Gonçalves, J.L. & Sparovek, G. (2013). Köppen's climate classification map for Brazil. *Meteorol. Zeitschrift*, 22, 711–728.

Barber, M.J. (2007). Modularity and community detection in bipartite networks. *Phys. Rev. E*, 76, 066102.

Beca, G., Vancine, M.H., Carvalho, C.S., Pedrosa, F., Alves, R.S.C., Buscariol, D., *et al.* (2017). High mammal species turnover in forest patches immersed in biofuel plantations. *Biol. Conserv.*, 210, 352–359.

Bello, C., Galetti, M., Montan, D., Pizo, M.A., Mariguela, T.C., Culot, L., *et al.* (2017). ATLANTIC-FRUGIVORY: a plant-frugivore interaction dataset for the Atlantic Forest. *Ecology*, 98, 1729.

Bello, C., Galetti, M., Pizo, M.A., Magnago, L.F.S., Rocha, M.F., de Lima, R.A.F., *et al.* (2015). Defaunation affects carbon storage in tropical forests. *Sci. Adv.*, 1, e1501105.

Bender, D.J., Contreras, T.A. & Fahrig, L. (1998). Habitat loss and population decline: a meta-analysis of the patch size effect. *Ecology*, 79, 517–533.

Bender, I.M.A., Kissling, W.D., Blendinger, P.G., Böhning-Gaese, K., Hensen, I., Kühn, I., *et al.* (2018). Morphological trait matching shapes plant-frugivore networks across the Andes. *Ecography*, 41, 1910–1919.

Bertness, M.D. & Callaway, R.M. (1994). Positive interactions in communities. *Trends Ecol. Evol.*, 9, 191–193.

Bovendorp, R.S., Villar, N., Abreu-Junior, E.F. de, Bello, C., Regolin, A.L., Percequillo, A.R., *et al.* (2017). Atlantic small-mammal: A dataset of communities of rodents and marsupials of the Atlantic forests of South America. *Ecology*, 98, 2226.

Brook, B.W., Sodhi, N.S. & Bradshaw, C.J.A. (2008). Synergies among extinction drivers under global change. *Trends Ecol. Evol.*, 23, 453–460.

Burkle, L.A., Martin, J.C. & Knight, T.M. (2013). Plant-pollinator interactions over 120 years: loss of species, co-occurrence, and function. *Science*, 339, 1611–1615.

Cadotte, M.W. & Tucker, C.M. (2017). Should environmental filtering be abandoned? *Trends Ecol. Evol.*, 32, 429–437.

Cagua, E.F., Wootton, K.L. & Stouffer, D.B. (2019). Keystoneness, centrality, and the structural controllability of ecological networks. *J. Ecol.*, 107, 1779–1790.

CaraDonna, P.J., Petry, W.K., Brennan, R.M., Cunningham, J.L., Bronstein, J.L., Waser, N.M., *et al.* (2017). Interaction rewiring and the rapid turnover of plant–pollinator networks. *Ecol. Lett.*, 20, 385–394.

Cardinale, B.J., Nelson, K. & Palmer, M.A. (2000). Linking species diversity to the functioning of ecosystems: on the importance of environmental context. *Oikos*, 91, 175–183.

Caro, T. (2010). *Conservation by proxy - Indicator, umbrella, keystone, flagship and other surrogate* *species*. Island Press, Washington.

Castanho, C.T., Oliveira, A.A. & Prado, P.I. (2015). Does extreme environmental severity promote plant facilitation? An experimental field test in a subtropical coastal dune. *Oecologia*, 178, 855–866.

Chacoff, N.P., Resasco, J. & Vázquez, D.P. (2018). Interaction frequency, network position, and the temporal persistence of interactions in a plant-pollinator network. *Ecology*, 99, 21–28.

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B.C., *et al.* (2014). Improved allometric models to estimate the aboveground biomass of tropical trees. *Glob. Chang. Biol.*, 20, 3177–3190.

Culot, L., Pereira, L.A., Agostini, I., Almeida, M.A.B. de, Alves, R.S.C., Aximoff, I., *et al.* (2018). ATLANTIC-PRIMATES: a dataset of communities and occurrences of primates in the Atlantic Forests of South America. *Ecology*, 1.

Damgaard, C. (2019). A critique of the space-for-time substitution practice in community ecology. *Trends Ecol. Evol.*, 34, 416–421.

Dehling, D.M., Töpfer, T., Schaefer, H.M., Jordano, P., Böhning-Gaese, K. & Schleuning, M. (2014). Functional relationships beyond species richness patterns: trait matching in plant-bird mutualisms across scales. *Glob. Ecol. Biogeogr.*, 23, 1085–1093.

Diamond, J.M. (1975). Assembly of species communities. In: *Ecology and evolution of communities* (eds. Cody, M.L. & Diamond, J.M.). Harvard University Press, Cambridge, pp. 342–444.

Diamond, J.M. (1984). 'Normal' extinction of isolated populations. In: *Extinctions* (ed. Nitecki, M.H.). Chicago University Press, Chicago, pp. 191–246.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B. & Collen, B. (2014). Defaunation in the Anthropocene. *Science*, 345, 401–406.

Donatti, C.I., Guimarães, P.R., Galetti, M., Pizo, M.A., Marquitti, F.M.D. & Dirzo, R. (2011). Analysis of a hyper-diverse seed dispersal network: modularity and underlying mechanisms. *Ecol. Lett.*, 14, 773–781.

Dormann, C.F., Bobrowski, M., Dehling, D.M., Harris, D.J., Hartig, F., Lischke, H., *et al.* (2018). Biotic interactions in species distribution modelling: ten questions to guide interpretation and avoid false conclusions. *Glob. Ecol. Biogeogr.*, 27, 1004–1016.

Doughty, C.E., Wolf, A., Morueta-Holme, N., Jørgensen, P.M., Sandel, B., Violle, C., *et al.* (2016). Megafauna extinction, tree species range reduction, and carbon storage in Amazonian forests. *Ecography (Cop.).*, 39, 194–203.

Dunn, R.R., Harris, N.C., Colwell, R.K., Koh, L.P. & Sodhi, N.S. (2009). The sixth mass coextinction: are most endangered species parasites and mutualists? *Proc. R. Soc. B Biol. Sci.*, 276, 3037–3045.

Dunne, J.A., Williams, R.J. & Martinez, N.D. (2002). Food-web structure and network theory: the role of connectance and size. *Proc. Natl. Acad. Sci.*, 99, 12–17.

Eklöf, A., Jacob, U., Kopp, J., Bosch, J., Castro-Urgal, R., Chacoff, N.P., *et al.* (2013). The dimensionality of ecological networks. *Ecol. Lett.*, 16, 577–583.

Emer, C., Galetti, M., Pizo, M.A., Guimarães, P.R., Moraes, S., Piratelli, A., *et al.* (2018). Seed-dispersal interactions in fragmented landscapes - a metanetwork approach. *Ecol. Lett.*, 21, 484–493.

Fick, S.E. & Hijmans, R.J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.*, 37, 4302–4315.

Fischer, G., Nachtergaele, F., Prieler, S., van Velthuizen, H.T., Verelst, L. & Wiberg, D. (2008). *Global agro-ecological zones assessment for agriculture (GAEZ 2008)*. IIASA & FAO, Laxenburg & Rome.

Fleming, T.H., Breitwisch, R. & Whitesides, G.H. (1987). Patterns of tropical vertebrate frugivore diversity. *Annu. Rev. Ecol. Syst.*, 18, 91–109.

Fleming, T.H. & Kress, W.J. (2013). *The ornaments of life: coevolution and conservation in the tropics*. University of Chicago Press, Chicago.

Fukami, T. (2015). Historical contingency in community assembly: integrating niches, species pools, and priority effects. *Annu. Rev. Ecol. Evol. Syst.*, 46, 1–23.

Fukami, T., Bezemer, T.M., Mortimer, S.R. & Van Der Putten, W.H. (2005). Species divergence and trait convergence in experimental plant community assembly. *Ecol. Lett.*, 8, 1283–1290.

Fundação SOS Mata Atlântica. (2014). *Atlas dos remanescentes florestais da Mata Atlântica: período 2012-2013*. Fundação SOS Mata Atlântica, Instituto Nacional de Pesquisas Espaciais.

Galetti, M., Brocardo, C.R., Begotti, R.A., Hortenci, L., Rocha-Mendes, F., Bernardo, C.S.S., *et al.* (2017a). Defaunation and biomass collapse of mammals in the largest Atlantic forest remnant. *Anim. Conserv.*, 20, 270–281.

Galetti, M., Pires, A.S., Brancalion, P.H. & Fernandez, F.A.S. (2017b). Reversing defaunation by trophic rewilding in empty forests. *Biotropica*, 49, 5–8.

Genes, L., Cid, B., Fernandez, F.A.S. & Pires, A.S. (2017). Credit of ecological interactions: A new conceptual framework to support conservation in a defaunated world. *Ecol. Evol.*, 7, 1892–1897.

Guimarães, P.R., Jordano, P. & Thompson, J.N. (2011). Evolution and coevolution in mutualistic networks. *Ecol. Lett.*, 14, 877–885.

Hansen, M.C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., *et al.* (2013). High-resolution global maps of 21st-century forest cover change. *Science*, 342, 850–854.

Harmon, L.J., Andreazzi, C.S., Débarre, F., Drury, J., Goldberg, E.E., Martins, A.B., *et al.* (2019). Detecting the macroevolutionary signal of species interactions. *J. Evol. Biol.*, 32, 769–782.

Harvey, E., Gounand, I., Ward, C.L. & Altermatt, F. (2016). Bridging ecology and conservation: from ecological networks to ecosystem function. *J. Appl. Ecol.*, 54, 371–379.

Hasui, É., Metzger, J.P., Pimentel, R.G., Silveira, L.F., de Abreu Bovo, A.A., Martensen, A.C., *et al.* (2018). ATLANTIC BIRDS: a dataset of bird species from the Brazilian Atlantic Forest. *Ecology*, 99, 497.

Hegland, S.J., Grytnes, J.A. & Totland, Ø. (2009). The relative importance of positive and negative interactions for pollinator attraction in a plant community. *Ecol. Res.*, 24, 929–936.

Hérault, B. (2007). Reconciling niche and neutrality through the Emergent Group approach. *Perspect. Plant Ecol. Evol. Syst.*, 9, 71–78.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.*, 25, 1965–1978.

Hubbell, S.P. (2001). *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton.

IUCN. (2019). *The IUCN Red List of Threatened Species. Version 2019-2*. Available at: http://www.iucnredlist.org. Last accessed 7 August 2019.

Janzen, D.H. (1970). Herbivores and the number of tree species in tropical forests. *Am. Nat.*, 104, 501–528.

Johnson, E.A. & Miyanishi, K. (2008). Testing the assumptions of chronosequences in succession. *Ecol. Lett.*, 11, 419–431.

Jordano, P. (1987). Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. *Am. Nat.*, 129, 657–677.

Kraft, N.J.B. & Ackerly, D.D. (2010). Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. *Ecol. Monogr.*, 80, 401–422.

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., *et al.* (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.*, 7, 601–613.

Lima, F., Beca, G., Muylaert, R.L., Jenkins, C.N., Perilli, M.L.L., Paschoal, A.M. de O., *et al.* (2017). ATLANTIC-CAMTRAPS: a dataset of medium and large terrestrial mammal communities in the Atlantic Forest of South America. *Ecology*, 98, 2979.

Lutz, J.A., Furniss, T.J., Johnson, D.J., Davies, S.J., Allen, D., Alonso, A., *et al.* (2018). Global importance of large-diameter trees. *Glob. Ecol. Biogeogr.*, 27, 849–864.

MacArthur, R. & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.*, 101, 377–385.

Magurran, A.E. (2007). Species abundance distributions over time. *Ecol. Lett.*, 10, 347–354.

Magurran, A.E. (2016). How ecosystems change. *Science (80-.).*, 351, 448–449.

Markl, J.S., Schleuning, M., Forget, P.M., Jordano, P., Lambert, J.E., Traveset, A., *et al.* (2012). Meta-analysis of the effects of human disturbance on seed dispersal by animals. *Conserv. Biol.*, 26, 1072–1081.

Miles, L., Grainger, A. & Phillips, O. (2004). The impact of global climate change on tropical forest biodiversity in Amazonia. *Glob. Ecol. Biogeogr.*, 13, 553–565.

Morales-Castilla, I., Matias, M.G., Gravel, D. & Araújo, M.B. (2015). Inferring biotic interactions from proxies. *Trends Ecol. Evol.*, 30, 347–356.

Morueta-Holme, N., Blonder, B., Sandel, B., McGill, B.J., Peet, R.K., Ott, J.E., *et al.* (2016). A network approach for inferring species associations from co-occurrence data. *Ecography (Cop.).*, 39, 1139–1150.

Muylaert, R.L., Bovendorp, R.S., Sabino-Santos, G.J., Prist, P.R., Melo, G.L., de Fátime Priante, C., *et al.* (2019). Hantavirus host assemblages and human disease in the Atlantic Forest. *PLoS Negl. Trop. Dis.*, 13, e0007655.

Muylaert, R.L., Stevens, R.D., Esbérard, C.E.L., Mello, M.A.R., Garbino, G.S.T., Varzinczak, L.H., *et al.* (2017). ATLANTIC BATS: a dataset of bat communities from the Atlantic Forests of South America. *Ecology*, 98, 3227.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858.

Naeem, S. & Li, S. (1997). Biodiversity enhances ecosystem reliability. *Nature*, 390, 507–509.

Olesen, J.M., Bascompte, J., Dupont, Y.L. & Jordano, P. (2007). The modularity of pollination networks. *Proc. Natl. Acad. Sci.*, 104, 19891–19896.

Olesen, J.M., Bascompte, J., Elberling, H. & Jordano, P. (2008). Temporal dynamics in a pollination network. *Ecology*, 89, 1573–1582.

Oliveira, M.A., Grillo, A.S. & Tabarelli, M. (2004). Forest edge in the Brazilian Atlantic forest: drastic changes in tree species assemblages. *Oryx*, 38, 389–394.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., *et al.* (2001). Terrestrial ecoregions of the world: a new map of life on Earth. *Bioscience*, 51, 933–938.

Ovaskainen, O., Abrego, N., Halme, P. & Dunson, D. (2016). Using latent variable models to identify large networks of species-to-species associations at different spatial scales. *Methods Ecol. Evol.*, 7, 549–555.

Ovaskainen, O., Tikhonov, G., Norberg, A., Blanchet, F.G., Duan, L., Dunson, D., *et al.* (2017). How to make more out of community data? A conceptual framework and its implementation as models and software. *Ecol. Lett.*, 20, 561–576.

Paine, R.T. (1966). Food web complexity and species diversity. *Am. Nat.*, 100, 65–75.

Perea, R., Delibes, M., Polko, M., Suárez-Esteban, A. & Fedriani, J.M. (2013). Context-dependent fruit-frugivore interactions: partner identities and spatio-temporal variations. *Oikos*, 122, 943–951.

Peres, C.A., Emilio, T., Schietti, J., Desmoulière, S.J.M. & Levi, T. (2016). Dispersal limitation induces long-term biomass collapse in overhunted Amazonian forests. *Proc. Natl. Acad. Sci.*, 201516525.

Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., *et al.* (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, 344, 1246752.

Pires, M.M. (2017). Rewilding ecological communities and rewiring ecological networks. *Perspect. Ecol. Conserv.*, 15, 257–265.

Poisot, T., Stouffer, D.B. & Gravel, D. (2015). Beyond species: why ecological interaction networks vary through space and time. *Oikos*, 124, 243–251.

Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J. & Hirota, M.M. (2009). The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. *Biol. Conserv.*, 142, 1141–1153.

Ries, L., Fletcher, R.J., Battin, J. & Sisk, T.D. (2004). Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annu. Rev. Ecol. Evol. Syst.*, 35, 491–522.

Saavedra, S., Rohr, R.P., Dakos, V. & Bascompte, J. (2013). Estimating the tolerance of species to the effects of global environmental change. *Nat. Commun.*, 4, 2350.

Sazatornil, F.D., Moré, M., Benitez-Vieyra, S., Cocucci, A.A., Kitching, I.J., Schlumpberger, B.O., *et al.* (2016). Beyond neutral and forbidden links: morphological matches and the assembly of mutualistic hawkmoth–plant networks. *J. Anim. Ecol.*, 85, 1586–1594.

Scheffer, M. & van Nes, E.H. (2006). Self-organized similarity, the evolutionary emergence of groups of similar species. *Proc. Natl. Acad. Sci.*, 103, 6230–6235.

Schleuning, M., Fründ, J. & García, D. (2015). Predicting ecosystem functions from biodiversity and mutualistic networks: an extension of trait-based concepts to plant-animal interactions. *Ecography*, 38, 380–392.

Sebastián-González, E. (2017). Drivers of species' role in avian seed-dispersal mutualistic networks. *J. Anim. Ecol.*, 86, 878–887.

Soares-Filho, B.S., Lima, L.S., Hissa, L.B., Costa, W.L.S., Rodrigues, H.O., Ferreira, B.M., *et al.* (2013). *OTIMIZAGRO: Uma plataforma integrada de modelagem de uso e mudanças no uso da terra* *para o Brasil.* 1st edn. IGC/UFMG, Brasilia.

Strassburg, B.B.N., Beyer, H.L., Crouzeilles, R., Iribarrem, A., Barros, F., de Siqueira, M.F., *et al.* (2019). Strategic approaches to restoring ecosystems can triple conservation gains and halve costs. *Nat. Ecol. Evol.*, 3, 62–70.

Svenning, J.-C., Pedersen, P.B.M., Donlan, C.J., Ejrnæs, R., Faurby, S., Galetti, M., *et al.* (2016). Science for a wilder Anthropocene: synthesis and future directions for trophic rewilding research. *Proc. Natl. Acad. Sci.*, 113, 898–906.

Thompson, J.N. (2005). *The Geographic Mosaic of Coevolution*. The University of Chicago Press, Chicago.

Tylianakis, J.M., Laliberté, E., Nielsen, A. & Bascompte, J. (2010). Conservation of species interaction networks. *Biol. Conserv.*, 143, 2270–2279.

Valdovinos, F.S. (2019). Mutualistic networks: moving closer to a predictive theory. *Ecol. Lett.*, 22, 1517–1534.

Valiente-Banuet, A., Aizen, M.A., Alcántara, J.M., Arroyo, J., Cocucci, A., Galetti, M., *et al.* (2015). Beyond species loss: the extinction of ecological interactions in a changing world. *Funct. Ecol.*, 29, 299–307.

Warton, D.I., Blanchet, F.G., O'Hara, R.B., Ovaskainen, O., Taskinen, S., Walker, S.C., *et al.* (2015). So many variables: joint modeling in community ecology. *Trends Ecol. Evol.*, 30, 766–779.

Weiher, E. & Keddy, P.A. (1995). Assembly rules, null models, and trait dispersion: new questions from old patterns. *Oikos*, 74, 159–164.

Wildlife Conservation Society & Center for International Earth Science Information Network. (2005). *Global Human Influence Index (Geographic), v2 (1995-2004)*. NASA Socioeconomic Data and Applications Center (SEDAC), Palisades.

Willison, M.F., Irvine, A.K. & Walsh, N.G. (1989). Vertebrate dispersal syndromes in some Australian and New Zealand plant communities, with geographic comparison. *Biotropica*, 21, 133–147.

Zurell, D., Pollock, L.J. & Thuiller, W. (2018). Do joint species distribution models reliably detect interspecific interactions from co-occurrence data in homogenous environments? *Ecography (Cop.).*, 41, 1812–1819.

PAPER I

A framework linking trait-based processes to the assembly of bipartite networks

Emma-Liina Marjakangas[1,*], Gabriel Muñoz[2,*], Shaun Turney[2], Jean-Philippe Lessard[2]

[1] Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of Science and Technology, Trondheim, Norway
[2] Department of Biology, Faculty of Arts and Sciences, Concordia University, Montreal, Canada
[*] These authors contributed equally to this study
Corresponding author: emma-liina.marjakangas@ntnu.no, orcid 0000-0002-5245-3779

Keywords: bipartite network, bottom-up effect, environmental filtering, limiting similarity, modularity, nestedness, neutral process, null model, species interaction, top-down effect

Abstract

The structures of ecological networks relate to the stability and resilience of communities, making them of focal interest in the context of intensifying anthropogenic pressures. The emergent structures of networks arise from a suite of interrelated processes that can be studied with trait-based approaches. Here, we propose a conceptual and methodological framework that extends trait-based approaches from single trophic levels to bipartite networks of resource and consumer trophic levels. Our approach is unique in that it (1) quantifies the determinants of network structure in relation to the assembly processes within trophic levels and to the formation of pairwise interactions between trophic levels, and (2) introduces null models that allow identifying the exact processes structuring observed networks. We explored the ecological relevance of our framework with simulations. We show that the interaction assembly generally plays a more important role in structuring bipartite networks than assembly of resource and consumer trophic levels. The within-trophic level assembly processes determine bipartite network structure mainly when their strengths differ between trophic levels. When within-trophic level processes have symmetric strengths, the process governing pairwise interactions is the main driver of network structure. We also show how our stepwise null models can be used to test observed networks against null expectations to determine the drivers of the observed network structure. By explicitly linking assembly processes and network structure, we provide means to determine the mechanisms that influence network assembly and the ecosystem functions embedded within networks. Conceptually and analytically, our framework facilitates exploration of many topical questions in network ecology. Practically, our framework can be used to guide conservation efforts to those processes most crucial for maintaining the stability of networks.

1 INTRODUCTION

Species interactions provide ecosystems with many fundamental functions, including pollination, nutrient cycling, and population regulation (IPBES 2019). The collection of interactions between species in an ecological community can be described as a network, with species as nodes and interspecific interactions as links between nodes. Distinct configurations of aggregated multi-species interactions between resource (e.g., plant or prey) and consumer (e.g., pollinator or predator) trophic levels are usually described using bipartite networks, where interactions among species only occur between the two trophic levels. The ability of these networks to buffer ecosystems against perturbations is crucial in the context of changing climate, introduction of invasive species, and other anthropogenic pressures (Tylianakis *et al.* 2010). In general, network architecture regulates the degree of stability and resilience of communities (Okuyama & Holland 2008; Thébault & Fontaine 2010; Gravel *et al.* 2016). Increasing connectance, nestedness and modularity of networks (see Box 1 for network metric definitions) increase the stability and resilience of the community in the face of disturbances (Thébault & Fontaine 2010; Tylianakis *et al.* 2010). For example, specialist species are especially vulnerable to extinction (Henle *et al.* 2004), but in highly connected networks secondary extinctions are unlikely as the remaining species will still have other species with which to interact. Thus, understanding the architectural properties of multi-species interaction networks provide invaluable information to quantify the stability and resilience of natural communities in relation to forecasted global change scenarios.

Network structure is thought to be shaped by assembly processes operating within and between trophic levels, as well as through interactions of such processes (Bascompte & Stouffer 2009; Ponisio *et al.* 2019). Although inferences of assembly processes usually focus on one trophic level at the time, all ecological assemblages are part of a larger network, such as a food web (Cavender-Bares *et al.* 2009). Assembly processes at a single trophic level have been studied in relation to network structure, indicating that changes in the interaction network structure are introduced through changes in community composition, interaction frequencies, and coevolutionary patterns (e.g., environmental filtering effects on networks reviewed by Tylianakis & Morris, 2017). Some recent studies have succeeded in expanding beyond one trophic level and in integrating networks and assembly processes (Albrecht *et al.* 2018; Godoy *et al.* 2018; Ponisio *et al.* 2019), but a comprehensive conceptual picture of drivers behind network structure is yet to be developed. For example, Ponisio and colleagues (2019) evaluate the effects of network structure on species' assemblages. From the other direction, the role of assembly processes in driving network structure has largely been ignored, in favor of an emphasis on the role of network dynamics, such as selection for stable networks (Maynard *et al.* 2018). To extend the current knowledge, our framework aims to synthesize and unify two important building blocks of community ecology theory: the links between assembly processes and functional trait space (e.g., Kraft & Ackerly, 2010) and between functional trait space and network structure (e.g., Laigle et al., 2018).

Network ecology offers concepts and tools to study communities across multiple trophic levels. Network approaches provide an opportunity to gain a better understanding of the role that trophic interactions play in the assembly of communities as a whole (Ponisio *et al.* 2019). It has become increasingly common to quantify one of several metrics (Box 1) to describe the often complex structure of networks, such as bipartite plant-pollinator and host-parasite networks (e.g., Fortuna et al., 2010). Although increasingly often used in novel ecological literature, it remains unclear what these metrics tell us about the processes involved in the assembly of multi-trophic communities. As such, network ecology tends to be descriptive and rely on *post hoc* interpretation of the quantified network metrics, rather than deciphering the actual processes behind observed patterns. Developing a predictive framework for network ecology is key to implementing management strategies that might take multi-trophic interactions into consideration. Processes determining community assembly, the interactions between species in networks, and biodiversity-ecosystem function relationships operate sequentially and in concert (Schleuning *et al.* 2015). Hence, gaining a better understanding of these processes that determine the assembly of interaction network is not only an ongoing challenge in community ecology, but also a necessary step in order to predict how network structure might vary in space and time, and how ecosystem functioning depends on biodiversity.

Trait-based approaches are widely used in community ecology to study assembly processes (e.g., Ackerly & Cornwell, 2007; Kraft & Ackerly, 2010). While the approaches have been criticized for their shortcomings in identifying trait-environment relationships, the simplicity of interpretation and application makes them useful (HilleRisLambers *et al.* 2012). The development of new methodologies can circumvent some issues in the application of these approaches and increase the power of inference (e.g., HilleRisLambers et al., 2012; Lessard, Belmaker, Myers, Chase, & Rahbek, 2012). Nevertheless, most of the trait-based approaches focus on one trophic level at the time, ignoring interactions between trophic levels (Godoy *et al.* 2018). This is a particular problem as it is widely accepted that species' functional traits "set the blueprint of the pairwise interactions" in form of functional trait matching between interacting species (Albrecht *et al.* 2018). Therefore, to distinguish processes behind network assembly, there is a need for extending traditional trait-based approaches across trophic levels.

Moving beyond descriptive network ecology and *post hoc* interpretation of network metrics requires a framework that links patterns to processes and enables hypothesis testing and inference of whole-network assembly processes. The integration of trait-based ecology concepts into network ecology could offer such conceptual platform (e.g., Ponisio et al., 2019). Because trait-based ecology is deeply rooted in niche-based ecology (MacArthur & Levins 1967; Diamond 1975), and because niche-related traits often determine the pairwise interaction of two partners in a network (Bender *et al.* 2018; Sonne *et al.* 2019), trait-based ecology can be extended to multi-trophic communities. Here, we propose a conceptual framework wherein network assembly is determined by the assembly of each trophic level and by the assembly of pairwise interactions between trophic levels. As such, assembly processes occur within each trophic level independently, while interactions are assembled based on functional trait matching of one trophic level with the other. With our framework, we want to understand how different assembly processes, within and between trophic levels, influence structural properties of bipartite networks. In this paper, we first introduce the conceptual framework and connect it to community ecology theory (section 2). Next, we illustrate the ecological relevance of the framework with simulations and show that different combinations of assembly process types and strengths within and between trophic levels produce distinct network structures (section 3). Then, we present a stepwise null model method for testing observed networks against null expectations (section 4). Finally, we highlight topical questions in network ecology to be addressed with our framework, and test two of them with observed networks (section 4). We conclude the paper by discussing the limitations and potential applications of the conceptual and analytical parts of the framework.

2 A CONCEPTUAL FRAMEWORK FOR NETWORK ASSEMBLY

We identify three building blocks that shape bipartite network structure: assembly processes at the resource trophic level, assembly processes at the consumer trophic level, and interaction assembly processes (Figure 1). Assembly processes at the resource and consumer trophic levels independently influence the assemblage composition at the respective trophic levels. Interaction assembly processes determine the pairwise interactions among species pairs present in the local resource and consumer assemblages. In case of obligate relationships (e.g., fig tree-fig wasp mutualism; Herre, 1996), interaction assembly processes also indirectly determine species compositions within trophic levels. We categorize the different assembly processes to be either niche-based or neutral. This follows the current paradigm that emphasizes the synergies between different niche-based mechanisms rather than separating them (Cadotte & Tucker 2017). Together, niche-based and neutral processes encompass all possible assembly processes because all such processes are necessarily either dependent on species' niches (niche-based processes) or are independent of species' niches (neutral processes). However, while current ecological research treats niche and neutral processes categorically, the rules that govern the assembly processes are likely to fall within a continuous gradient, varying from fully neutral to fully determined by species' identities (Gravel *et al.* 2006; Krishna *et al.* 2008; Fournier *et al.* 2017). While neutral processes are stochastic relative to species' identities, they can be deterministic relative to other variables, such as biogeography (dispersal limitation; Hubbell, 2001) or abundance (neutral interaction assembly; Vázquez et al., 2007). Together the three building blocks determine the structure of bipartite networks.

2.1 Within-trophic level assembly processes

According to the ecological filtering concept, the structure and composition of assemblages within a trophic level are determined by assembly processes ("filters") acting on a regional species pool (Figure 1; Cadotte & Tucker, 2017; Kraft et al., 2015; Weiher & Keddy, 1995). These community assembly processes govern how species in a region are distributed at a local spatial scale, and can be either neutral or niche-based. Under neutral processes, community assembly is stochastic relative to species' niches (Hubbell 2001). Under niche-based processes, the probability that an individual or species is present or absent in an assemblage is dependent on its niche properties. Environmental filtering is a niche-based process whereby species are excluded from the local assemblage if their niches are not compatible with the local environmental conditions (van der Valk 1981; Keddy 1992). That is, at the niche level, environmental filtering is driven by niche filtering. Here we use a broad definition of environmental filtering, such that it encompasses both biotic (e.g., presence of facultative symbionts) and abiotic (e.g., climatic filtering) constraints (Cadotte & Tucker 2017). Thus, environmental filtering may encompass biotic interactions other than those directly related to the interaction type of interest. Under limiting similarity, another niche-based process, species are unable to coexist in an assemblage if their niches are too similar, due to competitive exclusion (Gause 1934; MacArthur & Levins 1967). That is, at the niche level, limiting similarity is driven by niche partitioning. These neutral and niche-based processes determine which species are present in an assemblage and (for niche-based processes) the resources they consume, affecting network structure in ways that are yet to be investigated. The ecological filtering paradigm treats assembly processes as discrete from one another, which is a simplification of the interacting effects of ecological processes in nature (HilleRisLambers et al., 2012; see Section 5: Limitations). Despite its limitations, this paradigm is pervasive and a useful tool when used carefully and with consideration of other recent advancements (e.g., Cadotte & Tucker, 2017; Li et al., 2018).

Predicting and understanding ecological processes from species' traits is considered a "holy grail" of ecology (Lavorel & Garnier 2002; Suding & Goldstein 2008; Funk *et al.* 2017). In the past three decades, trait-based approaches have yielded important advancements in our understanding of many ecological processes (e.g., (Reich *et al.* 1997; Wright *et al.* 2004; Kraft *et al.* 2008; Violle *et al.* 2014), including community assembly. The community assembly processes taking place in a region can be inferred from the distribution of functional traits across and within local assemblages (Weiher & Keddy 1995; Rosenfeld 2002; Li *et al.* 2018). Neutral processes are inferred if the distribution of functional traits in an observed assemblage does not differ from that of a random set of species from the regional species pool (i.e., null models of community structure; Lessard et al., 2012). If the local functional trait distribution deviates from null expectation, the presence of niche-based processes is inferred. More specifically, environmental filtering is inferred if the distribution of functional traits in local assemblages is more convergent than null expectation (Keddy 1992; Díaz *et al.* 1998). Limiting similarity is inferred if the distribution of functional traits in local assemblages are more divergent than null expectation (e.g., Stubbs & Wilson, 2004). To our knowledge, our framework is the first to allow the inference of the effects of assembly processes on network structure from both trait and network index distributions.

2.2 Interaction assembly processes

Interaction assembly processes can strongly influence the overall structure of networks (Figure 1). Interaction assembly processes determine the occurrences of interactions between species pairs at resource and consumer trophic levels (i.e., pairwise interactions), while within-trophic level assembly processes filter the set of species occurring within the assemblages. However, interaction assembly processes have not been thoroughly investigated in comparison to the assembly processes occurring within-trophic levels. The influence of interaction assembly processes on pairwise interactions is determined by the degree of functional trait matching between species at the resource and consumer trophic levels (i.e., the degree of complementarity between traits of interacting species; Dehling et al., 2014). Functional trait matching is tightly linked with the degree of specialization between interaction partners (Dehling *et al.* 2014). Indeed, species' specialization to a resource is considered to be a function of its degree of trait matching with the interaction partners (Dehling *et al.* 2016), abundance (Simmons *et al.* 2019) and intensity of competition with other species (MacArthur & Levins 1967). In general, some species have specialized requirements for their habitat or food resources (e.g., host-specific parasites), whereas others are generalists that thrive under diverse conditions (e.g., omnivorous scavengers). In particular, highly specialized species tend to have narrow interaction niches (Junker *et al.* 2013), that can be defined with the range of trait values that the interaction partners of the focal species express (Box 2; Albrecht et al., 2018). Strong trait matching implies that niche-based processes restrict pairwise interactions, thus resulting in a higher partitioning of interactions between consumer and resources trophic levels. For example, matching traits between animals (e.g., body size, gape size, beak morphology) and plants (e.g., fruit diameter, seed size, flower morphology) have shown to influence the occurrence of mutualistic interactions in the tropics (e.g., Bender et al., 2018; Sonne et al., 2019). On the other hand, weak trait matching implies that pairwise interactions are assembled neutrally. That is, interactions are determined by encounter probabilities among individuals in a community (Vázquez *et al.* 2007). Thereby, interactions are more likely to occur between abundant than rare species (e.g., Chacoff, Resasco, & Vázquez, 2018). The relationship between interaction assembly and interaction niche properties may provide new insights to understanding the relative contributions of various processes on network structure.

Several hypotheses have been proposed in order to predict pairwise interactions based on functional trait matching among species (Morales-Castilla *et al.* 2015; Sazatornil *et al.* 2016). The morphological matching hypothesis assumes restrictive criteria for the formation of specialized interactions (Sazatornil *et al.* 2016). Under this hypothesis, focal species' interaction niche breadth is constrained bidirectionally. That is, the interaction partner traits must fall within both a minimum and maximum trait value. With morphological matching, the probability of a pairwise interaction is determined by the trait distribution of interacting species instead of the abundance based encounter probabilities between individuals (Sazatornil *et al.* 2016). Degree of constraint in trait matching may determine how likely local networks are to be rewired after changes in species composition (Poisot *et al.* 2015). For example, highly constrained trait matching between a plant and a pollinator may prevent any other pollinator from interacting with the plant in case of local extinction of its original pollinator. Alternatively, the forbidden links hypothesis (Morales-Castilla *et al.* 2015) assumes that functional trait matching limits the breadth of species-specific interaction niche unidirectionally. That is, traits of the focal species' interaction partners must either fall above a minimum or below a maximum trait value. Unidirectional trait matching is typically observed in food webs with size-related traits. For example, predators can generally only consume prey objects smaller than themselves (Cohen *et al.* 1993). By far, these two hypotheses have mainly been studied with mutualistic plant-animal interactions (e.g., Bender et al., 2018; Sazatornil et al., 2016).

2.3 Bottom-up and top-down drivers of bipartite network structure

Since Hairston and colleagues' (1960) "green world" hypothesis of natural enemies, rather than plant defences, keeping herbivores in check, community ecologists have debated over whether multitrophic communities are controlled from bottom-up or top-down (e.g., Pace, Cole, Carpenter, & Kitchell, 1999). In general, bottom-up effects are inferred when the lower trophic level regulates the flow of energy to the upper trophic level, and top-down effects are inferred when the upper trophic level regulates the populations at the lower trophic level. Empirical support has been found for both bottom-up (e.g., Scherber et al., 2010) and top-down effects (e.g., Ripple & Beschta, 2012), which would imply that the structure of the focal networks is primarily affected by the assembly processes at one of the trophic levels at a time. Despite a more complex picture being likely, mechanistic understanding of the pathways that regulate the relative contributions of bottom-up and top-down effects on communities is limited. Testing for the relative contributions of different assembly processes to bipartite network structure, and the mechanisms that determine the relative importance of bottom-up and top-down effects, may advance this debate. By quantifying the relative strengths of such effects, it is possible to infer generalities about network assembly along broad-scale gradients and in different regions of the world (Lessard *et al.* 2012).

In this paper, we extend the aforementioned definition and view the effects of resource assembly processes on interaction network structure as being bottom-up and the effects of consumer assembly processes on interaction network structure as being top-down. The relative importance of bottom-up and top-down effects would hence be determined by the difference in strengths of the assembly processes between trophic levels. Accordingly, our framework allows quantifying the relative contributions of bottom-up and top-down effects of within-trophic level assembly processes to bipartite network structure. We assess relative importance of bottom-up and top-down effects as the degree of symmetry in the strengths of the niche-based assembly processes at resource and consumer trophic levels. In addition to quantifying the relative contributions of bottom-up and top-down effects on interaction network structure, the driving mechanism behind the observed contributions is of great interest. We argue that the properties of species-specific interaction niches could contribute to determining how strongly a network is bottom-up or top-down regulated (Box 2). More specifically, the trophic level with more constrained interaction niches is the one that regulates the network structure more. However, the links between interaction assembly and bottom-up versus top-down effects are still to be investigated empirically.

Although most often presented separately, within-trophic level and interaction assembly processes shape networks in synergy. For instance, distinct environmental factors can independently constrain the formation of consumer and resource assemblages. For example, Albrecht and colleagues (2018) found that temperature filtered the trait distribution of pollinators, whereas precipitation shaped the trait distribution of plants in plant-pollinator networks along an elevational gradient in the Kilimanjaro mountain. This decoupled shift in trait distributions between trophic levels leads to differences in the formation of pairwise interactions, scaling up to different network structures (Albrecht *et al.* 2018). Furthermore, distinct niche-based assembly processes within trophic levels may also act independently between resources and consumers in terms of strength or type of assembly process. For example, resource assemblage may be filtered by climatic variables, while consumer assemblage may be determined through limiting similarity. In summary, drivers of the assemblages at individual trophic levels (within-trophic level processes) operate in concert with the ones governing the interactions among species (between-trophic levels processes) to form the structure of bipartite networks. Regardless of the interconnected processes within and between trophic levels, the interactions and synergies of different assembly processes have rarely been tested with empirical or simulated data.

3 TRAIT-BASED SIMULATIONS OF NETWORK ASSEMBLY

During the past decade, research on ecological networks has focused on describing a series of non-random emergent patterns in bipartite network structure (Box 1; Fortuna et al., 2010; Olesen, Bascompte, Dupont, & Jordano, 2007). Bipartite networks show considerable geographic variation in their structural properties across local and regional scales (Trøjelsgaard *et al.* 2015; Galiana *et al.* 2019; Muñoz *et al.* 2019). Alongside this variation, particular network structures are over-represented (e.g., highly modular configurations), which was initially attributed to selective processes responsible for the formation of stable communities (Thébault & Fontaine 2010). However, the emergence of such non-random architectures have more recently been linked to the intrinsic assembly process governing the formation of species assemblages that conform interaction networks (Maynard *et al.* 2018; Valverde *et al.* 2018). Thus, the general processes governing the turnover in structural patterns of observed networks remain unclear (Gravel *et al.* 2016, 2019).

Recent efforts have related various within-trophic level assembly processes to observed network structures (e.g., Alcántara, Pulgar, Trøjelsgaard, Garrido, & Rey, 2018; Fournier, Mouly, & Gillet, 2016; Maynard et al., 2018). However, the global shortage of ecological data on species' traits and interactions (i.e., Raunkiæran and Eltonian knowledge gaps; Hortal et al., 2015) is perhaps the main factor that hinders the development of general frameworks to relate community and interaction assembly processes with empirical patterns of network structure. Simulating synthetic bipartite networks under different assembly scenarios enables partitioning the contributions of distinct assembly processes that generate different network structures. Despite representing a compromise of the intrinsic complexity of natural systems, simulations can contribute greatly to overcoming data limitation issues and setting hypotheses for further empirical testing (Kraft & Ackerly 2010; Barbier *et al.* 2018).

We simulated synthetic bipartite networks under different combinations of neutral and niche-based scenarios of within-trophic level and interaction assembly processes (Figure 2). Resource and consumer assemblages were simulated under environmental filtering and limiting similarity scenarios to represent the effects of niche-based assembly within trophic levels on network structure. Niche-based interaction assembly effects were introduced through interaction probabilities defined by two distinct functional trait matching hypothesis (see section 2). We quantified the relative contributions of niche-based assembly processes within and between trophic levels to network structure by measuring the deviations of network metrics from the expected values of neutral scenarios. Moreover, we partitioned the variance in the magnitude of niche-based effects on network structure into components attributable to the five simulation parameters: type of within-trophic level assembly process, interaction assembly process hypothesis, assembly process strength at resource trophic level, assembly process strength at consumer trophic level, and symmetry of the assembly process strengths between trophic levels. We did this in two separate steps. First, we modelled modularity and nestedness as functions of the aforementioned simulation parameters and estimated the contribution of each parameter to the variation in the network metric values. Second, we partitioned the variation in relative magnitude of niche-based assembly process effects on network structure into unique and common effects of the simulation parameters. For details on the simulations and all combinations of simulated scenarios, see Appendix S1 (Table S1a-e).

Based on preceding literature and the conceptual framework presented in Figure 1, we predict that (1) both within-trophic level and interaction assembly processes contribute to the variation in bipartite network structure. We base this prediction on separate findings that show links between within-trophic level assembly processes and network structure (Tylianakis & Morris 2017), and between trait matching and network structure (Sazatornil *et al.* 2016; Laigle *et al.* 2018). We also predict that (2) when the assembly of interactions between trophic levels is constrained by functional trait matching, networks have more modular structures. This is because traits limit pairwise interactions to occur among matching sets of species, which leads to reduction in the average interaction niche breadth and overlap in the network (Box 2). In other words, the functional specialization of species in the network increases with more constrained trait matching (Lewinsohn *et al.* 2006; Dehling *et al.* 2016), creating more modular networks compared to networks where pairwise interactions are assembled neutrally. Finally, we predict that (3) the symmetry in the strengths of niche-based assembly processes forming resource and consumer assemblages regulates the magnitude of effects that niche-based assembly within trophic levels have on network structure. Niche-based assembly processes within trophic levels can greatly impact the final distribution of functional traits at both consumer and resource trophic levels, ultimately constraining the availability of species within trophic levels to form interactions among trophic levels. For example, asymmetric assembly process strengths between trophic levels result in asymmetric interaction niches, which can lead to stronger partitioning of pairwise interactions. Hence, bipartite networks with asymmetric assembly process strengths between resource and consumer trophic levels may have more different network structures from expected neutral scenarios compared to those networks with symmetric assembly process strengths.

3.1 Drivers of network structure

3.1.1 Assembly processes within and between trophic levels jointly shape network structure

In agreement with prediction (1), we found that the structure of simulated networks depended on the assembly processes taking place within and between trophic levels (Appendix S2, Tables S2). The type of interaction assembly hypothesis significantly correlated with the variation in modularity ($R^2 = 0.93$) and nestedness ($R^2 = 0.92$), as well as with their variances (SD) across scenarios (modularity: $R^2 = 0.25$; nestedness: $R^2 = 0.81$). On the other hand, within-trophic level assembly process significantly correlated with modularity and nestedness, but did not with their variances across scenarios (Appendix S2, Table S2). Niche-based assembly processes had significant effects on network structure (Figure 3a,b,e,f). In general, bipartite networks with interactions determined by morphological matching produced more modular and anti-nested structures than networks with interactions assembled neutrally (Figure 3; Appendix S2, Figure S1). Bipartite networks with interactions assembled under the forbidden link hypothesis were generally more nested, but equally modular compared to networks with interactions assembled neutrally (Figure 3; Appendix S2, Figure S1). The type of within-trophic level assembly process partly explained the variance of the relative magnitudes of niche-based assembly effects (Figure 3d,h; Appendix S2, Table S2). For example, limiting similarity generally produced more modular but similarly nested networks compared to environmental filtering (Figures 3a,b,e,f; Appendix S2, Figure S1). In addition, the range of variation in network structure induced by niche-based interaction assembly process (i.e., variation within convex hulls in Figure 3a,b) was much larger than the range of variation in network structure induced by within-trophic level assembly (i.e., variation between convex hulls in Figure 3e,f). Finally, interaction assembly hypothesis and within-trophic assembly process type were both significant predictors of the variance in magnitude of niche-based assembly effects (Figure 3d,h; Appendix S2, Table S2). For instance, niche-based assembly effects on network structure were larger in under limiting similarity and forbidden links (Figure 3b). Thereby, our results indicate that the interaction assembly generally plays a more important role in structuring bipartite networks than assembly of resource and consumer trophic levels. However, the scale of niche-based interaction assembly process effects (i.e., size of convex hulls in Figure 3a,b) was larger compared to those effects from within-trophic assembly process (i.e., size of convex hulls in Figure 3e,f). Hence, to a certain extent, niche-based assembly processes within trophic levels may limit the magnitude and direction of interaction assembly effects on network structure.

3.1.2 Niche-based interaction assembly leads to modular and nested network structure

Parallel to prediction (2), networks under niche-based interaction assembly were significantly more modular than networks under neutral interaction assembly (Figure 3a,b). This finding is parallel to a global study of plant-pollinator networks, where 57 % of analyzed networks were significantly more modular than networks of similar size with random interactions (Olesen *et al.* 2007). In addition, more specialized plant-herbivore and plant-ant networks showed much more modular patterns than less specialized plant-pollinator networks (Olesen *et al.* 2007). This suggests that niche-based interaction assembly processes can scale up to produce more modular network structures. On the other hand, the resulting nested structures differed between the distinct hypotheses of functional trait matching. Bipartite networks with interactions assembled according to morphological matching hypothesis were typically more anti-nested than networks with interactions assembled neutrally (Figure 3a). Conversely, bipartite networks with interactions assembled according to forbidden links hypothesis were largely more nested than networks with interactions assembled neutrally (Figure 3b). In agreement with our results, a conspicuous anti-nested network structure have been observed in below-ground networks of highly specialized mycorrhizal symbionts of plants (Toju *et al.* 2015). For other mutualistic interaction networks, including plant-pollinator or plant-seed disperser networks, nestedness is a prevalent pattern. Size-related traits tend to unidirectionally regulate the occurrence of pairwise interactions of such networks (e.g., Bender et al., 2018) Following the forbidden link hypothesis, the most abundant species with the largest interaction niche breaths are more likely generalists. Similarly, those species with narrow interaction niche breaths and low abundances are more likely specialists. As such, niches of generalists will overlap niches of more specialized ones, thus creating nested network structures where the core of interactions consists of interactions among species with the highest total overlap in their interaction niches.

3.1.3 Process strength symmetry dictates the effect of niche-based within-trophic level assembly processes on bipartite network structure

Contrary to prediction (3), the symmetry in the strength of niche-based assembly process forming consumer and resource assemblages modulated the magnitude of within-trophic niche-based assembly effects, but not the magnitude of niche-based interaction assembly effects on network structure (Figure 3c,d,g,h). After accounting for interaction assembly effects, processes creating asymmetrical interaction niches increased the within-trophic assembly effects on network structure, creating structures that deviate the most from neutral scenarios. In addition, asymmetric interaction niches may also increase the likelihood of bipartite networks being either bottom-up or top-down controlled through increasing within-trophic level assembly effects on network structure (Box 2). Finally, the degree of process strength forming resource and consumer assemblages also contributed to the variation in the magnitude of within-trophic niche-based assembly effects on network structure (Figure 3h; Appendix S2, Table S2). Altogether these results show that the congruence of the relationship between resource and consumer interaction niches, defined by the strengths of the assembly processes creating local assemblages, may partly modulate network structures at finer scales.

3.2 Conclusions arising from the simulations

Our simulation results show that within- and between-trophic level assembly processes affect network structure in important and predictable ways. In order to understand how ecological networks are formed and what determines their structure, it is clear that we must therefore consider the role of assembly processes. It is especially important to consider and model consumer, resource, and interaction assembly processes together. Additionally, our simulation results may provide important application possibilities for conservation and management of biodiversity. For example, high morphological matching could make networks less stable and prone to secondary extinctions by decreasing nestedness, which translates to decreased redundancy of interactions. Furthermore, nestedness and modularity may be tightly linked with the degree of specialization in the assemblage (Danieli-Silva *et al.* 2012; Nuismer *et al.* 2013), metanetwork dynamics (Emer *et al.* 2018) and priority effects (i.e., effect that a species has on community assembly due to prior arrival at a site; Fukami, Bezemer, Mortimer, & Van Der Putten, 2005), all which are important components when prioritizing conservation areas, restoration efforts and species (re)introductions (e.g., Devoto, Bailey, Craze, & Memmott, 2012; Ribeiro da Silva et al., 2015).

4 HYPOTHESES FOR TESTING THE DRIVERS OF NETWORK STRUCTURE

4.1 Null models

In nature, within-trophic level and interaction assembly processes take place simultaneously (Bascompte & Stouffer 2009; Albrecht *et al.* 2018). Therefore, under different combinations of assembly processes we expect the network structure to vary in distinct ways, as seen in our simulations. Our simulations demonstrate that in order to understand the mechanisms driving network structure, it is necessary to consider the effect of all assembly processes, both within-trophic levels and in interaction assembly. We illustrate the potential use of our framework by introducing a null model approach for testing the influence of different assembly processes on observed bipartite network structure (Figure 5). In general, null models are statistical approaches that quantify how the studied response deviates from random expectations by constructing a model that deliberately excludes the mechanism being tested (Gotelli 2001; Lessard *et al.* 2012). Null models have been widely used in community ecology to study patterns of biodiversity measures and species co-occurrences (Gotelli 2001) and to infer the effects of within-trophic level processes on community assembly (e.g., Cornwell, Schwilk, & Ackerly, 2006; Kraft & Ackerly, 2010). The use of null models in network ecology, however, has largely been limited to investigating variation in network metrics (e.g., Dormann, Fründ, Bluthgen, & Gruber, 2009; Vázquez & Aizen, 2003). Here, we propose stepwise null models that allow determining the effects of niche-based assembly processes on network structure. The stepwise approach consists of detecting niche-based assembly processes consecutively at resource trophic level, at consumer trophic level, and in pairwise interactions. These null models will solve many crucial issues in community ecology by uniting currently separated theoretical avenues of within and between trophic level processes. Our approach is novel and unique as it combines null models that are traditionally used separately to infer assembly processes within trophic levels and variation in network structure.

In the first step, the trait distributions of resource, consumer, and interaction assemblages are compared to distributions generated from stochastic sampling of the appropriate regional pool to detect the relative influence of neutral and niche-based assembly processes (Figure 5). Within trophic levels, trait convergence indicates environmental filtering (Keddy 1992; Díaz *et al.* 1998) and divergence indicates limiting similarity (Gause 1934; MacArthur & Levins 1967). For resource and consumer assemblages, the species pool is the set of all resource species in the region (Lessard *et al.* 2012). To detect the influence of niche-based processes in the interaction assemblage, the functional trait matching of the observed interactions is compared to that of null interactions, simulated with unweighted (presence-absence data) or abundance-weighted probabilities (Bartomeus *et al.* 2016). Trait matching is inferred if there is a greater trait correlation (Spitz *et al.* 2014) between consumer and resource traits for observed interactions than for null interactions.

In the second step, the effect of niche-based assembly processes on network structure are inferred by comparing the network index values of null and observed networks (Figure 5). The null networks are selected based on which components of the observed network (consumer, resource, or interaction) were found to be influenced by niche-based assembly processes in the first step (Figure 4). We define null networks as simulated networks with at least one component being generated from a simulated neutral process by stochastic sampling of the appropriate regional pool. For example, suppose that in the first step, limiting similarity is detected at the consumer level, with no niche-based processes detected at the resource or interaction levels. In this case, null networks are generated containing the observed resource assemblage, the observed (regional) interactions, and a null consumer assemblage composed of species randomly drawn from the regional species pool. We refer to this set of null network as $R_oC_nI_o$, where R = resource, C = consumer, I = interaction; subscript o = observed; subscript n = null. If the influence of niche-based processes was detected in multiple network components (e.g., at the consumer and interaction level), then null networks with all combinations of null and observed components are compared to the observed network ($R_oC_nI_o$, $R_oC_oI_n$, and $R_oC_nI_n$; Figure 4). Once the appropriate null networks are generated, the network metric values (modularity, nestedness, or any metric of interest) of the null networks are compared to the observed network by calculating a standardized effect size of the network index (N_{SES}) for each null network set:

$$N_{SES} = (N_{obs} - \text{mean}\ (N_{null})) \ /\ \text{standard deviation}\ (N_{null})$$

where, N is the network metric of interest. Depending on whether N_{SES} is significantly different from 0 (i.e., $|N_{SES}| > 1.96$), it is inferred that the niche-based assembly process in the null component(s) of the null network affect ($N_{SES} \neq 0$) or do not affect ($N_{SES} = 0$) the network structure as measured by the network metric of interest (Table 1).

In order to apply our null model approach, adequate data of local and regional species pools of both trophic levels with species' functional traits are needed. At minimum, mean trait values of each species in the regional species pool are required. Importantly, the included functional traits should be relevant for the interaction type in question. For example, flower nectar depth and proboscis length are focal traits for plant-pollinator networks (Sazatornil *et al.* 2016).

4.2 Topical questions to address with the framework

Community ecology, and network ecology in particular, would benefit from conceptual and methodological approaches that encompass currently separated theoretical avenues. To facilitate the usage of our framework and the presented null models, we list topical questions within network ecology to be addressed with the help of the framework (Table 2). With our framework, both general and more specific questions within network ecology can be answered. Using the stepwise null model approach allows identifying the exact processes shaping the studied network, whereas partitioning the variation in network metrics into different assembly processes within and between trophic levels is an efficient way of gaining more knowledge on the relative importance of the drivers behind the observed network.

5 LIMITATIONS

Despite the achievements of our framework, our approach poses some limitations. At a general level, difficulties with inferring assembly processes from local trait distributions reflect the difficulty of inferring process from pattern. From the perspective of coexistence theory, functional niche differences can drive either coexistence or exclusion depending on whether the niche differences cause frequency-dependent population growth (i.e., stabilizing niche differences) or cause fitness differences, respectively (Chesson 2000; Mayfield & Levine 2010). In case that each species limits itself more than it limits the abundances of other species within the focal trophic level, all species can coexist regardless of being ecologically similar and sharing between-trophic level interactions (McPeek & Siepielski 2019). Thus density-regulated, but competition-driven assemblages may exhibit trait patterns similar to assemblages under environmental filtering. Furthermore, functional niche differences are influenced by, and themselves influence, both environmental and competitive factors (Kraft *et al.* 2015). As a result, it is not possible to separate the effects of different assembly processes using patterns of trait convergence and divergence alone (HilleRisLambers *et al.* 2012; Cadotte & Tucker 2017). Several authors have offered partial solutions to this challenge, including: incorporating experimental or physiological data (Kraft *et al.* 2015), incorporating demographic models (HilleRisLambers *et al.* 2012), using ecologically-explicit definitions of species pools (Lessard *et al.* 2012), selecting traits with environmental correlations (Cadotte & Tucker 2017), and testing hypotheses that involve multiple dimensions of functional niche occupancy (Li *et al.* 2018).

From a more practical point of view, our framework does not account for temporal variation in the local community or the effects of dynamics taking place at larger spatial and temporal scales. Problematically, the studied assembly processes and network configurations are known to be scale-dependent (Weiher & Keddy 1995; Galiana *et al.* 2018). Our "snapshot" perspective inevitably leads to assuming that the local assemblages are stable (i.e., no change in composition over time, such as due to competitive exclusion) and ignoring the evolutionary and biogeographical dynamics that take place within longer timespans. The advantage of this simplification is that the observed networks can be tested against the null models without requirement of extensive temporal data. However, data on pairwise interactions, regional species occurrences and functional traits are still needed in order to use our null model approach. In terms of interaction data, few trait dimensions are enough to predict majority of the occurrences of interactions between species pairs and to reconstruct the network structure (Eklöf *et al.* 2013). Nevertheless, such high quality data on various aspects of biodiversity tend to be scarce.

6 CONCLUSIONS AND FUTURE DIRECTIONS

In this paper, we have presented a novel conceptual and analytical framework for studying bipartite networks. We have shown the ecological relevance of the concepts with simulated assemblages and given guidance for applying the framework to observed networks. Our results indicate that the structure of bipartite networks tends to be governed by symmetry of niche-based assembly processes within trophic levels together with the strength of functional trait matching constraint between species pairs. Our approach also allows inferring bottom-up and top-down effects on network structure, thus contributing to the discussion over their relative importance. Finally, we outline potential questions to be addressed with the framework in order to better understand the roles of ecosystem stability, bottom-up versus top-down effects, trait matching constraints, and interaction type in shaping interaction networks.

Our framework provides conceptual advantages for understanding assembly of bipartite networks. Firstly and most importantly, we piece together within-trophic level and interaction assembly processes and thus help unifying the otherwise disorganized theory on ecological communities and networks. Secondly, our framework aligns with the current niche-based community assembly paradigm while expanding the idea of species' niches to their interactions (e.g., Albrecht et al., 2018). Here, species' niches are defined in terms of their interactions (Figure B1a), as well as than in terms of their responses to abiotic environment (Grinnellian niche; Grinnell, 1917). Thirdly, we account for species pool effects by comparing the local assemblages to the regional species pool in terms of community composition, trait distributions and network structure. To allow the incorporation of species pool -based null models into community ecology research, occurrences of species outside of the local sampling site need to be recorded more rigorously. Therefore, we encourage further data collection at this front to fill the knowledge gaps.

Our framework can be applied to estimate and predict spatial variation in network properties, such as modularity and nestedness, by comparison to appropriate null models. Network properties can indicate conservation needs of local networks and are hence an important tool for biodiversity conservation and management (Tylianakis *et al.* 2010). As we present a simple way for evaluating the relative contributions of different assembly processes on network structure, our approach could potentially be used to predict network structure patterns from assembly processes at any given location with available species' occurrence and trait data. These local patterns could thereafter be generalized across larger spatial scales. For instance, estimates of global variation in other biodiversity metrics, such as species richness, have proven useful at informing decision makers (Fleishman *et al.* 2006), and similar estimates on network structure would extend the conservation focus to species interactions. Knowing the exact processes shaping the networks can aid prioritization of conservation efforts to target the most crucial processes maintaining the networks.

To increase the applicability, our simulation approach can be extended to cover more scenarios, for example by assuming different assembly processes at each trophic level. Here, we only consider obligate interactions, but expanding to facultative ones is equally possible. In addition, it is possible to vary the regional and local species pool sizes or test directional and disruptive filtering scenarios instead of the stabilizing environmental filtering scenario. Network structure can also be quantified with numerous other metrics beyond modularity and nestedness. Indeed, to better understand the relationship of different metrics used to describe bipartite networks, we recommend comparing the results produced by network level, trophic level and species level metrics (Box 1; Delmas et al., 2019; Dormann et al., 2009). To add to the realism of our approach, we strongly encourage future work to account for the effect of interspecific interactions on species' traits, thereby allowing inclusion of effects of evolutionary dynamics on network structure, rather than just inferring the realized patterns of interactions in a stable community. Naturally, this requires computationally more demanding simulations (Munoz *et al.* 2018), but with rapidly increasing computational power this is unlikely to be a major limitation in the future. Finally, we recommend future research to expand from bipartite to multilevel networks, for example by considering two trophic levels at a time and comparing the results of all bipartite networks in a multilevel network.

To truly understand species interaction networks, we need to relate community assembly to network structure, something which we have accomplished here. As ecosystem functions are under extreme anthropogenic pressures globally, more mechanistic knowledge of their underlying components is urgently needed. We hope that our framework, which connects assembly processes to network structure, will be a helpful tool in the effort to predict ecosystem functioning from biodiversity data.

Acknowledgements

We thank Vidar Grøtan for his helpful comments on the manuscript. This work was partly supported by the Research Council of Norway through its Centres of Excellence Funding Scheme (223257) to EM. ST is supported by a FRQNT postdoctoral research scholarship (B3X). GM is supported by a Graduate Fellowship from Concordia University.

Data availability

Code used for simulations available at: https://github.com/lessardlab/niche2net

References

Ackerly, D.D. & Cornwell, W.K. (2007). A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. *Ecol. Lett.*, 10, 135–145.

Albrecht, J., Classen, A., Vollstädt, M.G.R., Mayr, A., Mollel, N.P., Schellenberger Costa, D., *et al.* (2018). Plant and animal functional diversity drive mutualistic network assembly across an elevational gradient. *Nat. Commun.*, 9.

Alcántara, J.M., Pulgar, M., Trøjelsgaard, K., Garrido, J.L. & Rey, P.J. (2018). Stochastic and deterministic effects on interactions between canopy and recruiting species in forest communities. *Funct. Ecol.*, 32, 2264–2274.

Almeida-Neto, M., Campassi, F., Galetti, M., Jordano, P. & Oliveira-Filho, A. (2008). Vertebrate dispersal syndromes along the Atlantic forest: broad-scale patterns and macroecological correlates. *Glob. Ecol. Biogeogr.*, 17, 503–513.

Barber, M.J. (2007). Modularity and community detection in bipartite networks. *Phys. Rev. E*, 76, 066102.

Barbier, M., Arnoldi, J.F., Bunin, G. & Loreau, M. (2018). Generic assembly patterns in complex ecological communities. *Proc. Natl. Acad. Sci. U. S. A.*, 115, 2156–2161.

Bartomeus, I., Gravel, D., Tylianakis, J.M., Aizen, M.A., Dickie, I.A. & Bernard-Verdier, M. (2016). A common framework for identifying linkage rules across different types of interactions. *Funct. Ecol.*, 30, 1894–1903.

Bascompte, J. & Stouffer, D.B. (2009). The assembly and disassembly of ecological networks. *Philos. Trans. R. Soc. B*, 364, 1781–1787.

Bender, I.M.A., Kissling, W.D., Blendinger, P.G., Böhning-Gaese, K., Hensen, I., Kühn, I., *et al.* (2018). Morphological trait matching shapes plant-frugivore networks across the Andes. *Ecography (Cop.).*, 41, 1910–1919.

Blonder, B., Lamanna, C., Violle, C. & Enquist, B.J. (2014). The n-dimensional hypervolume. *Glob. Ecol. Biogeogr.*, 23, 595–609.

Cadotte, M.W. & Tucker, C.M. (2017). Should environmental filtering be abandoned? *Trends Ecol. Evol.*, 32, 429–437.

Cavender-Bares, J., Kozak, K.H., Fine, P.V.A. & Kembel, S.W. (2009). The merging of community ecology and phylogenetic biology. *Ecol. Lett.*, 12, 693–715.

Chacoff, N.P., Resasco, J. & Vázquez, D.P. (2018). Interaction frequency, network position, and the temporal persistence of interactions in a plant-pollinator network. *Ecology*, 99, 21–28.

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.*, 31, 343–66.

Cohen, J.E., Pimm, S.L., Yodzis, P. & Saldaña, J. (1993). Body sizes of animal predators and animal prey in food webs. *J. Anim. Ecol.*, 62, 67–78.

Cornwell, W.K., Schwilk, D.W. & Ackerly, D.D. (2006). A trait-based test for habitat filtering: convex hull volume. *Ecology*, 87, 1465–1471.

Danieli-Silva, A., de Souza, J.M.T., Donatti, A.J., Campos, R.P., Vicente-Silva, J., Freitas, L., *et al.* (2012). Do pollination syndromes cause modularity and predict interactions in a pollination network in tropical high-altitude grasslands? *Oikos*, 121, 35–43.

Dehling, D.M., Jordano, P., Schaefer, H.M., Böhning-Gaese, K. & Schleuning, M. (2016). Morphology predicts species' functional roles and their degree of specialization in plant–frugivore interactions. *Proc. R. Soc. B Biol. Sci.*, 283, 20152444.

Dehling, D.M., Töpfer, T., Schaefer, H.M., Jordano, P., Böhning-Gaese, K. & Schleuning, M. (2014). Functional relationships beyond species richness patterns: trait matching in plant-bird mutualisms across scales. *Glob. Ecol. Biogeogr.*, 23, 1085–1093.

Delmas, E., Besson, M., Brice, M.H., Burkle, L.A., Dalla Riva, G. V., Fortin, M.J., *et al.* (2019). Analysing ecological networks of species interactions. *Biol. Rev.*, 94, 16–36.

Devoto, M., Bailey, S., Craze, P. & Memmott, J. (2012). Understanding and planning ecological restoration of plant-pollinator networks. *Ecol. Lett.*, 15, 319–328.

Diamond, J.M. (1975). Assembly of species communities. In: *Ecology and evolution of communities* (eds. Cody, M.L. & Diamond, J.M.). Harvard University Press, Cambridge, pp. 342–444.

Díaz, S., Cabido, M. & Casanoves, F. (1998). Plant functional traits and environmental filters at a regional scale. *J. Veg. Sci.*, 9, 113–122.

Dormann, C.F., Fründ, J., Bluthgen, N. & Gruber, B. (2009). Indices, graphs and null models: analyzing bipartite ecological networks. *Open Ecol. J.*, 2, 7–24.

Dunne, J.A., Williams, R.J. & Martinez, N.D. (2002). Food-web structure and network theory: the role of connectance and size. *Proc. Natl. Acad. Sci.*, 99, 12–17.

Eklöf, A., Jacob, U., Kopp, J., Bosch, J., Castro-Urgal, R., Chacoff, N.P., *et al.* (2013). The dimensionality of ecological networks. *Ecol. Lett.*, 16, 577–583.

Emer, C., Galetti, M., Pizo, M.A., Guimarães, P.R., Moraes, S., Piratelli, A., *et al.* (2018). Seed-dispersal interactions in fragmented landscapes - a metanetwork approach. *Ecol. Lett.*, 21, 484–493.

Fleishman, E., Noss, R.F. & Noon, B.R. (2006). Utility and limitations of species richness metrics for conservation planning. *Ecol. Indic.*, 6, 543–553.

Fortuna, M.A., Stouffer, D.B., Olesen, J.M., Jordano, P., Mouillot, D., Krasnov, B.R., *et al.* (2010). Nestedness versus modularity in ecological networks: two sides of the same coin? *J. Anim. Ecol.*, 79, 811–817.

Fournier, B., Mouly, A. & Gillet, F. (2016). Multiple assembly rules drive the co-occurrence of orthopteran and plant species in grasslands: combining network, functional and phylogenetic approaches. *Front. Plant Sci.*, 7, 1–12.

Fournier, B., Mouquet, N., Leibold, M.A. & Gravel, D. (2017). An integrative framework of coexistence mechanisms in competitive metacommunities. *Ecography (Cop.)*, 40, 630–641.

Fukami, T., Bezemer, T.M., Mortimer, S.R. & Van Der Putten, W.H. (2005). Species divergence and trait convergence in experimental plant community assembly. *Ecol. Lett.*, 8, 1283–1290.

Funk, J.L., Larson, J.E., Ames, G.M., Butterfield, B.J., Cavender-Bares, J., Firn, J., *et al.* (2017). Revisiting the Holy Grail: using plant functional traits to understand ecological processes. *Biol. Rev.*, 92, 1156–1173.

Galiana, N., Hawkins, B.A. & Montoya, J.M. (2019). The geographical variation of network structure is scale dependent: understanding the biotic specialization of host-parasitoid networks. *Ecography (Cop.)*, 1–13.

Galiana, N., Lurgi, M., Claramunt-López, B., Fortin, M.J., Leroux, S., Cazelles, K., *et al.* (2018). The spatial scaling of species interaction networks. *Nat. Ecol. Evol.*, 2, 782–790.

Gause, G.F. (1934). Experimental analysis of Vito Volterra's mathematical theory of the struggle for existence. *Science (80-.).*, 79, 16–17.

Godoy, O., Bartomeus, I., Rohr, R.P. & Saavedra, S. (2018). Towards the integration of niche and network theories. *Trends Ecol. Evol.*, 33, 287–300.

Gotelli, N.J. (2001). Research frontiers in null model analysis. *Glob. Ecol. Biogeogr.*, 10, 337–343.

Gravel, D., Albouy, C. & Thuiller, W. (2016). The meaning of functional trait composition of food webs for ecosystem functioning. *Philos. Trans. R. Soc. B Biol. Sci.*, 371, 20150268.

Gravel, D., Baiser, B., Dune, J.A., Kopelke, J.-P., Martinez, N.D., Nyman, T., *et al.* (2019). Bringing Elton and Grinnell together: a quantitative framework to represent the biogeography of ecological interaction networks. *Ecography (Cop.)*, 42, 401–415.

Gravel, D., Canham, C.D., Beaudet, M. & Messier, C. (2006). Reconciling niche and neutrality: the continuum hypothesis. *Ecol. Lett.*, 9, 399–409.

Grinnell, J. (1917). The niche-relationships of the California Thrasher. *Auk*, 34, 427–433.

Hairston, N.G., Smith, F.E. & Slobodkin, L.B. (1960). Community structure, population control, and competition. *Am. Nat.*, 94, 421–425.

Henle, K., Davies, K.F., Kleyer, M., Margules, C.R. & Settele, J. (2004). Predictors of species sensitivity to fragmentation. *Biodivers. Conserv.*, 13, 207–251.

Herre, E.A. (1996). An overview of studies on a community of Panamanian figs. *J. Biogeogr.*, 23, 593–607.

HilleRisLambers, J., Adler, P.B., Harpole, W.S., Levine, J.M. & Mayfield, M.M. (2012). Rethinking community assembly through the lens of coexistence theory. *Annu. Rev. Ecol. Evol. Syst.*, 43, 227–248.

Hortal, J., de Bello, F., Diniz-filho, J.A.F., Lewinsohn, T.M., Lobo, J.M. & Ladle, R.J. (2015). Seven shortfalls that beset large-scale knowledge of biodiversity. *Annu. Rev. Ecol. Evol. Syst.*, 46, 523–549.

Hubbell, S.P. (2001). *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton.

IPBES. (2019). *Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. IPBES Secretariat, Bonn.

Junker, R.R., Blüthgen, N., Brehm, T., Binkenstein, J., Paulus, J., Schaefer, H.M., *et al.* (2013). Specialization on traits as basis for the niche-breadth of flower visitors and as structuring mechanism of ecological networks. *Funct. Ecol.*, 27, 329–341.

Keddy, P.A. (1992). Assembly and response rules: two goals for predictive community ecology. *J. Veg. Sci.*, 3, 157–164.

Kraft, N.J.B. & Ackerly, D.D. (2010). Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. *Ecol. Monogr.*, 80, 401–422.

Kraft, N.J.B., Adler, P.B., Godoy, O., James, E.C., Fuller, S. & Levine, J.M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Funct. Ecol.*, 29, 592–599.

Kraft, N.J.B., Valencia, R. & Ackerly, D.D. (2008). Functional traits and niche-based tree community assembly in an Amazonian forest. *Science (80-.).*, 322, 580–582.

Krishna, A., Guimarães, P.R.J., Jordano, P. & Bascompte, J. (2008). A neutral-niche theory of nestedness in mutualistic networks. *Oikos*, 117, 1609–1618.

Laigle, I., Aubin, I., Digel, C., Brose, U., Boulangeat, I. & Gravel, D. (2018). Species traits as drivers of food web structure. *Oikos*, 127, 316–326.

Lavorel, S. & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct. Ecol.*, 16, 545–556.

Lessard, J.-P., Belmaker, J., Myers, J.A., Chase, J.M. & Rahbek, C. (2012). Inferring local ecological processes amid species pool influences. *Trends Ecol. Evol.*, 27, 600–607.

Lewinsohn, T.M., Prado, P.I., Jordano, P., Bascompte, J. & Olesen, J.M. (2006). Structure in plant-animal interaction assemblages. *Oikos*, 113, 174–184.

Li, Y., Shipley, B., Price, J.N., Dantas, V. de L., Tamme, R., Westoby, M., *et al.* (2018). Habitat filtering determines the functional niche occupancy of plant communities worldwide. *J. Ecol.*, 106, 1001–1009.

MacArthur, R. & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.*, 101, 377–385.

Mayfield, M.M. & Levine, J.M. (2010). Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecol. Lett.*, 13, 1085–1093.

Maynard, D.S., Serván, C.A. & Allesina, S. (2018). Network spandrels reflect ecological assembly. *Ecol. Lett.*, 21, 324–334.

McPeek, M.A. & Siepielski, A.M. (2019). Disentangling ecologically equivalent from neutral species: the mechanisms of population regulation matter. *J. Anim. Ecol.*

Morales-Castilla, I., Matias, M.G., Gravel, D. & Araújo, M.B. (2015). Inferring biotic interactions from proxies. *Trends Ecol. Evol.*, 30, 347–356.

Munoz, F., Grenié, M., Denelle, P., Taudière, A., Laroche, F., Tucker, C., *et al.* (2018). ecolottery: simulating and assessing community assembly with environmental filtering and neutral dynamics in R. *Methods Ecol. Evol.*, 9, 693–703.

Muñoz, G., Trøjelsgaard, K. & Kissling, W.D. (2019). A synthesis of animal-mediated seed dispersal of palms reveals distinct biogeographical differences in species interactions. *J. Biogeogr.*, 46, 466–484.

Nuismer, S.L., Jordano, P. & Bascompte, J. (2013). Coevolution and the architecture of mutualistic networks. *Evolution (N. Y).*, 67, 338–354.

Okuyama, T. & Holland, J.N. (2008). Network structural properties mediate the stability of mutualistic communities. *Ecol. Lett.*, 11, 208–216.

Olesen, J.M., Bascompte, J., Dupont, Y.L. & Jordano, P. (2007). The modularity of pollination networks. *Proc. Natl. Acad. Sci.*, 104, 19891–19896.

Pace, M.L., Cole, J.J., Carpenter, S.R. & Kitchell, J.F. (1999). Trophic cascades revealed in diverse ecosystems. *Trends Ecol. Evol.*, 14, 483–488.

Poisot, T., Stouffer, D.B. & Gravel, D. (2015). Beyond species: why ecological interaction networks vary through space and time. *Oikos*, 124, 243–251.

Ponisio, L.C., Valdovinos, F.S., Allhoff, K.T., Gaiarsa, M.P., Barner, A., Guimarães, P.R.J., *et al.* (2019). A network perspective for community assembly. *Front. Ecol. Evol.*, 7.

Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1997). From tropics to tundra: global convergence in plant functioning. *Proc. Natl. Acad. Sci.*, 94, 13730–13734.

Ribeiro da Silva, F., Montoya, D., Furtado, R., Memmott, J., Pizo, M.A. & Rodrigues, R.R. (2015). The restoration of tropical seed dispersal networks. *Restor. Ecol.*, 23, 852–860.

Ripple, W.J. & Beschta, R.L. (2012). Trophic cascades in Yellowstone: the first 15 years after wolf reintroduction. *Biol. Conserv.*, 145, 205–213.

Rosenfeld, J.S. (2002). Functional redundancy in ecology and conservation. *Oikos*, 98, 156–162.

Sazatornil, F.D., Moré, M., Benitez-Vieyra, S., Cocucci, A.A., Kitching, I.J., Schlumpberger, B.O., *et al.* (2016). Beyond neutral and forbidden links: morphological matches and the assembly of mutualistic hawkmoth–plant networks. *J. Anim. Ecol.*, 85, 1586–1594.

Scherber, C., Eisenhauer, N., Weisser, W.W., Schmid, B., Voigt, W., Fischer, M., *et al.* (2010). Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature*, 468, 553–556.

Schleuning, M., Fründ, J. & García, D. (2015). Predicting ecosystem functions from biodiversity and mutualistic networks: an extension of trait-based concepts to plant-animal interactions. *Ecography (Cop.).*, 38, 380–392.

Simmons, B.I., Vizentin-Bugoni, J., Maruyama, P.K., Cotton, P.A., Marin-Gomez, O.H., Lara, C., *et al.* (2019). Abundance drives broad patterns of generalisation in plant-hummingbird pollination networks. *Oikos*.

Sonne, J., Zanata, T.B., Martín González, A.M., Cumbicus Torres, N.L., Fjeldså, J., Colwell, R.K., *et al.* (2019). The distributions of morphologically specialized hummingbirds coincide with floral trait matching across an Andean elevational gradient. *Biotropica*, 51, 205–218.

Spitz, J., Ridoux, V. & Brind'Amour, A. (2014). Let's go beyond taxonomy in diet description: testing a trait-based approach to prey-predator relationships. *J. Anim. Ecol.*, 83, 1137–1148.

Stone, L. & Roberts, A. (1992). Competitive exclusion, or species aggregation? An aid in deciding. *Oecologia*, 91, 419–424.

Stubbs, W.J. & Wilson, J.B. (2004). Evidence for limiting similarity in a sand dune community. *J. Ecol.*, 92, 557–567.

Suding, K.N. & Goldstein, L.J. (2008). Testing the Holy Grail framework: using functional traits to predict ecosystem change. *New Phytol.*, 180, 559–562.

Thébault, E. & Fontaine, C. (2010). Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science (80-.).*, 329, 853–856.

Toju, H., Guimarães, P.R., Olesen, J.M. & Thompson, J.N. (2015). Below-ground plant-fungus network topology is not congruent with above-ground plant-animal network topology. *Sci. Adv.*, 1.

Trøjelsgaard, K., Jordano, P., Carstensen, D.W. & Olesen, J.M. (2015). Geographical variation in mutualistic networks: similarity, turnover and partner fidelity. *Proc. R. Soc. B*, 282.

Tylianakis, J.M., Laliberté, E., Nielsen, A. & Bascompte, J. (2010). Conservation of species interaction networks. *Biol. Conserv.*, 143, 2270–2279.

Tylianakis, J.M. & Morris, R.J. (2017). Ecological networks across environmental gradients. *Annu. Rev. Ecol. Evol. Syst.*, 48, 25–48.

van der Valk, A.G. (1981). Succession in wetlands: A Gleasonian approach. *Ecology*, 62, 688–696.

Valverde, S., Piñero, J., Corominas-Murtra, B., Montoya, J., Joppa, L. & Solé, R. (2018). The architecture of mutualistic networks as an evolutionary spandrel. *Nat. Ecol. Evol.*, 2, 94–99.

Vázquez, D.P. & Aizen, M.A. (2003). Null model analyses of specialization. *Ecology*, 84, 2493–2501.

Vázquez, D.P., Melián, C.J., Williams, N.M., Blüthgen, N., Krasnov, B.R. & Poulin, R. (2007). Species abundance and asymmetric interaction strength in ecological networks. *Oikos*, 116, 1120–1127.

Violle, C., Reich, P.B., Pacala, S.W., Enquist, B.J. & Kattge, J. (2014). The emergence and promise of functional biogeography. *Proc. Natl. Acad. Sci.*, 111, 13690–13696.

Weiher, E. & Keddy, P.A. (1995). Assembly rules, null models, and trait dispersion: new questions from old patterns. *Oikos*, 74, 159–164.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., *et al.* (2004). The worldwide leaf economics spectrum. *Nature*, 428, 821–827.

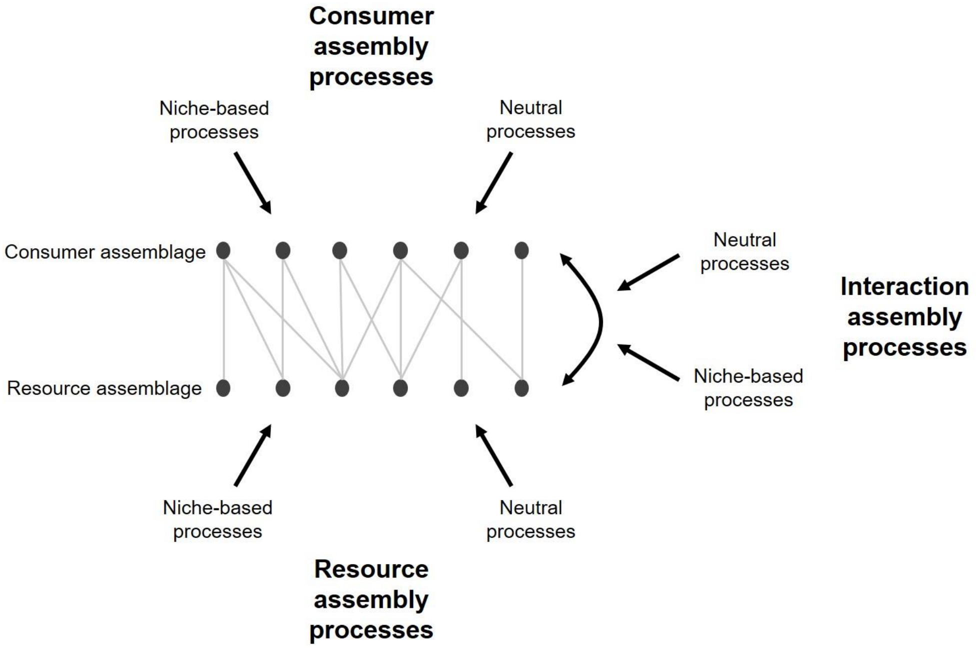


Figure 1. Processes driving bipartite network structure. Flowchart illustrates the within- and between-trophic level assembly processes that affect the focal interaction network. The upper row of grey circles represent consumer species, the lower row represents resource species, and the links represent consumer-resource interactions. Assembly processes at the resource and consumer trophic levels independently influence the species and trait compositions at the respective trophic level. Interaction assembly processes determine the occurrences of interactions among species pairs present in the assemblages. These assembly processes can be niche-based or neutral, their difference being the influence of species niches (inferred from functional trait distributions) on within-trophic level and interaction assembly. Combinations of different assembly mechanisms at different trophic levels, together with interaction assembly processes, lead to variation in the emergent structures of bipartite networks.

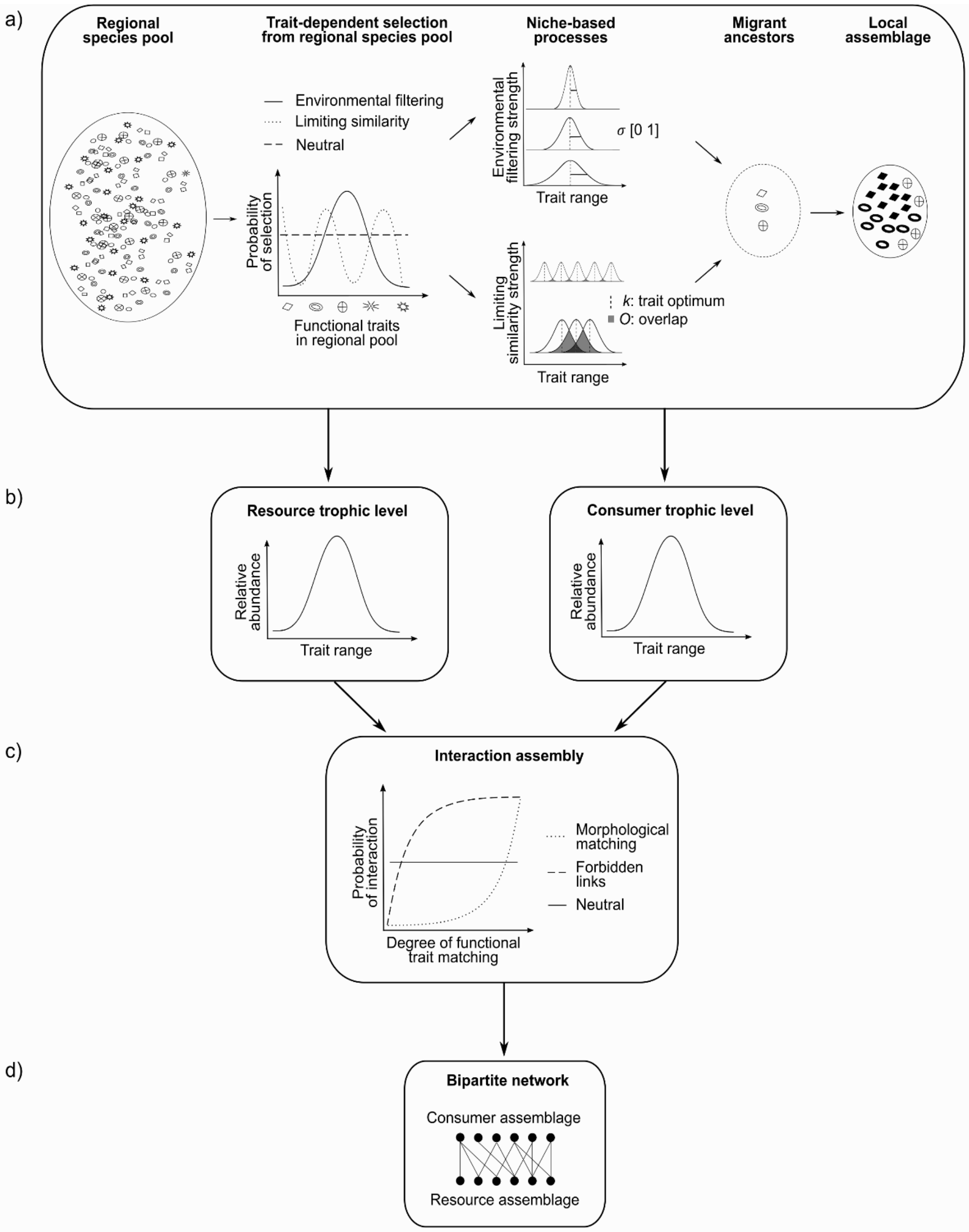


Figure 2. Illustrated workflow for simulation of within-trophic level and interaction assembly processes forming bipartite networks. Panels a) and b) illustrate the sampling of species from regional species pools to local assemblages of resource and consumer species separately. Species were sampled from the regional pool based on different trait selection

probability functions that mimic different intensities of environmental filtering and limiting similarity, as well as neutral (stochastic) processes. The probability functions were defined by different parameters depending on the assembly process in question. For simplicity, we assumed the same within-trophic level assembly process for both trophic levels. That is, species' probability to be selected from the regional pool depends on its trait value. Panel c) illustrates the simulation of pairwise interactions between the species in resource and consumer assemblages. After the resource and consumer assemblages were defined, the assembly of pairwise interactions between resource and consumer species was simulated by using three distinct linkage rules. These linkage rules either relate to species' traits, such that the probability of a pairwise interaction depends on the degree of functional trait matching between a pair of species (forbidden links and morphological matching) or on the species' relative abundances (neutral). These steps together lead to particular bipartite networks (panel d). For more details on simulation methods, see Appendix S1.

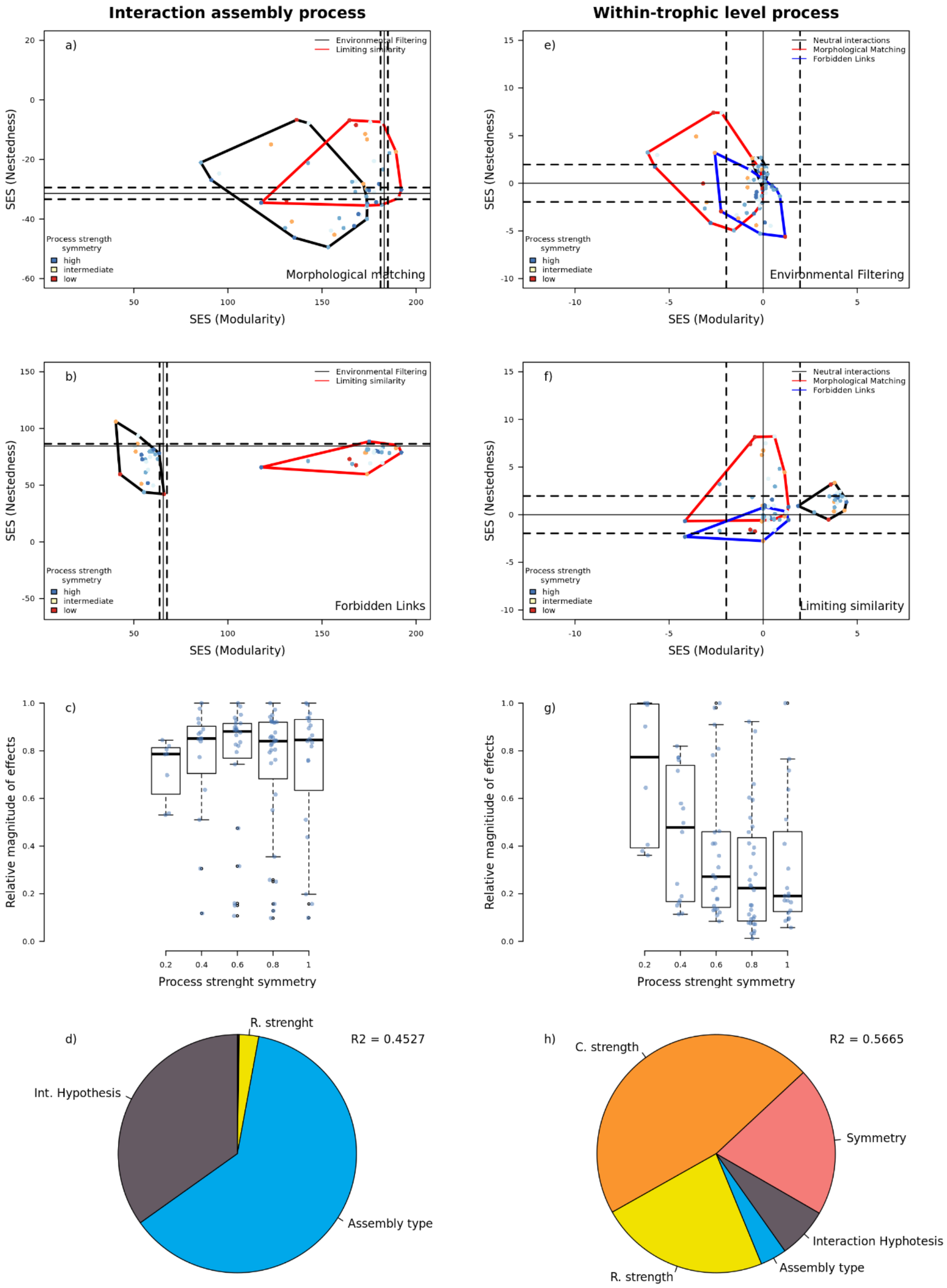

Interaction assembly process
Within-trophic level process
a)
b)
c)
d)
e)
f)
g)
h)
SES (Nestedness)
SES (Modularity)
Environmental Filtering
Limiting similarity
Neutral interactions
Morphological Matching
Forbidden Links
Process strength symmetry
high
intermediate
low
Morphological matching
Forbidden Links
Environmental Filtering
Limiting similarity
Relative magnitude of effects
Process strenght symmetry
0.2
0.4
0.6
0.8
1
R. strenght
R2 = 0.4527
Int. Hypothesis
Assembly type
C. strength
R2 = 0.5665
Symmetry
Interaction Hyphotesis
Assembly type
R. strength

Figure 3. Effects of niche-based assembly processes on modularity (Q Z-score) and nestedness (NODF Z-score) of simulated networks. Panels in the left column represent effects on network structure induced by interaction assembly processes (i.e., within-trophic level assembly effects are controlled for), whereas panels in the right column represent effects on network structure induced by within-trophic level assembly processes (i.e, interaction assembly effects are controlled for). Panels a) and b) illustrate the interaction assembly effects of morphological matching and forbidden links on the modular (x-axis) and nested (y-axis) structure of simulated networks, respectively. Panels e) and f) illustrate the within-trophic level assembly effects of environmental filtering and limiting similarity on the modular (x-axis) and nested (y-axis) structure of simulated networks, respectively. In panels a), b), e) and f), coordinates of points represent the magnitude of difference in network structure between niche-based and neutral network structures, measured as standardized effect sizes (SES). The coordinate points represent different assembly process scenarios (listed in Table S1a-e), where network metric values of modularity (Q Z-score) and nestedness (NODF Z-score) are averaged over 10 replicates of simulated networks. The magnitude of niche-based assembly effects is represented as vectors of Euclidean distances between the niche-based effects and the neutral effects of within-trophic assembly scenarios (neutral effect values of the within-trophic assembly are marked with horizontal and vertical solid lines, stippled lines mark confidence intervals of ±1.96 SES). The color gradient of coordinate points represents the process strength symmetry between trophic levels (dark red = highly asymmetric, dark blue = highly symmetric). Convex hulls illustrate grouping based on within-trophic assembly processes (panels a and b) interaction assembly processes (panels e and f). The effect of process strength symmetry (x-axis) on the relative differences in network structure between niche-based and neutral scenarios (y-axis) are illustrated with boxplots for effects attributed to interaction assembly processes (panel c) and within-trophic level assembly processes (panel g). The blue points are scaled to the maximum effect size observed for within-trophic level (panel c) and interaction (panel g) assembly processes. Panels d) and h) illustrate the percentage of the total explained variance (R^2) of the relative niche-based effects in network structure, after controlling for interaction assembly process (panel d) and within-trophic level assembly process (panel h), attributed to each of the five simulation parameters.

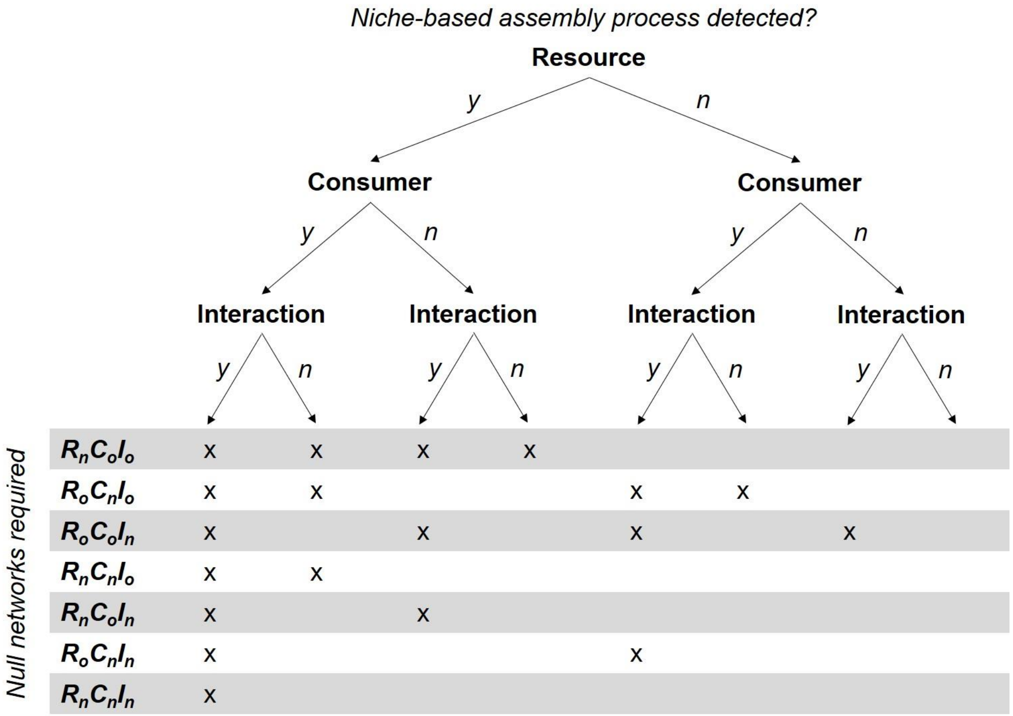


Figure 4. Decision tree to select appropriate null networks. The influence of niche-based assembly processes at the resource, consumer, and interaction level are separately tested for by comparing observed trait distributions to null trait distributions. The results of these tests determine the decision tree path (*y* = yes, the trait distribution is significantly different from null expectations, consistent with the effects of a niche-based process; *n* = no, the trait distribution is not significantly different from null expectations, consistent with the effects of a neutral process). The end point of the decision tree indicates the null networks to be tested (*R* = resource; *C* = consumer; *I* = interaction). The observed components of the null networks (subscript *o* = observed) remain as observed, while the null components of the null networks (subscript *n* = null) are generated from simulated neutral processes. The network metrics (e.g., modularity) of the null networks are compared to the observed network, generating standardized effect sizes (N_{SES}). The N_{SES} are interpreted to evaluate the effect of consumer, resource, and interaction assembly processes on network structure (Table 1).

Table 1. Ecological interpretations of standardized effect sizes (N_{SES}) of network metrics. The N_{SES} are calculated as the difference between the network metric value (e.g., modularity) of the observed network and the null networks, divided by the standard deviation of the null networks. For the null networks, R = resource, C = consumer, and I = interaction. The observed components of the null networks (subscript o = observed) remain as observed, while the null components of the null networks (subscript n = null) are generated from simulated neutral processes. Interpretation of the N_{SES} depends on whether it is significantly different from 0 ($p < 0.05$). If N_{SES} differs significantly from 0, its directionality determines the direction of the effect of niche-based assembly process on the network index.

Null network	**Interpretation**	
	$N_{SES} = 0$	**$N_{SES} \neq 0$**
$R_nC_oI_o$	No effect of niche-based resource assembly alone on network metric.	Niche-based resource assembly process affects network metric.
$R_oC_nI_o$	No effect of niche-based consumer assembly alone on network metric.	Niche-based consumer assembly process affects network metric.
$R_oC_oI_n$	No effect of niche-based interaction assembly alone on network metric.	Niche-based interaction assembly process affects network metric.
$R_nC_nI_o$	No effect on network metric when effects of niche-based resource and consumer assembly are combined. An antagonistic effect must be present if $N_{SES} \neq 0$ for $R_nC_oI_o$ and/or $R_oC_nI_o$.	Niche-based resource and consumer assembly processes act separately and/or synergistically to affect network metric. A synergistic effect must be present if $N_{SES} = 0$ for both $R_nC_oI_o$ and $R_oC_nI_o$.
$R_nC_oI_n$	No effect on network metric when effects of niche-based resource and interaction assembly are combined. An antagonistic effect must be present if $N_{SES} \neq 0$ for $R_nC_oI_o$ and/or $R_oC_oI_n$.	Niche-based resource and interaction assembly processes act separately and/or synergistically to affect network metric. A synergistic effect must be present if $N_{SES} = 0$ for both $R_nC_oI_o$ and $R_oC_oI_n$.
$R_oC_nI_n$	No effect on network metric when effects of niche-based consumer and interaction assembly are combined. An antagonistic effect must be present if $N_{SES} \neq 0$ for $R_oC_nI_o$ and/or $R_oC_oI_n$.	Niche-based consumer and interaction assembly processes act separately and/or synergistically to affect network metric. A synergistic effect must be present if $N_{SES} = 0$ for both $R_oC_nI_o$ and $R_oC_oI_n$.
$R_nC_nI_n$	No effect on network metric when effects of niche-based resource, consumer, and interaction assembly are combined. A three-way antagonistic effect must be present if $N_{SES} \neq 0$ for $R_nC_nI_o$, $R_nC_oI_n$, and/or $R_oC_nI_n$.	Niche-based resource, consumer, and interaction assembly processes act separately and/or synergistically to affect network metric. A three-way synergistic effect must be present if $N_{SES} = 0$ for $R_nC_nI_o$, $R_nC_oI_n$, and $R_oC_nI_n$.

Table 2. Topical questions in network ecology, an outline on how to address them with our framework, and examples of specific study questions for future research.

General question	Addressing the question	Example of a specific study question
How is variation in network structure attributed to different assembly processes?	Using the null model approach to determine the underlying assembly processes and comparing network metric values between differently assembled networks, partitioning variation among niche-based processes	How does an elevational gradient in the intensity of environmental filtering affect the connectance of alpine plant-mycorrhizae networks?
Is network structure regulated bottom-up, top-down, both, or neither?	Using the null model approach for evaluating the strength of niche-based within-trophic level and interaction assembly processes, studying the properties of interaction niches (Box 2), partitioning variation among niche-based processes	How strong is the assembly process at plant trophic level compared to that at pollinator trophic level?
What is the role of trait matching in shaping the structure of a network?	Using the null model approach for evaluating the contribution of niche-based processes to interaction assembly, comparing network metric values of networks under different trait matching constraints	How does size-based matching of consumer-resource interactions affect food web nestedness?
Which combinations of assembly processes produce most stable networks?	Using the null model approach to determine the underlying assembly processes and comparing network metric values between differently assembled networks to find those with highest values of connectance, nestedness and modularity	How does the intensity of environment filtering of plants affect plant-pollinator network stability?
Are antagonistic and mutualistic interactions assembled differently?	Using the null model approach to determine the underlying assembly processes and comparing network metric values between differently assembled networks, partitioning variation among niche-based processes	Which within-trophic level and interaction assembly processes affect food webs and pollination networks?

Glossary

Assembly process = Assembly rules are processes that explain the local (co-)occurrence of species in a community.

Bipartite network = Network where nodes are divided into two sets and only interactions between sets are allowed; mutualistic or antagonistic.

Bottom-up effect = Processes at lower trophic levels determine dynamics at higher trophic levels.

Environmental filtering = A process whereby environmental conditions determine the local assemblage composition by selecting those species capable of survival and persistence under those conditions.

Limiting similarity = A process whereby interspecific competition determines the local assemblage composition by imposing a maximum level of niche overlap between two species allowing continued co-occurrence.

Neutral process = Ecological processes that are independent of species' niches. These processes can be stochastic or they can be dependent on variables unrelated to species' niches.

Niche-based process = Ecological processes that are dependent on species' niches.

Top-down effect = Processes at higher trophic levels determine dynamics at lower trophic levels.

Trait matching = Network interaction assembly processes that depend on the trait values of both potential partners in an interaction.

Box 1. Different metrics to quantify network structure.

The realized configuration of pairwise interactions in a local assemblage, i.e. the structure of an interaction network, can be defined and measured in various ways. Different network metrics depict distinct characteristics of network structure, but lack of consistency between studies and clarity as to when each metric is most appropriate has lead to coexistence of complementary yet rather confusing set of metrics. In particular, it is not clear which of the many available metrics have actual ecological meaning (Delmas *et al.* 2019). In our framework, we consider the full network scale, but wish to highlight the multiple scales that structural metrics can be calculated at: the full network, the trophic level, and the species scale (Table B1). At the full network scale, properties of a network are measured for all species and all interaction links in the network. At the trophic level scale, network properties are measured either as an average or as a total for the species within a trophic level. Finally, at the species (node) scale, each species is assigned a value representing its interactions within the full realized network. In order to gain a comprehensive understanding of the structure of an observed network, measuring properties at different scales is necessary. Benefits of calculating different structural metrics include having additional tools to describe communities and ecosystem functioning as well as to predict structure of communities through prediction of interactions (Delmas *et al.* 2019). Our framework allows using any of the example metrics as response variables when inferring network structure of differently assembled resource-consumer networks.

Table B1. Examples of widely used metrics to describe (bipartite) network structure.

Metric	**Scale**	**Definition**	**Reference(s)**
Connectance	Network	Proportion of realized interaction links in the local assemblage	Dunne *et al.* 2002
Modularity (Q Z-score)	Network	The extent to which interactions cluster into groups, relative to a null model	Barber 2007
Nestedness (NODF)	Network	Metric based on overlap and decreasing fill, relative to a null model	Almeida-Neto *et al.* 2008
Interaction evenness	Network	Shannon's evenness of all interactions in the network	Dormann *et al.* 2009
Specialization (H2)	Network	Measure of discrimination, i.e. calculated in comparison of no specialization	Dormann *et al.* 2009
Average interaction niche breadth	Trophic level	Range of trait values that species' interaction partners express, averaged over all species within the trophic level	Albrecht *et al.* 2018; Li *et al.* 2018
Average interaction	Trophic level	Overlap of trait values that species' interaction partners express, averaged over all species	Albrecht *et al.* 2018; Li *et al.* 2018

niche overlap		within the trophic level	
Total interaction niche breadth	Trophic level	Range covered by the species-specific interaction niches within trophic level	Albrecht *et al.* 2018; Li *et al.* 2018
C score	Trophic level	Mean number of checkerboard combinations across all species of the trophic level (chekcerboardness = a high mutual exclusion by species)	Stone & Roberts 1992
Interaction diversity	Species	Shannon's diversity for interactions per species	Dormann *et al.* 2009
Species degree (normalized)	Species	Number of interaction links per species, scaled with the number of possible interaction partners	Dormann *et al.* 2009

Box 2. Interaction niche congruence determines the relative influence of bottom-up and top-down effects in bipartite resource-consumer networks.

In addition to the metrics at network scale, trophic-level-specific metrics can describe important characteristics of interactions in local communities (Box 1). Measuring species' interaction niches within trophic levels provides another angle to understanding the bottom-up versus top-down regulation of networks. Mechanistic understanding of the pathways that govern the relative contributions of bottom-up and top-down effects on communities and networks is limited. We suggest that the deviation from the linear relationship between the interaction niche properties at resource and consumer trophic levels determines whether the bipartite network structure is controlled from resource or consumer trophic level (Figure B1). The species-specific interaction niche corresponds to the range of trait values that its interaction partners express, whereas the trophic-level-specific interaction niche is the average (or median) of the species-specific range (Figure B1a). The interaction niche overlap of a species pair can be calculated for example as the intersection of their hypervolumes in interaction niche space (similarly to Blonder *et al.* 2014), whereas the trophic-level-specific overlap is the average of the pairwise overlap. Finally, the total interaction niche for the focal trophic level is simply measured as the trait range covered by the species-specific interaction niches.

We predict that if the interaction niche properties at different trophic levels have equal average breadth or overlap, the bipartite network structure will neither be bottom-up nor top-down controlled, but the interactions in the network will rather be determined by the interaction assembly processes (Figure B1b). In case that the interaction niche breadth or overlap of the consumers is much larger than that of the resources, we expect the network structure to be bottom-up controlled. That is, for example in pollination networks, if the pollinators on average interact with functionally more diverse set of plants than plants in terms of pollinators, we expect the network structure to be controlled from bottom-up. This would be the case because the persistence of pollinators in the local community is restricted to those that have functional traits matching with the interaction niches of the more specialized plants. Similarly, if the average interaction niche of the resources is much larger than that of the consumers, we expect that the network is top-down controlled. In general, environmental filtering and limiting similarity asymmetry would create bottom-up and top-down effects (see section 3.1).

Using within-trophic level metrics in addition to network scale metrics could open a new avenue to study bottom-up and top-down effects. The relative importance of top-down and bottom-up effects could potentially be evaluated even without knowing the precise interaction network, with the help of trait matching models (Dehling *et al.* 2016). Interaction niche properties also relate to other ecological processes. For example, in highly specialized networks, co extinctions keep the average interaction niche breadth constant, but the total interaction niche breadth changes. The study of interaction niche properties therefore has potential to lend insight to areas of ecology beyond network structure.

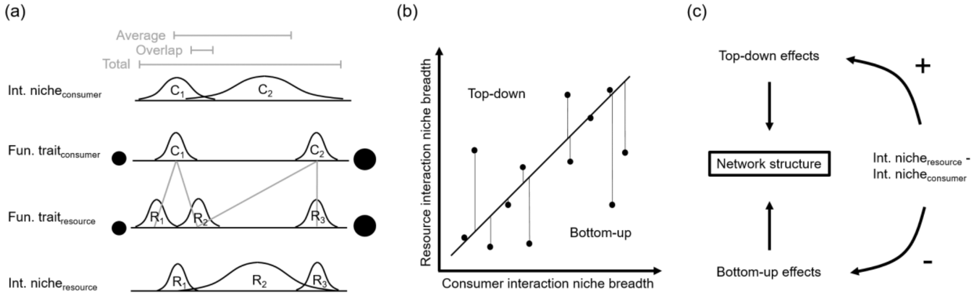


Figure B1. Potential effects of interaction niche properties on network structure. Panel (a) summarizes three different interaction niche (Int. niche) metrics calculated for the species at the focal trophic level: average niche breadth, average niche overlap, and total niche range (modified from Albrecht *et al.* 2018). We show an example of a bipartite resource-consumer network, where species are ordered along two functional trait (Fun. trait) axes according to their sizes (illustrated by black circles). The grey lines represent resource-consumer interactions that are constrained by functional trait matching. Trait matching determines the realized interaction niches of resources and consumers (represented on the trait axis of the other trophic level). From top down, the grey horizontal lines represent the average interaction niche breadth, the average interaction niche overlap, and the total interaction niche range of consumers, respectively. Panel (b) illustrates the effect of interaction niche discrepancies between trophic levels. If the interaction niche properties of resource and consumer species correspond to each other linearly, the network structure is likely neither bottom-up nor top-down controlled, but interactions are expected to be determined by interaction assembly processes. If the residual between the interaction niche properties between trophic levels differs from zero, the network structure may be determined by bottom-up or top-down properties. Panel (c) illustrates the feedback loop from the discrepancy in trophic-level specific interaction niche properties to network structure through bottom-up and top-down effects. For example, if the resource species' average interaction niche breadth is much larger than that of the consumers, the network is assumed to be structured through top-down effects.

A framework linking trait-based processes to the assembly of bipartite networks

Emma-Liina Marjakangas, Gabriel Muñoz, Shaun Turney, Jean-Philippe Lessard

Supplementary material Appendix S1: Simulating synthetic bipartite networks

1 Defining the species pools

We simulated regional species pools separately for synthetic consumer (C) and resource (R) assemblages. Each pool $J_P\,(C|R)$ consisted of 5000 individuals, belonging to 500 species $S_P\,(C|R)$. Each species was assigned a trait mean distribution from a uniform distribution [0 1]. We included intraspecific trait variation around the species-specific trait mean by drawing trait values from a normal distribution (mean = species-specific, SD = 0.001) for the 10 individuals of each of the 500 species.

2 Creating local assemblages

We used a coalescent-based algorithm to form local consumer and resource assemblages of $J_A\,(C|R) = 500$ individuals from a regional species pool of $J_P\,(C|R)$ individuals of $S_P\,(C|R)$ species. The coalescent-based algorithm simulates the genealogy of individuals, such that the occurrence and abundance of a species in a local assemblage is dependent both on the successful immigration of ancestor individuals from the species pool and subsequent survival of descendant individuals. However, we set the migratory rate (*m)* parameter to 0.5 to reduce the effect of genealogy in the local assemblage and thus mimic conditions where local assemblages are formed mainly by the initial migrant individuals (Munoz *et al.* 2017; Figure 2 in the main text). We sampled individuals from the regional resource and consumer pools to local assemblages based on probabilistic functions around a trait optima (Munoz et al. 2019). To remove potential species pool effects on the assembly of resource and consumer trophic levels (Lessard et al. 2012), we selected trait optima randomly from a uniform distribution [0 1] for each assembly process scenario and set the trait optima identical for the two trophic levels. We simulated distinct scenarios of niche-based assembly processes (i.e., environmental filtering and limiting similarity) by modifying the type and strength of the probabilistic function for selection of individuals while maintaining the regional pool constant. We simulated distinct scenarios in order to produce general expectations of bipartite network structure under different combinations of assembly processes within and between trophic levels. By varying the strengths of niche-based processes at resource and consumer trophic levels we varied the relative contributions of bottom-up and top-down effects (i.e., process strength symmetry) to bipartite network structures. We used the *ecolottery* package (Munoz *et al.* 2017) for the R software (version 3.5.3; R Core Team 2019) to perform the coalescent-based simulations of local assemblages.

2.1 Simulating within-trophic assembly processes

2.1.1 Environmental filtering

To simulate the effects of environmental filtering, we establish the probability of selection (*p*) of individual migrants with traits (*t*) as a Gaussian distribution around an arbitrarily set trait optimum (t_{opt}) between 0 and 1 ($t_{opt} = 0.2$) (Figure 2 in the main text). That is:

Equation 1. $p = e^{-(t-topt)^{2}/(2\sigma opt)^{2}}$,

where we introduced different gradients environmental filtering intensity by modulating the parameter σ_{opt}. We used five different values of σ_{opt} at both trophic levels, from weak ($\sigma_{opt} = 0.9$) to strong ($\sigma_{opt} = 0.1$), to allow a gradient of filtering strengths but to maintain the number of scenario combinations reasonable.

2.1.2 Limiting similarity

We also simulated the assembly of local consumer and resource assemblages under limiting similarity assumptions. To this end, we first created frequency distributions of normally distributed traits around two or more equally spaced trait optima. We constructed such distributions to reflect both the expected limiting similarity (*k*: total number of t_{opt}) and the selective pressure around optimal traits (*O*: overlap between individual t_{opt} distributions). We gradually increased the total niche partitioning (*k*: total number of t_{opt}), while lowering the selective pressures (*O*: overlap of distributions around t_{opt}) to simulate the intensity of the limiting similarity effects in local assemblages. We used 5 different values for *k* and 5 different values for *O*, resulting in 25 scenario combinations for limiting similarity between resource and consumer assemblages. Finally, to sample individuals from the regional species pool, we used the observed trait frequency density curves as probability functions for migrant selection.

2.2 Simulating pairwise interaction probabilities

We simulated the probability of interaction between individuals of consumer (*C*) and resource (*R*) assemblages under different interaction assembly rules reflecting neutral and niche-based (i.e., functional trait matching) assembly processes.

2.2.1 Neutral interaction assembly

Under neutral assumptions of interaction assembly, pairwise interaction probability $P(C_iR_j)$ depends only on the relative abundances of C_i and R_j, such that interactions occur more frequently between the most abundant species (Morales-Castilla *et al.* 2015; Chacoff *et al.* 2018). That is:

Equation 2. $P(C_iR_j) = rAC_i * rAR_j$,

where $P(C_iR_j)$ is the probability of pairwise interaction between individuals at the consumer *i* and resource *j* trophic level. rAC_i and rAR_j correspond to their relative abundances.

2.2.2 Functional trait matching

With the objective to simulate niche-based process between trophic levels, we assembled pairwise interaction probabilities following two distinct, but not mutually exclusive, hypotheses of functional trait matching. The first interaction hypothesis is commonly known as *forbidden links* (Morales-Castilla *et al.* 2015). Here, interaction partners are constrained to species within a certain range of traits at the opposite trophic level. Within this constrained set of potential partners, species' relative abundances define pairwise interaction probabilities. We constricted the trait range of interacting partners of consumer and resource species to represent real-life scenarios where traits constrain interactions between trophic levels unidirectionally. For example, the mechanical limitations that size-related traits impose on the formation of certain biotic interactions (e.g., large beaked birds can still eat smaller fruits but small beaked birds cannot handle big ones). That is:

Equation 3. if $tC_i-tR_j \leqq 0 \rightarrow P(C_iR_j) = 0$
if $tC_i-tR_j > 0 \rightarrow P(C_iR_j) = rAC_i * rAR_j$,

where interaction probability $P(C_iR_j)$ is zero, when the difference between consumer trait value tC_i and resource trait value tR_j is smaller than or equal to 0. When the difference between consumer and resource trait values is larger than zero, the interaction probability between consumer species *i* and resource species *j* is defined as the product of their relative abundances. In the second interaction assembly hypothesis, namely *morphological matching* (Sazatornil *et al.* 2016), pairwise interactions only occur whenever a strong functional trait matching is present between species across trophic levels (Maglianesi *et al.* 2014; Sazatornil *et al.* 2016). In contrast with the previous scenario, species relative abundances play no role in defining pairwise interactions between species under this hypothesis. As such, the hypothesis represents scenarios where the evolution of matching traits has resulted from resource competition effects favouring convergence and specialization between interacting species pairs (e.g., insect proboscis length - corolla length; Sazatornil *et al.* 2016). Here, interaction probabilities depend on the frequency distribution of trait dissimilarities among trophic levels. That is:

Equation 4. $P(C_iR_j) = 1-|tC_i-tR_j|/|max(tC-tR)|$,

where the probability of interaction $P(C_iR_j)$ between consumer and resource species is given by the absolute difference between the consumer trait value tC_i and resource trait value tR_j relative to the maximum absolute difference between the mean trait values tC and tR of consumers and resources, respectively.

3 Assembling bipartite networks

Following the assembly of pairwise interactions, we end up with a probabilistic bipartite network that we turn into binary one by selecting those interactions within the highest 5th percentile as realized interactions. Realized interactions between species in the final (C x R) bipartite matrices were set to 1, whereas non-realized interactions were set to 0.

4 Quantifying bipartite network structure

We calculated modularity and nestedness to assess the overall network structure of simulated bipartite binary networks. We quantified the modular configuration of simulated bipartite networks using a label-propagation algorithm (Liu and Murata 2010; Beckett 2016), which maximises Barber's modularity (Q; Barber 2007). Q metric values are not independent of intrinsic network properties, such as network size and connectance. Hence, to make them comparable among simulation scenarios we calculated Q Z-scores by comparing the Q values to a null distribution of 100 independent network rewires that were constrained to preserve the richness and frequencies of consumer species interactions constant (model 'r1' implemented in *vegan* R package) (Oksanen *et al.* 2013; Delmas et al. 2019). That is, we restricted the degree of resource specialization at the consumer level in each network rewire. We quantified nestedness of simulated networks using the NODF metric (Almeida-Neto *et al.* 2008). NODF values were transformed into NODF Z-scores by comparing them with a null-distribution of NODF values constructed under the same conditions as described for Q Z-scores. Functions to calculate modularity and nestedness were implemented from the *bipartite* package for R (Dormann *et al.* 2009).

5 Quantifying the effects of niche-based assembly processes on network structure

We quantified the effect of distinct niche-based assembly processes on the formation of synthetic bipartite network structures. We defined a two-dimensional field representing the niche-based effect on network structure as the difference in modular (x-axis) and nested (y-axis) network structures in relation to neutrally observed scenarios (Figure 3 in the main text). Within this field, we first measured the niche-based interaction assembly effects defining bipartite network structure. We did this by comparing the observed metrics of networks assembled under morphological matching and forbidden link hypotheses to the expected metric values of networks under neutrally assembled interactions (i.e, pairwise interactions determined by relative abundances). We repeated the process for all different assumptions of within-trophic level assembly (i.e., environmental filtering, limiting similarity, stochastically assembled assemblages). Second, we measured the niche-based within-trophic level assembly effects defining bipartite network structure. To this end, we compared the observed metric values of networks assembled under different types of within-trophic level assembly (i.e., environmental filtering, limiting similarity, stochastically assembled assemblages) to the metric values expected under neutral within-trophic level assembly (i.e., stochastically assembled resource and consumer assemblages). We repeated the process for all different hypothesis of interaction assembly (i.e., morphological matching, forbidden links, neutral interactions); We considered process strength symmetry (Ps) as the absolute differences between trophic levels in the strength of the assembly process operating within-trophic levels (Equation 5). We quantified the magnitude of both niche-based assembly effects as Euclidean distances between the observed niche-based effects and the expected effects under neutral within-trophic processes.

Equation 5. $Ps = |Consumer\ strength\text{-}Resource\ strength|$

6 Partitioning the variance in network structure metrics and niche-based assembly process effects

We used multivariate linear regression models (Eq 6.1-6.6) to quantify the relationships of distinct simulation parameters with (a) network structure metrics and (b) the relative magnitude of the effects of niche-based assembly processes. We used the following multiple linear regression model equations:

Equation 6.1. $YQZscorex = b_0 + b_1X_1 + b_2X_2 + b_3X_3 + b_4X_4 + b_5X_5$

Equation 6.2. $YQZscoresSD = b_0 + b_1X_1 + b_2X_2 + b_3X_3 + b_4X_4 + b_5X_5$

Equation 6.3. $YNODFx = b_0 + b_1X_1 + b_2X_2 + b_3X_3 + b_4X_4 + b_5X_5$

Equation 6.4. $YNODFsd = b_0 + b_1X_1 + b_2X_2 + b_3X_3 + b_4X_4 + b_5X_5$

Equation 6.5. $Y\ NBAEint = b_0 + b_1X_1 + b_2X_2 + b_3X_3 + b_4X_4 + b_5X_5$

Equation 6.6. $Y\ NBAEwith = b_0 + b_1X_1 + b_2X_2 + b_3X_3 + b_4X_4 + b_5X_5$

where **Y(n)** is the dependent variable: average Q Z-score (modularity) across replicates (in equation 6.1.); standard deviation of Q Z-score across replicates (in equation 6.2); average NODF Z-score (nestedness) across replicates (in equation 6.3); standard deviation of NODF Z-score across replicates (in equation 6.4); relative magnitude of interaction niche-based effects in network structure (in equation 6.5); and relative magnitude of within-trophic level niche-based effects in network structure (in equation 6.6). **X(n)** are the predictors: (1) type of within-trophic level assembly process (EF, LS, NL); (2) interaction assembly process hypothesis (MM, FL, NL); (3) assembly process strength at resource trophic level [0-1]; (4) assembly process strength at consumer trophic level [0-1]; and (5) symmetry of the assembly process strengths between trophic levels (*Ps*, see description above). ***b*** is the regression coefficient and **b0** is the coefficient when **Xn** = 0. We used commonality analysis (Nimon et al. 2008) to decompose the explained variance in **Yn** (given by the R^2**(Yn)**) into components of independent variation attributable to the individual predictors **Xn** (Appendix S2, Table S2). Multivariate regressions and commonality coefficients were obtained using the packages *stats* (R Core Team 2019) and *yhat* (Nimon et al. 2008) for R environment.

References

Almeida-Neto, M., Campassi, F., Galetti, M., Jordano, P. & Oliveira-Filho, A. (2008). Vertebrate dispersal syndromes along the Atlantic forest: broad-scale patterns and macroecological correlates. *Glob. Ecol. Biogeogr.*, 17, 503–513.

Barber, M.J. (2007). Modularity and community detection in bipartite networks. *Phys. Rev. E*, 76, 066102.

Chacoff, N.P., Resasco, J. & Vázquez, D.P. (2018). Interaction frequency, network position, and the temporal persistence of interactions in a plant-pollinator network. *Ecology*, 99, 21–28.

Delmas, E., Besson, M., Brice, M.H., Burkle, L.A., Dalla Riva, G. V., Fortin, M.J., *et al.* (2019). Analysing ecological networks of species interactions. *Biol. Rev.*, 94, 16–36.

Dormann, C.F., Fründ, J., Bluthgen, N. & Gruber, B. (2009). Indices, graphs and null models: analyzing bipartite ecological networks. *Open Ecol. J.*, 2, 7–24.

Lessard, J.-P., Belmaker, J., Myers, J.A., Chase, J.M. & Rahbek, C. (2012). Inferring local ecological processes amid species pool influences. *Trends Ecol. Evol.*, 27, 600–607.

Liu, X. & Murata, T. (2010). An efficient algorithm for optimizing bipartite modularity in bipartite networks. *J. Adv. Comput. Intell. Intell. Informatics*, 14, 408–415.

Maglianesi, M.A., Blüthgen, N., Böhning-Gaese, K. & Schleuning, M. (2014). Morphological traits determine specialization and resource use in plant-hummingbird networks in the neotropics. *Ecology*, 95, 3325–3334.

Morales-Castilla, I., Matias, M.G., Gravel, D. & Araújo, M.B. (2015). Inferring biotic interactions from proxies. *Trends Ecol. Evol.*, 30, 347–356.

Munoz, F., Grenié, M., Denelle, P., Taudière, A., Laroche, F., Tucker, C., *et al.* (2018). ecolottery: simulating and assessing community assembly with environmental filtering and neutral dynamics in R. *Methods Ecol. Evol.*, 9, 693–703.

Nimon, K., Lewis, M., Kane, R. & Haynes, R.M. (2008). An R package to compute commonality coefficients in the multiple regression case: an introduction to the package and a practical example. *Behav. Res. Methods*, 40, 457–466.

Oksanen, J., Blanchet, F.G., Roeland, R., Legendre, P., Minchin, P.R., O'Hara, R.B., *et al.* (2013). Community Ecology Package vegan, R package version 2.0-7.

R Core Team. (2019). R: a language and environment for statistical computing.

Sazatornil, F.D., Moré, M., Benitez-Vieyra, S., Cocucci, A.A., Kitching, I.J., Schlumpberger, B.O., *et al.* (2016). Beyond neutral and forbidden links: morphological matches and the assembly of mutualistic hawkmoth–plant networks. *J. Anim. Ecol.*, 85, 1586–1594.

Table S1a. Scenarios simulating niche-based bipartite network assembly under environmental filtering of different filtering intensities (σ) at each trophic level. Pairwise interactions are assembled under distinct hypothesis of functional trait matching. Each scenario was replicated 100 independent times.

Consumer assembly process	**Resource assembly process**	**Pairwise interaction hypothesis**	$\sigma_{consumer}$	$\sigma_{resource}$
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Forbidden Links	0.1	0.1
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Forbidden Links	0.3	0.1
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Forbidden Links	0.5	0.1
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Forbidden Links	0.7	0.1
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Forbidden Links	0.9	0.1
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Forbidden Links	0.1	0.3
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Forbidden Links	0.3	0.3

Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Forbidden Links	0.5	0.3
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Forbidden Links	0.7	0.3
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Forbidden Links	0.9	0.3
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Forbidden Links	0.1	0.5
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Forbidden Links	0.3	0.5
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Forbidden Links	0.5	0.5
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Forbidden Links	0.7	0.5
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Forbidden Links	0.9	0.5
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Forbidden Links	0.1	0.7
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Forbidden Links	0.3	0.7
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Forbidden Links	0.5	0.7
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Forbidden Links	0.7	0.7
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Forbidden Links	0.9	0.7
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Forbidden Links	0.1	0.9
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Forbidden Links	0.3	0.9
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Forbidden Links	0.5	0.9
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Forbidden Links	0.7	0.9
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Forbidden Links	0.9	0.9
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Morphological Match	0.1	0.1
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Morphological Match	0.3	0.1
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Morphological Match	0.5	0.1

Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Morphological Match	0.7	0.1
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Morphological Match	0.9	0.1
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Morphological Match	0.1	0.3
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Morphological Match	0.3	0.3
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Morphological Match	0.5	0.3
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Morphological Match	0.7	0.3
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Morphological Match	0.9	0.3
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Morphological Match	0.1	0.5
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Morphological Match	0.3	0.5
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Morphological Match	0.5	0.5
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Morphological Match	0.7	0.5
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Morphological Match	0.9	0.5
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Morphological Match	0.1	0.7
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Morphological Match	0.3	0.7
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Morphological Match	0.5	0.7
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Morphological Match	0.7	0.7
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Morphological Match	0.9	0.7
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Morphological Match	0.1	0.9
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Morphological Match	0.3	0.9
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Morphological Match	0.5	0.9
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Morphological Match	0.7	0.9

Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Morphological Match	0.9	0.9

Table S1b. Scenarios simulating niche-based bipartite network assembly under limiting similarity with different intensities of niche partitioning (*k*) and overlap (*O*) at each trophic level. Pairwise interactions are assembled under distinct hypothesis of functional trait matching. Each scenario was replicated 100 independent times.

Consumer assembly process	**Resource assembly process**	**Pairwise interaction hypothesis**	$k_{consumer}$	$k_{resource}$	$O_{consumer}$	$O_{resource}$
Limiting Similarity	Limiting Similarity	Forbidden Links	2	2	0.5	0.5
Limiting Similarity	Limiting Similarity	Forbidden Links	3	2	0.37525	0.5
Limiting Similarity	Limiting Similarity	Forbidden Links	4	2	0.2505	0.5
Limiting Similarity	Limiting Similarity	Forbidden Links	5	2	0.12575	0.5
Limiting Similarity	Limiting Similarity	Forbidden Links	6	2	0.001	0.5
Limiting Similarity	Limiting Similarity	Forbidden Links	2	3	0.5	0.37525
Limiting Similarity	Limiting Similarity	Forbidden Links	3	3	0.37525	0.37525
Limiting Similarity	Limiting Similarity	Forbidden Links	4	3	0.2505	0.37525
Limiting Similarity	Limiting Similarity	Forbidden Links	5	3	0.12575	0.37525
Limiting Similarity	Limiting Similarity	Forbidden Links	6	3	0.001	0.37525
Limiting Similarity	Limiting Similarity	Forbidden Links	2	4	0.5	0.2505
Limiting Similarity	Limiting Similarity	Forbidden Links	3	4	0.37525	0.2505
Limiting Similarity	Limiting Similarity	Forbidden Links	4	4	0.2505	0.2505
Limiting Similarity	Limiting Similarity	Forbidden Links	5	4	0.12575	0.2505
Limiting Similarity	Limiting Similarity	Forbidden Links	6	4	0.001	0.2505
Limiting Similarity	Limiting Similarity	Forbidden Links	2	5	0.5	0.12575

Limiting Similarity	Limiting Similarity	Forbidden Links	3	5	0.37525	0.12575
Limiting Similarity	Limiting Similarity	Forbidden Links	4	5	0.2505	0.12575
Limiting Similarity	Limiting Similarity	Forbidden Links	5	5	0.12575	0.12575
Limiting Similarity	Limiting Similarity	Forbidden Links	6	5	0.001	0.12575
Limiting Similarity	Limiting Similarity	Forbidden Links	2	6	0.5	0.001
Limiting Similarity	Limiting Similarity	Forbidden Links	3	6	0.37525	0.001
Limiting Similarity	Limiting Similarity	Forbidden Links	4	6	0.2505	0.001
Limiting Similarity	Limiting Similarity	Forbidden Links	5	6	0.12575	0.001
Limiting Similarity	Limiting Similarity	Forbidden Links	6	6	0.001	0.001
Limiting Similarity	Limiting Similarity	Morphological Match	2	2	0.5	0.5
Limiting Similarity	Limiting Similarity	Morphological Match	3	2	0.37525	0.5
Limiting Similarity	Limiting Similarity	Morphological Match	4	2	0.2505	0.5
Limiting Similarity	Limiting Similarity	Morphological Match	5	2	0.12575	0.5
Limiting Similarity	Limiting Similarity	Morphological Match	6	2	0.001	0.5
Limiting Similarity	Limiting Similarity	Morphological Match	2	3	0.5	0.37525
Limiting Similarity	Limiting Similarity	Morphological Match	3	3	0.37525	0.37525
Limiting Similarity	Limiting Similarity	Morphological Match	4	3	0.2505	0.37525
Limiting Similarity	Limiting Similarity	Morphological Match	5	3	0.12575	0.37525
Limiting Similarity	Limiting Similarity	Morphological Match	6	3	0.001	0.37525
Limiting Similarity	Limiting Similarity	Morphological Match	2	4	0.5	0.2505
Limiting Similarity	Limiting Similarity	Morphological Match	3	4	0.37525	0.2505

Limiting Similarity	Limiting Similarity	Morphological Match	4	4	0.2505	0.2505
Limiting Similarity	Limiting Similarity	Morphological Match	5	4	0.12575	0.2505
Limiting Similarity	Limiting Similarity	Morphological Match	6	4	0.001	0.2505
Limiting Similarity	Limiting Similarity	Morphological Match	2	5	0.5	0.12575
Limiting Similarity	Limiting Similarity	Morphological Match	3	5	0.37525	0.12575
Limiting Similarity	Limiting Similarity	Morphological Match	4	5	0.2505	0.12575
Limiting Similarity	Limiting Similarity	Morphological Match	5	5	0.12575	0.12575
Limiting Similarity	Limiting Similarity	Morphological Match	6	5	0.001	0.12575
Limiting Similarity	Limiting Similarity	Morphological Match	2	6	0.5	0.001
Limiting Similarity	Limiting Similarity	Morphological Match	3	6	0.37525	0.001
Limiting Similarity	Limiting Similarity	Morphological Match	4	6	0.2505	0.001
Limiting Similarity	Limiting Similarity	Morphological Match	5	6	0.12575	0.001
Limiting Similarity	Limiting Similarity	Morphological Match	6	6	0.001	0.001

Table S1c. Scenarios simulating niche-based bipartite network assembly under environmental filtering of different filtering intensities (σ) at each trophic level. Pairwise interactions are assembled under neutral assumptions. Each scenario was replicated 100 independent times.

Consumer assembly process	**Resource assembly process**	**Pairwise interaction hypothesis**	$\sigma_{consumer}$	$\sigma_{resource}$
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Neutrally Assembled Interactions	0.1	0.1
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Neutrally Assembled Interactions	0.3	0.1
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Neutrally Assembled Interactions	0.5	0.1
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Neutrally Assembled Interactions	0.7	0.1
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Neutrally Assembled Interactions	0.9	0.1

Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Neutrally Assembled Interactions	0.1	0.3
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Neutrally Assembled Interactions	0.3	0.3
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Neutrally Assembled Interactions	0.5	0.3
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Neutrally Assembled Interactions	0.7	0.3
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Neutrally Assembled Interactions	0.9	0.3
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Neutrally Assembled Interactions	0.1	0.5
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Neutrally Assembled Interactions	0.3	0.5
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Neutrally Assembled Interactions	0.5	0.5
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Neutrally Assembled Interactions	0.7	0.5
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Neutrally Assembled Interactions	0.9	0.5
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Neutrally Assembled Interactions	0.1	0.7
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Neutrally Assembled Interactions	0.3	0.7
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Neutrally Assembled Interactions	0.5	0.7
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Neutrally Assembled Interactions	0.7	0.7
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Neutrally Assembled Interactions	0.9	0.7
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Neutrally Assembled Interactions	0.1	0.9
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Neutrally Assembled Interactions	0.3	0.9
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Neutrally Assembled Interactions	0.5	0.9
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Neutrally Assembled Interactions	0.7	0.9
Stabilizing Environmental Filtering	Stabilizing Environmental Filtering	Neutrally Assembled Interactions	0.9	0.9

Table S1d. Scenarios simulating niche-based bipartite network assembly under limiting similarity with different intensities of niche partitioning (k) and overlap (O) at each trophic level. Pairwise interactions are assembled under neutral assumptions. Each scenario was replicated 100 independent times.

Consumer assembly process	**Resource assembly process**	**Pairwise interaction hypothesis**	$k_{consumer}$	$k_{resource}$	$O_{consumer}$	$O_{resource}$
Limiting Similarity	Limiting Similarity	Neutrally assembled interactions	2	2	0.5	0.5
Limiting Similarity	Limiting Similarity	Neutrally assembled interactions	3	2	0.37525	0.5
Limiting Similarity	Limiting Similarity	Neutrally assembled interactions	4	2	0.2505	0.5
Limiting Similarity	Limiting Similarity	Neutrally assembled interactions	5	2	0.12575	0.5
Limiting Similarity	Limiting Similarity	Neutrally assembled interactions	6	2	0.001	0.5
Limiting Similarity	Limiting Similarity	Neutrally assembled interactions	2	3	0.5	0.37525
Limiting Similarity	Limiting Similarity	Neutrally assembled interactions	3	3	0.37525	0.37525
Limiting Similarity	Limiting Similarity	Neutrally assembled interactions	4	3	0.2505	0.37525
Limiting Similarity	Limiting Similarity	Neutrally assembled interactions	5	3	0.12575	0.37525
Limiting Similarity	Limiting Similarity	Neutrally assembled interactions	6	3	0.001	0.37525
Limiting Similarity	Limiting Similarity	Neutrally assembled interactions	2	4	0.5	0.2505
Limiting Similarity	Limiting Similarity	Neutrally assembled interactions	3	4	0.37525	0.2505
Limiting Similarity	Limiting Similarity	Neutrally assembled interactions	4	4	0.2505	0.2505
Limiting Similarity	Limiting Similarity	Neutrally assembled interactions	5	4	0.12575	0.2505
Limiting Similarity	Limiting Similarity	Neutrally assembled interactions	6	4	0.001	0.2505
Limiting Similarity	Limiting Similarity	Neutrally assembled interactions	2	5	0.5	0.12575
Limiting Similarity	Limiting Similarity	Neutrally assembled interactions	3	5	0.37525	0.12575
Limiting Similarity	Limiting Similarity	Neutrally assembled interactions	4	5	0.2505	0.12575
Limiting Similarity	Limiting Similarity	Neutrally assembled interactions	5	5	0.12575	0.12575

Limiting Similarity	Limiting Similarity	Neutrally assembled interactions	6	5	0.001	0.12575
Limiting Similarity	Limiting Similarity	Neutrally assembled interactions	2	6	0.5	0.001
Limiting Similarity	Limiting Similarity	Neutrally assembled interactions	3	6	0.37525	0.001
Limiting Similarity	Limiting Similarity	Neutrally assembled interactions	4	6	0.2505	0.001
Limiting Similarity	Limiting Similarity	Neutrally assembled interactions	5	6	0.12575	0.001
Limiting Similarity	Limiting Similarity	Neutrally assembled interactions	6	6	0.001	0.001

Table S1e. Neutral scenarios with simulated effects of neutral within-trophic level assembly (i.e., stochastically assembled resource and consumer assemblages). Pairwise interactions were assembled under morphological matching, forbidden links and neutral hypotheses. Each scenario was replicated 100 independent times.

Resource assembly process	**Consumer assembly process**	**Pairwise interaction hypothesis**
Neutrally assembled communities	Neutrally assembled communities	Forbidden Links
Neutrally assembled communities	Neutrally assembled communities	Morphological Matching
Neutrally assembled communities	Neutrally assembled communities	Neutrally assembled interactions

A framework linking trait-based processes to the assembly of bipartite networks

Emma-Liina Marjakangas, Gabriel Muñoz, Shaun Turney, Jean-Philippe Lessard

Supplementary material Appendix S2: Additional results

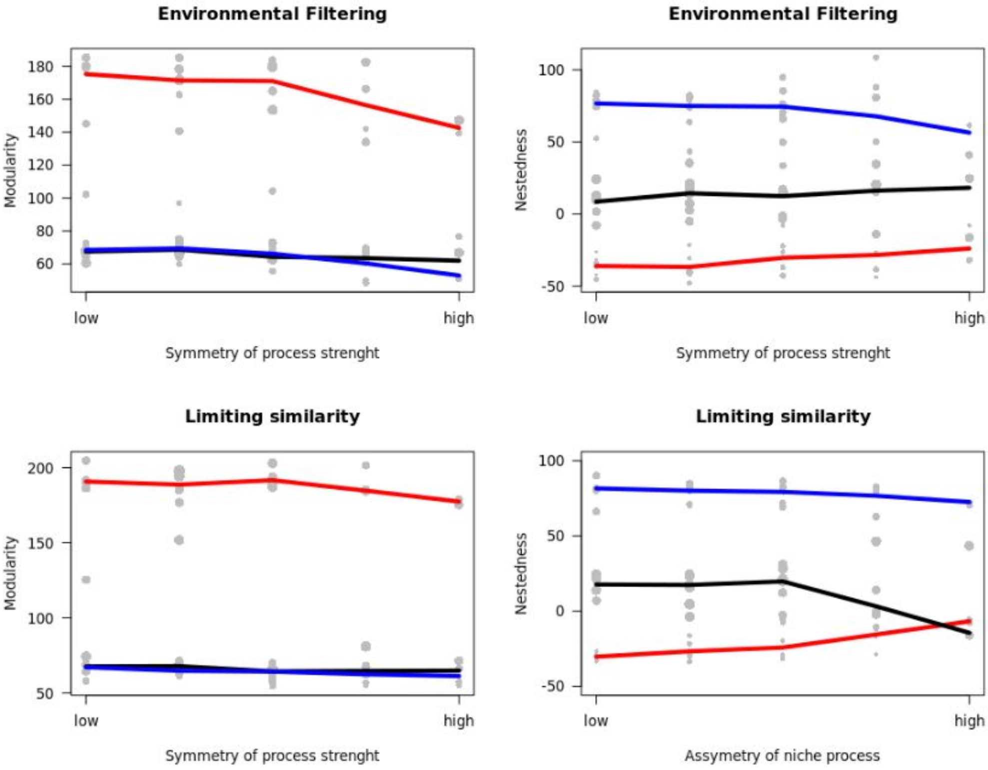


Figure S1. Changes in modularity and nestedness in relation to the varying strength of symmetry of niche-based within-trophic level assembly process. Points represent individual combinations of assembly scenarios to form synthetic bipartite networks. Colors represent the different scenarios of interaction assembly: red = morphological match, blue = forbidden links, and black = neutrally assembled interactions. Lines show the tendency, calculated with smoothed local regression of the network metric values in relation to the symmetry of niche-based within level assembly process between trophic levels. The size of points is drawn in relation to the variation (standard deviation) of the metric values across replicates of the similar assembly scenarios.

Table S2a. Regression coefficients from the multivariate linear regression of the relationships between the distinct simulation parameters and the average modularity Z-scores across simulation scenarios.

Parameter	DF	SumSq	MeanSumSq	F-Value	p	
Process strength symmetry	1.00E+00	4.34E+05	3.09E+03	1.56E+01	1.22E-04	***
Consumer process strength	1.00E+00	4.35E+04	2.70E+01	1.34E-01	7.15E-01	
Resource process strength	1.00E+00	-2.92E+05	1.10E+03	5.55E+00	1.98E-02	*
Interaction assembly hypothesis	2.00E+00	2 385536	1.93E+05	9.74E+02	< 2.2e-16	***
Within-trophic level process type	2.00E+00	8.19E+05	2.07E+03	1.05E+01	5.72E-05	***

Table S2b. Regression coefficients from the multivariate linear regression of the relationships between the distinct simulation parameters and the amount of variance in modularity Z-scores across simulation scenarios.

Parameter	DF	SumSq	MeanSumSq	F-Value	p	
Process strength symmetry	1.00E+00	1.86E+01	1.87E+01	6.76E-01	4.12E-01	
Consumer process strength	1.00E+00	1.33E+01	1.33E+01	4.83E-01	4.88E-01	
Resource process strength	1.00E+00	1.24E+02	1.23E+02	4.48E+00	3.61E-02	*
Interaction assembly hypothesis	2.00E+00	1.09E+03	5.43E+02	1.97E+01	2.76E-08	***
Within-trophic level process type	2.00E+00	1.32E+02	6.58E+01	2.39E+00	9.56E-02	

Table S2c. Regression coefficients from the multivariate linear regression of the relationships between the distinct simulation parameters and the average nestedness Z-scores across simulation scenarios.

Parameter	DF	SumSq	MeanSumSq	F-Value	p	
Process strength symmetry	1.00E+00	5.00E+02	5.00E+02	3.39E+00	6.76E-02	.
Consumer process strength	1.00E+00	4.20E+01	4.20E+01	2.83E-01	5.96E-01	
Resource process strength	1.00E+00	1.21E+03	1.21E+03	8.19E+00	4.84E-03	**
Interaction assembly hypothesis	2.00E+00	2.75E+05	1.37E+05	9.31E+02	< 2.2e-16	***
Within-trophic level process type	2.00E+00	1.33E+03	6.65E+02	4.51E+00	1.26E-02	*

Table S2d. Regression coefficients from the multivariate linear regression of the relationships between the distinct simulation parameters and the amount of variance in nestedness Z-scores across simulation scenarios.

Parameter	DF	SumSq	MeanSumSq	F-Value	p	
Process strength symmetry	1.00E+00	5.20E+00	5.18E+00	6.31E-01	4.28E-01	
Consumer process strength	1.00E+00	4.79E+01	4.79E+01	5.84E+00	1.69E-02	*
Resource process strength	1.00E+00	4.00E-01	3.90E-01	4.79E-02	8.27E-01	
Interaction assembly hypothesis	2.00E+00	5.32E+03	2.66E+03	3.24E+02	< 2e-16	***
Within-trophic level process type	2.00E+00	4.19E+01	2.10E+01	2.55E+00	8.15E-02	.

Table S2e. Regression coefficients from the multivariate linear regression of the relationships between the distinct simulation parameters and within-trophic niche-based assembly effects

Parameter	DF	SumSq	MeanSumSq	F-Value	p	
Process strength symmetry	1	51.436	51.436	24.736	2.96E-06	***
Consumer process strength	1	103.13	103.13	49.596	3.08E-10	***
Resource process strength	1	47.22	47.22	22.709	6.85E-06	***
Interaction assembly hypothesis	1	78.207	78.207	37.611	2.02E-08	***
Within-trophic level process type	1	8.602	8.602	4.137	0.04477	*

Table S2f. Regression coefficients from the multivariate linear regression of the relationships between the distinct simulation parameters and interaction niche-based assembly effects

Parameter	DF	SumSq	MeanSumSq	F-Value	p	
Process strength symmetry	1	0.0038	0.00384	0.0973	0.7558	
Consumer process strength	1	0.0039	0.00388	0.0983	0.7545	
Resource process strength	1	1.0688	1.06884	27.1024	1.13E-06	***
Interaction assembly hypothesis	1	0.0807	0.08074	2.0472	0.1558	
Within-trophic level process type	1	1.9095	1.90945	48.4177	4.57E-10	***

Table S2g. Commonality coefficients corresponding to percentages of variance in the network metric averages and stochasticity explained by the simulation parameters.

Parameter	Modularity mean	Modularity variance	Nestedness mean	Nestedness variance
Interaction assembly hypothesis	98	88	99	99
Within-trophic level process type	1	6	1	0.00
Process strength symmetry	1	2	0.00	0.00
Consumer process strength	0.00	2	0.00	0.00
Resource process strength	0.00	2	0.00	0.00

Table S2h. Commonality coefficients corresponding to percentages of variance in the magnitude of niche-based assembly effects explained by the simulation parameters.

Parameter	Interaction assembly effects	Within-trophic level assembly effects
Interaction assembly hypothesis	0.13	18
Within-trophic level process type	0.13	36
Process strength symmetry	2.63	17
Consumer process strength	62.26	27
Resource process strength	34.85	3

PAPER II

Co-occurrences of tropical trees: disentangling abiotic and biotic forces

Running title: Tropical tree co-occurrences

Emma-Liina Marjakangas[1,*], Otso Ovaskainen[1,2], Nerea Abrego[3], Vidar Grøtan[1], Alexandre A. de Oliveira[4], Paulo I. Prado[4], and Renato A. F. de Lima[4,5]

[1] Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of Science and Technology, N-7491 Trondheim, Norway
[2] Organismal and Evolutionary Biology Research Programme, PO Box, 65, FI-00014 University of Helsinki, Finland
[3] Department of Agricultural Sciences, PO Box 27, FI-00014 University of Helsinki, Finland
[4] Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, 05508-090, São Paulo, Brazil
[5] Biodiversity Dynamics group, Naturalis Biodiversity Center, 2333 CR Leiden, The Netherlands
Correspondence: emma-liina.marjakangas@ntnu.no, orcid: 0000-0002-5245-3779

Keywords: assembly process, environmental filtering, functional trait, limiting similarity, phylogenetic distance, species association

Abstract

Aim: Species co-occurrences in local assemblages can arise neutrally or dependent on species' niches. However, the role of these mechanisms when generalized to large, biogeographical scales has not been thoroughly deciphered, probably due to combined shortcomings of data and methodology. Here, we explored the relative importance of two central hypotheses related to assembly of species communities and co-occurrences: environmental filtering and limiting similarity.
Location: Eastern South America
Taxon: Trees
Methods: We modelled jointly the occurrences and co-occurrences of 1016 tropical tree species with abundance data compiled from forest inventories of 574 localities. We estimated species co-occurrences as raw and residual associations by building models that exclude and include the effects of environmental factors on the species' co-occurrences, respectively.
Results: We found overarching evidence that the abiotic environment is the most important driver of tree species occurrences and co-occurrences across Eastern South America. We found the number of estimated raw associations to be higher than that of the residual associations, the difference being attributed to those observed species co-occurrences that stem from their shared responses to the environment. Negative residual associations were more prevalent in the transitional zones between biogeographical regions, indicating a possible establishment barrier

founded on negative species interactions. Contrary to the predictions of the limiting similarity hypothesis, phylogenetic relatedness or functional similarity did not limit tree species co-occurrences.

Main conclusions: We conclude that the importance of environmental filtering exceeds that of limiting similarity in shaping tree species' co-occurrences when local patterns are generalized to large spatial extents. However, the spatial patterns of the residual associations within local communities indicate that species interactions may play a role in shaping the limits of biogeographical regions. The estimated residual species associations pose interesting hypotheses for direct and indirect ecological interactions of tropical trees to be tested in the future.

1 Introduction

The immense diversity of tropical tree communities and its drivers have intrigued scientists for centuries. Research on the topic has focused on mechanisms allowing species to occur together despite the limited resources available for growth and reproduction (e.g., Chesson, 2000; Diamond, 1975; Hardin, 1960). Studying tropical tree co-occurrences may reveal the relative importance of the ecological and biogeographical processes underlying the observed patterns. In general, the processes that define which species occur in the local tree assemblage are either neutral (Hubbell, 2001) or dependent on species' niches (MacArthur & Levins, 1967; van der Valk, 1981). These community assembly processes govern how species in a regional pool are distributed into local assemblages, and thereby determine the co-occurrences of species within the local assemblages.

Under neutral processes, assembly of communities is stochastic relative to species' niches (Hubbell, 2001). Under niche-based processes, the presence and abundance of a species in an assemblage is dependent on the properties of its niche. Environmental filtering is a niche-based process that excludes species from the assemblage if their niches are not suited to the local environmental conditions (Keddy, 1992; van der Valk, 1981). Thereby, at the niche level, environmental filtering is driven by niche filtering (Cadotte & Tucker, 2017), such as through climatic factors or presence of facultative symbionts. Limiting similarity is a niche-based process that prevents species from co-occurring in an assemblage if their niches are too similar, due to competitive exclusion (MacArthur & Levins, 1967). Thereby, at the niche level, limiting similarity is driven by niche partitioning. In practice, species with the same set of life-history traits are expected to compete and not to co-occur in space and time (Kraft, Valencia, & Ackerly, 2008; Wilson & Stubbs, 2012). However, niche-based processes have gained criticism for being difficult to differentiate in terms of the biodiversity patterns that they produce (Cadotte & Tucker, 2017). Despite the criticism towards niche-based processes, they have distinct value for inferring the role of the environment and species characteristics in community structure. In this paper, we focus on the niche-based processes behind tropical tree co-occurrences: the environmental filtering (Cadotte & Tucker, 2017; Weiher & Keddy, 1995; Zobel, 1997) and the limiting similarity (MacArthur & Levins, 1967) hypotheses.

At large observation scales, species' co-occurrences may depend on the biogeographical processes, for example on the time since last glacial period (Adams & Woodward, 1989) or even on the continental drift-induced distributions of major taxonomic lineages. Furthermore, priority effects, i.e. randomly determined order of species' arrival to the local community, may affect the final composition of the community (Fukami, Bezemer, Mortimer, & Van Der Putten, 2005). Therefore, linking local and regional community dynamics as well as ecological and biogeographical processes in generating diversity is essential. For example, increased regional species richness can result only from dispersal of species into a region or from *in situ* speciation, processes that are best identified using historical biogeography (Wiens & Donoghue, 2004). However, the majority of studies on species co-occurrence patterns are conducted at the scale of single forest patches and not generalized to larger spatial extents (e.g., McFadden et al., 2019; Seidler & Plotkin, 2006; Wiegand, Gunatilleke, & Gunatilleke, 2007). In addition to the scale-dependency of mechanisms behind co-occurrence patterns, different factors may explain spatial variations of plant species presence-absences and abundances: dispersal is an important predictor for presence-absences, while biotic interactions are important predictors for abundances (Boulangeat, Gravel, & Thuiller, 2012). Data on species presence-absences may allow capturing the potential competitive exclusion among species, while data on species abundances rather capture potential pairwise interactions within a local assemblage. Therefore, both presence-absence and abundance data are needed to infer the mechanisms behind species co-occurrence patterns. Probably due to combined shortcomings of available abundance data and statistical methodology, the mechanisms that define species' co-occurrences when generalized to large spatial scales have not been thoroughly deciphered. In order to gain insight into co-occurrences and their drivers at biogeographical scales, both spatially and taxonomically extensive data and computationally efficient methods are imperative.

Using comprehensive data on tropical tree abundances across a large spatial scale, we investigate how niche-based assembly processes, namely environmental filtering and limiting similarity, affect the co-occurrence patterns in species-rich tree communities. Following the preceding literature on patterns within single forest patches (see above), we expect abiotic environment to be important in explaining variation in species occurrences and co-occurrences when generalized to large spatial scales. Furthermore, we investigate whether the species co-occurrences are structured according to phylogenetic relatedness or functional similarity of species. We predict that functionally similar and closely-related species occur together less often and in lower abundances than expected due to niche overlap. Finally, we study the proportions of positive and negative co-occurrences across varying biogeographical regions. Since major biogeographical regions have substantial differences in their vegetation structures and species compositions, we expect to observe spatial variation in pairwise species co-occurrences among the regions.

2 Methods

2.1 Data

The studied tree communities are located in various biogeographical regions in Eastern South America, including the Atlantic Forest, Caatinga, Cerrado, Pampa and Pantanal (Figure 1). Eastern South America is characterised by a coast-inland gradient of precipitation and seasonality and a north-south gradient of temperature minimum. These climatic gradients coupled with the variation in geomorphologic and edaphic conditions result in a wide spectrum of woodland types ranging from tall rainforests to open canopy savannas. The study region includes forests with different proportions of deciduous trees and soil properties, growing in altitudes varying from sea level to 2300 m a.s.l.

2.1.1 Species occurrences

We retrieved abundance data of 1016 tree species from 574 community surveys (totalling 961184 individuals) from the Neotropical Tree Community database (TreeCo; http://labtrop.ib.usp.br/doku.php?id=projetos:treeco:start) using the methods described in de Lima et al. (2015). For this specific study, we selected the surveys including trees from the dominant/adult stratum of the vegetation, which were defined to include trees with diameter at breast height (DBH) ≥ 5 cm for closed canopy forests and DBH ≥ 3 cm or DGH (diameter at ground height) ≥ 5 cm for open canopy forests and savannas. We included only surveys that met the following criteria: minimum sampling effort of 0.5 ha, data published after 2000 and with a minimum 90 % of trees identified to species level. We did not consider planted or early secondary forests. Furthermore, we selected those surveys for which the available spatial coordinates were accurate enough to allow determination of the size of the focal forest fragment and to obtain reliable covariate values. Within these surveys, we selected for the analyses only the records of species with available phylogenetic and functional trait data after completing the trait matrix with upper-taxon averages (see details below), and a minimum of six occurrence records to ensure sufficient model fit. Here we define tree species as those plants with free-standing stems that can grow at least 4 meters tall, including trees, treelets, palms, tree ferns and cacti.

2.1.2 Environmental covariates and spatial structure

To study the possible abiotic effects on species co-occurrences patterns, we obtained climate, topography, soil and landscape covariates for each survey based on the information provided by the authors of the original surveys or on the spatial coordinates of the survey. Following preliminary analyses, we selected a set of uncorrelated variables to avoid collinearity in the model fitting. Climate covariates consisted of mean annual precipitation (mm), mean annual temperature (°C) (Alvares, Stape, Sentelhas, & de Moraes Gonçalves, 2013), and bioclimatic stress measured as a function of temperature seasonality, precipitation seasonality and climatic water deficit (for details, see Chave et al., 2014). As topography covariates, we included slope declivity (0-90 degrees) and aspect (0-360 degrees), both at 30 m resolution, built based on 2000 NASA Shuttle Radar Topography Mission using GDAL-QGIS software (version 3.4.4). As a soil property measure, we included soil quality, defined qualitatively with nutrient availability, nutrient retention capacity, rooting conditions, oxygen availability to roots, excess salts, toxicity and workability (Fischer et al., 2008). To account for the effects of forest patch metrics and human-induced disturbances, we obtained the area of the forest fragment surveyed (ha) and human influence index (Wildlife Conservation Society & Center for International Earth Science Information Network, 2005). Area of the fragment was obtained from the original publication and cross-checked using the SOS Mata Atlântica / INPE Atlantic Forest fragments mapping (Fundação SOS Mata Atlântica, 2014). We did not include landscape forest cover due to its strong correlation with forest fragment size that better corresponds to local patch quality. Finally, we included sampling effort (ha) and sampling method (point-centered quadrant, plot) to account for potential sampling effects.

We compiled species occurrence data hierarchically at ecoregion and sampling site scales (Figure 1). At the larger scale, we included ecoregions without spatial coordinates. Ecoregions were obtained and simplified from the Nature Conservancy (TNC) definitions (ecoregion scale, N = 10; Olson et al., 2001). Although the ecoregions, such as Cerrado and Caatinga, are distinguished from each other by biotic and abiotic differences, the borders between them are arbitrarily set, and transitional zones generally exist between the regions. At the smaller scale, we included the hierarchical level of sampling site with its spatial coordinates (site scale, N = 574).

2.1.3 Species characteristics

To study the effect of shared evolutionary history on species co-occurrence patterns, we built the phylogenetic tree based on the stored megatree R20120829 from Phylomatic (version 3; http://phylodiversity.net/phylomatic). The tree was calibrated using 'bladj' algorithm in Phylocom software (Webb, Ackerly, & Kembel, 2008), which is based on node ages suggested by Bell et al. (2010) and Magallón et al. (2015). We eliminated polytomies by generating random dichotomies with length 0.001 between sister species. To solve polytomies we used the 'ape' package in R software (version 3.5.0; Paradis, Claude, & Strimmer, 2004). Finally, we constructed a matrix of evolutionary distances in million years across all species pairs.

To assess the effect of functional similarity on species' co-occurrences, we obtained from the TreeCo database those plant traits that reflect the major axes of variation in ecological strategies (Díaz et al., 2015; Martins, dos Santos Seger, Wiegand, & dos Santos, 2018) and are relevant for species distribution modelling: seed length (cm), wood density (g/cm^3), maximum growth height (m), leaf area (cm^2), leaf type (compound, simple), dispersal syndrome (autochoric, anemochoric, barochoric, hydrochoric, zoochoric), successional group (pioneer, initial/late secondary, climax) and geographic distribution (local/regional endemic, central/southern/northern/western South America, Neotropical, Pantropical, exotic). Based on the assumption that closely related species tend to have similar trait values, we completed the trait matrix with genus level averages in cases of missing values of seed length, wood density and dispersal syndrome. We did not use genus level averages for traits that tend to have large variation within upper taxonomic levels, such as leaf area. We calculated a pairwise trait distance matrix using Gower distances in 'FD' package in R software (version 3.5.0; Laliberté & Legendre, 2010), thus allowing inclusion of categorical traits. Based on the distance matrix, we constructed a dendrogram using 'stats' package with UPGMA agglomeration method (R Core Team, 2019).

2.2 Statistical analyses

2.2.1 Joint species distribution modelling

We synthesised data on species occurrences, environmental and spatial variables, and species traits with Hierarchical Modelling of Species Communities framework (HMSC; Ovaskainen et al., 2017). HMSC is a joint species distribution model, and it thus models all species simultaneously. We fitted a hierarchically structured and spatially explicit Hurdle model to the species abundance data described above, meaning we first modelled presence-absences, and then only abundances conditional on presence. Fitting the model to both data separately allows deciphering the different ecological mechanisms that explain variations in species' presence-absences and abundances. We applied probit regression to presence-absence data and log-normal regression to abundance conditional on presence. We fitted the models within the Bayesian inference framework using the Matlab implementation of HMSC and the default prior distributions (for code and manual to fit the models, see https://www.helsinki.fi/en/researchgroups/statistical-ecology/hmsc). We evaluated the explanatory power of the HMSC model fit to presence-absence data by Tjur's R^2 (Tjur, 2009). To evaluate the explanatory power of the model fitted to the abundance data conditional on presence, we calculated the correlation between the data and predicted abundances.

Modelling species-rich communities is generally challenging as computation times increase exponentially with increasing number of species. HMSC allows circumventing this problem with a latent variable approach (Ovaskainen, Abrego, Halme, & Dunson, 2016; Ovaskainen, Tikhonov, Norberg, et al., 2017; Warton et al., 2015). We included latent variables at ecoregion level and spatially structured latent variables at sampling site level to account for spatial auto-correlation in the species occurrence data. Latent variables allow a representation of the species-to-species variance-covariance matrix (hereafter referred to as association matrix) through latent factors and their loadings. The factor loadings indicate patterns where two species co-occur less or more often or in higher or lower abundances than expected: if the loadings have the same sign, both species increase in occurrence probability or abundance, whereas if the factor loadings have opposite signs, one species declines while the other increases.

As oppose to traditional co-occurrence analyses (e.g., checkerboard scores by Stone & Roberts (1992)), HMSC allows modelling residual associations among species, thereby removing the underlying effect of environmental covariates. Therefore, we estimated association matrices with two alternative HMSC models: 1) model without the environmental covariates to produce raw associations and 2) model with the environmental covariates to produce residual associations. Raw associations represent the overall pairwise associations among species disregarding which factors drive the co-occurrences, while residual associations can be considered as hypotheses of species interactions, since the species' shared responses to the environmental covariates are controlled for. For these reasons, in the following analyses, we utilised raw associations when inferring mechanisms behind realised species co-occurrences and residual associations when inferring the potential species interactions. In particular, we use the residual associations obtained from the model fitted to the abundance data. This is because variation in species abundances better reflects the contemporary species interactions compared to their presence-absences that may rather be a realisation of past competitive exclusion or biogeographical barriers. Based on the raw and residual association matrices, we calculated the proportions of positive and negative associations among all species pairs with at least 95 % posterior probability.

2.2.2 Assessing spatial distribution of species co-occurrences

To infer potential hotspots of species interactions, we calculated for each local tree assemblage the percentages of residual positive and negative associations as sum of all significant associations of species pairs co-occurring in the assemblage. We plotted the spatial configurations of association percentages across Eastern South America and applied an analysis of variance test to study differences in average percentages among ecoregions. Furthermore, we assessed whether the transitional zones between ecoregions exhibited distinct percentages of positive and negative associations. We defined transitional zones as those areas within close proximity to established limits of ecoregions, where the assemblages are likely to exhibit characteristics of both ecoregions (McDonald et al., 2005; Smith et al., 2018).

2.2.3 Estimating effects of environmental filtering on species co-occurrences

We partitioned the explained variance in species occurrences among the environmental predictors and assessed how much of the responses were contributed to the covariates and the latent variables. In order to evaluate the relative role of environmental filtering, we compared the proportions of positive and negative associations between the raw and residual association matrices.

2.2.4 Estimating effects of phylogenetic relatedness and functional similarity on species co-occurrences

As opposed to the phylogenetic niche conservatism hypothesis (Harvey & Pagel, 1991), pairwise phylogenetic and trait distances did not correlate strongly ($r = 0.07$). Even when testing the correlation separately for phylogenetic distances and distances of each trait, we found correlation coefficients to be < 0.16. Thus we treated phylogenetic relatedness as an independent factor in the analyses, rather than as a proxy for species' functional space. To investigate the relationship of raw pairwise associations with pairwise phylogenetic and trait distances, we used Mantel test with 1000 permutations to calculate the correlations of the respective pairs of matrices. By ordering the raw association matrix according to the phylogenetic and trait distance dendrograms, we studied the clustering of raw positive and negative associations among the species visually.

Finally, we studied more closely the ecology of those species with the strongest residual positive ($N = 20$) and negative ($N = 20$) associations with other species to assess whether they represent distinctive trait combinations and whether their associations with other species could represent actual species interactions.

3 Results

The HMSC models fitted to the presence-absence data without and with environmental covariates explained 18.9 % and 24.9 % of the variation in species' presence-absences at the sampling site level, respectively. That is, the model explains species' occurrences and co-occurrences better when environmental factors are accounted for. The models fitted to the abundance data without and with environmental covariates explained 60.6 % and 71.5 % of the variation in species' abundances at the sampling site level, respectively. Note the different expressions of R^2 measure between models fitted to the presence-absence and abundance data (see section 2.2.1), so these numbers are not comparable as such.

We estimated more positive than negative associations. However, the estimated proportions of positive and negative associations differed between the studied spatial scales and between the models fitted to presence-absence and abundance data, as well as between models fitted without and with environmental covariates (Table 1). The observed associations were largely different at site and ecoregion scales, likely encompassing local assembly processes and biogeographical processes, respectively. Overall, we estimated more associations based on the models fitted to the presence-absence than to the abundance data. Furthermore, we estimated more associations at the sampling site than ecoregion level.

3.1 Effects of environmental filtering on and spatial configuration of species co-occurrences

According to the model fitted to the presence-absence data including environmental covariates, the selected environmental covariates corresponded to 36 % of the explained variation in species occurrences, whereas the remaining 64 % was attributed to the spatial latent factors. According to the model fitted to the abundance data including environmental covariates, the selected environmental covariates corresponded to 56 % of the explained variation, whereas the remaining 44 % was attributed to the spatial latent factors. With both models, the included climatic factors (mean annual precipitation, mean annual temperature and bioclimatic stress) were most important in explaining variation in species occurrences, on average corresponding to 25 % of the total explained variation (for full variance partitioning, see Appendix S1, Table S1).

Environmental filtering showed to be important in shaping tree species co-occurrences. The models including environmental covariates estimated fewer positive and negative associations than the models without environmental covariates, the positive associations from the model fitted to the presence-absence data being an exception (Table 1). The difference is attributed to those species co-occurrences that stem from species' shared responses to the environment.

According to the model fitted to the abundance data, we found the highest proportions of residual positive associations in Alto Parana and Uruguayan Savanna ecoregions, and the differences among the ecoregions in general were statistically significant (ANOVA: F = 63.3, df = 572, p < 0.01; Figure 2; Appendix S1, Figure S1). The proportions of residual negative associations were highest in Cerrado ecoregion and its transitional zones with other ecoregions, however, there were no statistically significant differences among the ecoregions (ANOVA: F = 0.29, df = 572, p = 0.29; Figure 2; Appendix S1, Figure S1).

3.2 Effects of phylogenetic relatedness and functional similarity on species co-occurrences

Phylogenetic and trait distances among species pairs showed weak relationships with raw association patterns based on the model fitted to the presence-absence data (Figure 3, panels (a)-(b)), while the relationships based on the model fitted to the abundance data were almost non-existent (Figure 3, panels (c)-(d)). Mantel correlation test showed no correlation between the matrices (Figure 3). Visual inspection of the raw associations ordered according to the distance dendrograms showed no distinct clustering according to the phylogenetic or trait distances, except for slight trait distance effects on raw associations according to the model fitted to the presence-absence data (Figure 4).

According to the model fitted to the abundance data, the species with the strongest positive associations was *Zanthoxylum rhoifolium*, whereas the species with the strongest negative associations was *Guarea guidonia* (see Appendix S1, Table S2 for the full lists of the species with the strongest associations). The trait spaces of the species with the strongest positive (20 species) and negative associations (20 species) did not differ significantly from each other (Appendix S1, Table S3). However, the species with the strongest positive associations were on average taller and more often of Neotropical distribution, while the species with the strongest negative associations had on average higher wood density and were more often late secondary and wind-dispersed species.

4 Discussion

Here, we used a comprehensive dataset of tropical trees to find that their co-occurrences are governed by environmental factors, rather than by phylogenetic relatedness or functional similarity. Furthermore, we found significant spatial variation in tree co-occurrences among the studied ecoregions. Our findings suggest that previously observed co-occurrence patterns at the scale of local forest patches can be generalized to large spatial extents.

Variation in species occurrences was best explained by the climatic variables, including mean temperature and precipitation as well as climate seasonality. This suggests that climate change may alter tree species distributions (similarly to Miles, Grainger, & Phillips, 2004), and the resulting co-occurrence patterns. In addition, we found that the effect of anthropogenic disturbances (here, forest fragment area and human influence) was larger on tree abundances than presence-absences, which may indicate declining population trends for some species and increasing population trends for others under intensifying anthropogenic pressures.

According to the limiting similarity hypothesis, the co-occurrences among closely related and functionally similar species should be predominantly negative. As oppose to preceding research (Kraft et al., 2008; Wilson & Stubbs, 2012, but see Silva & Batalha, 2009), we did not observe any constraints of limiting similarity, i.e. how phylogenetically related or functionally similar the species can be to co-occur. Competitive exclusion can take an extremely long time and the importance of limiting similarity in that may be overridden by speciation (Hubbell & Foster, 1986), leading to seemingly random patterns of species co-occurrences. Furthermore, outcomes of limiting similarity may be masked because we considered species occurrences at sampling site scale without information of the spatial configuration of individual trees within the site. Therefore, the modelled associations may not reflect the fine scale avoidance of similar species as they may still co-occur within the same sampling site.

Although useful for inferring drivers of community assembly and the consequent co-occurrences, different niche-based processes cannot be completely separated based on observed patterns of species co-occurrences. In general, functional niche differences are influenced by, and themselves influence, environmental and competitive factors (Kraft et al., 2015). Both environmental filtering and competition among species may select for functionally similar species to occur together locally. Environmental filtering would produce this pattern by filtering the local species pool according to species' abilities to disperse and establish in particular environmental conditions (Bazzaz, 1991; Kraft et al. 2015). On the other hand, competition among species can drive the local co-occurrence of functionally similar species if trait differences drive fitness differences (Chesson, 2000). Indeed, competition may exclude more functionally different and less related species, even when the traits underlying the species differences are phylogenetically conserved (Mayfield & Levine, 2010). Particular plant traits, such as stem size and leaf economics, are important for adaptation to the local environmental conditions across the phylogeny (Díaz et al., 2015). Especially species-saturated communities, such as tropical tree assemblages, may be characterised by convergent evolution and invasion of "look-a-likes" (Scheffer & van Nes, 2006). Potentially, environment is filtering emergent groups (Hérault, 2007), i.e. groups of species that are functionally similar, which then drives functional differences among local communities at larger spatial scales. In particular, climatic conditions and habitat filtering within the ecoregions may select for a set of common characteristics (Echeverría-Londoño et al., 2018; Li et al., 2018). Finally, difficulties with inferring assembly processes from local co-occurrences reflects the general difficulty of inferring process from pattern.

Our results indicate that species interactions (hypothesised based on residual associations) may play a significant role in shaping the limits of ecoregions. Tree communities with the highest proportions of negative associations were located in the transitional zones between major biogeographical regions, suggesting a dispersal and/or establishment barrier between the regions, possibly founded on species interactions. Indeed, interactions among species can act as gate keepers to new species, i.e. other species would prevent dispersal or establishment of immigrants through competitive superiority or historical priority effects (Fukami, 2015; Fukami et al., 2005). More specifically, as the estimated associations based on the abundance data by default require co-occurrence within sampling sites, we expect the respective negative associations to reflect establishment rather than dispersal barriers. Moreover, 75 % of the studied tree species are animal-dispersed, a dispersal syndrome known to be efficient (Myers, Vellend, Gardescu, & Marks, 2004), making dispersal limitation the less plausible mechanism. Despite occurring rarely (C. J. Clark, Poulsen, Bolker, Connor, & Parker, 2005; J. S. Clark, Silman, Macklin, & HilleRisLambers, 1999), long distance seed dispersal events may be key to colonization of new ecoregions. However, tree occurrences are mainly driven by establishment and growth, which are affected by many ecological factors, such as seed predation and light conditions (Janzen, 1970; Rüger, Berger, Hubbell, Vieilledent, & Condit, 2011). Transitional zones between ecoregions are highly variable and may therefore induce different effects on species' co-occurrences and interactions. For example, the transitional zone between Cerrado and Caatinga is likely to stem from their difference in length of the dry season, whereas the transitional zones between Bahia, Serra do Mar, and Araucaria are likely founded on temperature differences (Alvares et al., 2013; Liebmann et al., 2007). We note that the observed pattern may also be generated by a barrier by combined effects of multiple factors preventing species from establishing to a new ecoregion beyond the transitional zones. However, as we included a wide range of environmental covariates in our model, it is unlikely that the observed pattern would be solely produced by these barriers.

Fitting the model to presence-absence and abundance data separately yielded additional evidence for the importance of biogeographical scale mechanisms: there were more negative associations according to the model fitted to the presence-absence data than to the model fitted to the abundance data. This indicates that it is more common for species not to co-occur due to biogeographical limitations (the likely mechanism behind species presence-absences) than it is for them to co-occur locally and still have a negative association (the likely mechanism behind species abundances). However, the difference between the negative associations estimated by different models may also be due to a statistical artefact. This is because detecting negative associations with HMSC requires considerable amount of data and the model fitted to the abundance data conditional on presence utilises a smaller set of data than that of presence-absence data.

Disentangling the mechanisms maintaining tropical tree diversity is challenging, spatially and taxonomically unevenly distributed data hindering general conclusions. We overcame one of the main challenges within the field of biodiversity maintenance by utilising high quality data on species occurrences at a large spatial scale. In this study, we used the occurrence data to model residual species-to-species associations, meaning that the effects of species' similar responses to the environmental covariates were eliminated in the estimation of associations. However, interpreting residual species-to-species associations as species interactions from non-manipulative occurrence data is problematic as unmeasured environmental covariates may drive the association patterns instead (Dormann et al., 2018; Freilich, Wieters, Broitman, Marquet, & Navarrete, 2018). On the other hand, indirect species interactions, such as apparent competition, are few in the literature and research tends to focus on the observed networks of direct interactions. As a result, significant associations are often disregarded as false positives or negatives in co-occurrence analyses (e.g., Freilich et al., 2018). Thus, our estimated residual associations pose interesting hypotheses of direct and indirect ecological interactions to be tested in the future.

Due to data and model structures, we considered the net outcome of the species-to-species association and treated the associations as stationary and symmetrical. However, a pair of species may simultaneously be associated both positively and negatively (e.g., Bimler, Stouffer, Lai, & Mayfield, 2018; Brooker et al., 2008), their responses to each other may be unbalanced (Frederickson, 2013) and they are likely to experience spatial variation in their association (Tikhonov, Abrego, Dunson, & Ovaskainen, 2017). For example, a negative association via light competition may be masked by a stronger positive association introduced by nitrogen fixing or mycorrhizal fungi facilitation (Verdú & Valiente-Banuet, 2011) or similar species may together attract pollinators more efficiently, thus increasing the benefits of co-occurrence even when competing over other resources (Hegland, Grytnes, & Totland, 2009). In our study, we did not model the spatial variation in associations of individual species pairs, leading to the spatial patterns of local associations being driven by community composition. This takes us one step closer to the actual mechanisms, but to further improve the understanding of co-occurrence patterns in the tropics, we recommend future research to develop ways to account for the non-stationary and asymmetrical associations among species (similarly to Ovaskainen, Tikhonov, Dunson, et al., 2017 and Tikhonov et al., 2017). Additionally, to explain the possible dispersal and establishment barriers between major biogeographical regions, more detailed understanding on spatial trait composition and variation in relation to positive and negative associations in local communities is needed.

Understanding how the abiotic environment drives tree species' occurrences and co-occurrences has both conservational and methodological applications. Firstly, shifts in tree occurrences due to environmental factors need to be accounted for in conservation prioritisation as future distributions of species may not match the current ones (Miles et al., 2004). Secondly, presence-absence data alone may not suffice for inferring effects of environmental change on species communities as the negative population trends may be masked until (local) extinctions of species unless abundance data is obtained. Finally, when inferring species interactions from co-occurrences, including environmental covariates in the model is essential. Otherwise, estimated raw co-occurrences (here, associations) will largely represent species' shared responses to the abiotic environment rather than actual pairwise interactions.

Acknowledgements

We thank André Amorim, João L.F. Batista, Marcelo Pansonato, Mariana C. Pardgurschi and Ricardo R. Rodrigues for providing their published or unpublished tree abundance data. We thank Luiz F.S. Magnago for providing additional trait information for several species. We also thank Gregory Pitta, Danilo Mori, Markus Gastauer, Carolina Bello, Natália Targhetta and Geison Castro for helping with the compilation of abundance and trait data from the literature. This work was partly supported by the Research Council of Norway through its Centres of Excellence Funding Scheme (223257) to EM, VG & OO via Centre for Biodiversity Dynamics, by the Academy of Finland grants to OO (284601, 273253 and 309581), and by São Paulo Research Foundation (FAPESP) grant 2013/08722-5 to RAFL. RAFL also received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Sklodowska-Curie Grant Agreement No. 795114. The data collection of some of the major forest plots was supported by grants 99/08515-0 and 99/09635-0 (FAPESP).

Data availability

The utilised data are stored in Neotropical Tree Communities (TreeCo) database and are available by request through the database.

References

Adams, J. M., & Woodward, F. I. (1989). Patterns in tree species richness as a test of the glacial extinction hypothesis. *Nature*, *339*(6227), 699–701. https://doi.org/10.1038/339699a0

Alvares, C. A., Stape, J. L., Sentelhas, P. C., & de Moraes Gonçalves, J. L. (2013). Modeling monthly mean air temperature for Brazil. *Theoretical and Applied Climatology*, *113*(3–4), 407–427. https://doi.org/10.1007/s00704-012-0796-6

Bazzaz, F. A. (1991). Habitat selection in plants. *American Naturalist*, *137*, 116–130. https://doi.org/10.1086/285142

Bell, C. D., Soltis, D. E., & Soltis, P. S. (2010). The age and diversification of the angiosperms re-revisited. *American Journal of Botany*, *97*(8), 1296–1303. https://doi.org/10.3732/ajb.0900346

Bimler, M. D., Stouffer, D. B., Lai, H. R., & Mayfield, M. M. (2018). Accurate predictions of coexistence in natural systems require the inclusion of facilitative interactions and environmental dependency. *Journal of Ecology*, *106*(5), 1839–1852. https://doi.org/10.1111/1365-2745.13030

Boulangeat, I., Gravel, D., & Thuiller, W. (2012). Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. *Ecology Letters*, *15*(6), 584–593. https://doi.org/10.1111/j.1461-0248.2012.01772.x

Brooker, R. W., Maestre, F. T., Callaway, R. M., Lortie, C. L., Cavieres, L. A., Kunstler, G., … Michalet, R. (2008). Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology*, *96*(1), 18–34. https://doi.org/10.1111/j.1365-2745.2007.01295.x

Cadotte, M. W., & Tucker, C. M. (2017). Should environmental filtering be abandoned? *Trends in Ecology and Evolution*, *32*(6), 429–437. https://doi.org/10.1016/j.tree.2017.03.004

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M. S., Delitti, W. B. C., … Vieilledent, G. (2014). Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology*, *20*(10), 3177–3190. https://doi.org/10.1111/gcb.12629

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, *31*, 343–366. https://doi.org/10.1146/annurev.ecolsys.31.1.343

Clark, C. J., Poulsen, J. R., Bolker, B. M., Connor, E. F., & Parker, V. T. (2005). Comparatie seed shadows of bird-, monkey-, and wind-dispersed trees. *Ecology*, *86*(10), 2684–2694. https://doi.org/10.1890/04-1325

Clark, J. S., Silman, R., Macklin, E., & HilleRisLambers, J. (1999). Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology*, *80*(5), 1475–1494. https://doi.org/10.1890/0012-9658(1999)080[1475:SDNAFP]2.0.CO;2

Diamond, J. M. (1975). Assembly of species communities. In M. L. Cody & J. M. Diamond (Eds.), *Ecology and evolution of communities* (pp. 342–444). Cambridge: Harvard University Press.

Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., … Gorné, L. D. (2015). The global spectrum of plant form and function. *Nature*, *529*(7585), 167–171. https://doi.org/10.1038/nature16489

Dormann, C. F., Bobrowski, M., Dehling, D. M., Harris, D. J., Hartig, F., Lischke, H., … Kraan, C. (2018). Biotic interactions in species distribution modelling: ten questions to guide interpretation and avoid false conclusions. *Global Ecology and Biogeography*, *27*(9), 1004–1016. https://doi.org/10.1002/adsc.201

Echeverría-Londoño, S., Enquist, B. J., Neves, D. M., Violle, C., Boyle, B., Kraft, N. J. B., … Wiser, S. K. (2018). Plant functional diversity and the biogeography of biomes in North and South America. *Frontiers in Ecology and the Environment*, *6*, 219. https://doi.org/10.3389/fevo.2018.00219

Fischer, G., Nachtergaele, F., Prieler, S., van Velthuizen, H. T., Verelst, L., & Wiberg, D. (2008). *Global agro-ecological zones assessment for agriculture (GAEZ 2008)*. Laxenburg & Rome: IIASA & FAO.

Frederickson, M. E. (2013). Rethinking mutualism stability: cheaters and the evolution of sanctions. *The Quarterly Review of Biology*, *88*(4), 269–295. https://doi.org/10.1177/0959354311432905

Freilich, M. A., Wieters, E., Broitman, B. R., Marquet, P. A., & Navarrete, S. A. (2018). Species co-occurrence networks: can they reveal trophic and non-trophic interactions in ecological communities? *Ecology*, *99*(3), 690–699. https://doi.org/10.1002/ecy.2142

Fukami, T. (2015). Historical contingency in community assembly: integrating niches, species pools, and priority effects. *Annual Review of Ecology, Evolution, and Systematics*, *46*(1), 1–23. https://doi.org/10.1146/annurev-ecolsys-110411-160340

Fukami, T., Bezemer, T. M., Mortimer, S. R., & Van Der Putten, W. H. (2005). Species divergence and trait convergence in experimental plant community assembly. *Ecology Letters*, *8*(12), 1283–1290. https://doi.org/10.1111/j.1461-0248.2005.00829.x

Fundação SOS Mata Atlântica. (2014). *Atlas dos remanescentes florestais da Mata Atlântica: período 2012-2013*. Fundação SOS Mata Atlântica, Instituto Nacional de Pesquisas Espaciais.

Hardin, G. (1960). The competitive exclusion principle. *Science*, *131*(3409), 1292–1297. https://doi.org/10.1126/science.131.3409.1292

Harvey, P. H., & Pagel, M. D. (1991). *The comparative method in evolutionary biology*. New York: Oxford University Press.

Hegland, S. J., Grytnes, J. A., & Totland, Ø. (2009). The relative importance of positive and negative interactions for pollinator attraction in a plant community. *Ecological Research*, *24*(4), 929–936. https://doi.org/10.1007/s11284-008-0572-3

Hérault, B. (2007). Reconciling niche and neutrality through the Emergent Group approach. *Perspectives in Plant Ecology, Evolution and Systematics*, *9*(2), 71–78. https://doi.org/10.1016/j.ppees.2007.08.001

Hubbell, S.P., & Foster, R. B. (1986). Biology, chance, and history and the structure of tropical rain forest tree communities. In J. Diamond & T. J. Case (Eds.), *Community ecology* (pp. 314–329). New York: Harper and Row.

Hubbell, Stephen P. (2001). *The unified neutral theory of biodiversity and biogeography*. Princeton: Princeton University Press.

Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forests. *American Naturalist*, *104*(940), 501–528. https://doi.org/10.1086/282687

Keddy, P. A. (1992). Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science*, *3*(2), 157–164. https://doi.org/10.2307/3235676

Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., & Levine, J. M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*, *29*(5), 592–599. https://doi.org/10.1111/1365-2435.12345

Kraft, N. J. B., Valencia, R., & Ackerly, D. D. (2008). Functional traits and niche-based tree community assembly in an Amazonian forest. *Science*, *322*(5901), 580–582. https://doi.org/10.1126/science.1160662

Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, *91*, 299–305.

Li, Y., Shipley, B., Price, J. N., Dantas, V. de L., Tamme, R., Westoby, M., … Batalha, M. A. (2018). Habitat filtering determines the functional niche occupancy of plant communities worldwide. *Journal of Ecology*, *106*(3), 1001–1009. https://doi.org/10.1111/1365-2745.12802

Liebmann, B., Camargo, S. J., Seth, A., Marengo, J. A., Carvalho, L. M. V., Allured, D., … Vera, C. S. (2007). Onset and end of the rainy season in South America in observations and the ECHAM 4.5 atmospheric general circulation model. *Journal of Climate*, *20*(10), 2037–

2050. https://doi.org/10.1175/JCLI4122.1

MacArthur, R., & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist*, *101*, 377–385. https://doi.org/10.1086/282505

Magallón, S., Gómez-Acevedo, S., Sánchez-Reyes, L. L., & Hernández-Hernández, T. (2015). A metacalibrated time-tree documents the early rise of flowering plant phylogenetic diversity. *New Phytologist*, *207*(2), 437–453. https://doi.org/10.1111/nph.13264

Martins, V. F., dos Santos Seger, G. D., Wiegand, T., & dos Santos, F. A. M. (2018). Phylogeny contributes more than site characteristics and traits to the spatial distribution pattern of tropical tree populations. *Oikos*, *127*(9), 1368–1379. https://doi.org/10.1111/oik.05142

Mayfield, M. M., & Levine, J. M. (2010). Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*, *13*(9), 1085–1093. https://doi.org/10.1111/j.1461-0248.2010.01509.x

McDonald, R., McKnight, M., Weiss, D., Selig, E., O’Connor, M., Violin, C., & Moody, A. (2005). Species compositional similarity and ecoregions: Do ecoregion boundaries represent zones of high species turnover? *Biological Conservation*, *126*(1), 24–40. https://doi.org/10.1016/j.biocon.2005.05.008

McFadden, I. R., Bartlett, M. K., Wiegand, T., Turner, B. L., Sack, L., Valencia, R., & Kraft, N. J. B. (2019). Disentangling the functional trait correlates of spatial aggregation in tropical forest trees. *Ecology*, *100*(3), e02591. https://doi.org/10.1002/ecy.2591

Miles, L., Grainger, A., & Phillips, O. (2004). The impact of global climate change on tropical forest biodiversity in Amazonia. *Global Ecology and Biogeography*, *13*, 553–565. https://doi.org/10.1111/j.1466-822X.2004.00105.x

Myers, J. A., Vellend, M., Gardescu, S., & Marks, P. L. (2004). Seed dispersal by white-tailed deer: implications for long-distance dispersal, invasion, and migration of plants in eastern North America. *Oecologia*, *139*(1), 35–44. https://doi.org/10.1007/s00442-003-1474-2

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., … Kassem, K. R. (2001). Terrestrial ecoregions of the world: a new map of life on Earth. *BioScience*, *51*(11), 933–938. https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

Ovaskainen, O., Abrego, N., Halme, P., & Dunson, D. (2016). Using latent variable models to identify large networks of species-to-species associations at different spatial scales. *Methods in Ecology and Evolution*, *7*, 549–555. https://doi.org/10.1111/2041-210X.12501

Ovaskainen, O., Tikhonov, G., Dunson, D., Grøtan, V., Engen, S., Sæther, B.-E., & Abrego, N. (2017). How are species interactions structured in species-rich communities? A new method for analysing time-series data. *Proceedings of the Royal Society B: Biological Sciences*, *284*, 20170768. https://doi.org//10.1098/rspb.2017.0768

Ovaskainen, O., Tikhonov, G., Norberg, A., Blanchet, F. G., Duan, L., Dunson, D., … Abrego, N. (2017). How to make more out of community data? A conceptual framework and its implementation as models and software. *Ecology Letters*, *20*, 561–576. https://doi.org/10.1111/ele.12757

Paradis, E., Claude, J., & Strimmer, K. (2004). APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, *20*(2), 289–290. https://doi.org/10.1093/bioinformatics/btg412

R Core Team. (2019). R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. Retrieved from http://www.r-project.org/

Rüger, N., Berger, U., Hubbell, S. P., Vieilledent, G., & Condit, R. (2011). Growth strategies of tropical tree species: disentangling light and size effects. *PLoS ONE*, *6*(9), e25330.

https://doi.org/10.1371/journal.pone.0025330

Scheffer, M., & van Nes, E. H. (2006). Self-organized similarity, the evolutionary emergence of groups of similar species. *Proceedings of the National Academy of Sciences*, *103*(16), 6230–6235. https://doi.org/10.1073/pnas.0508024103

Seidler, T. G., & Plotkin, J. B. (2006). Seed dispersal and spatial pattern in tropical trees. *PLoS Biology*, *4*(11), 2132–2137. https://doi.org/10.1371/journal.pbio.0040344

Silva, I. A., & Batalha, M. A. (2009). Co-occurrence of tree species at fine spatial scale in a woodland cerrado, southeastern Brazil. *Plant Ecology*, *200*(2), 277–286. https://doi.org/10.1007/s11258-008-9452-8

Smith, J. R., Letten, A. D., Ke, P. J., Anderson, C. B., Hendershot, J. N., Dhami, M. K., … Daily, G. C. (2018). A global test of ecoregions. *Nature Ecology and Evolution*, *2*(12), 1889–1896. https://doi.org/10.1038/s41559-018-0709-x

Stone, L., & Roberts, A. (1992). Competitive exclusion, or species aggregation? An aid in deciding. *Oecologia*, *91*(3), 419–424. https://doi.org/10.1007/BF00317632

Tikhonov, G., Abrego, N., Dunson, D., & Ovaskainen, O. (2017). Using joint species distribution models for evaluating how species-to-species associations depend on the environmental context. *Methods in Ecology and Evolution*, *8*(4), 443–452. https://doi.org/10.1111/2041-210X.12723

Tjur, T. (2009). Coefficients of determination in logistic regression models - a new proposal: The coefficient of discrimination. *American Statistician*, *63*(4), 366–372. https://doi.org/10.1198/tast.2009.08210

van der Valk, A. G. (1981). Succession in wetlands: A Gleasonian approach. *Ecology*, *62*(3), 688–696.

Verdú, M., & Valiente-Banuet, A. (2011). The relative contribution of abundance and phylogeny to the structure of plant facilitation networks. *Oikos*, *120*(9), 1351–1356. https://doi.org/10.1111/j.1600-0706.2011.19477.x

Warton, D. I., Blanchet, F. G., O'Hara, R. B., Ovaskainen, O., Taskinen, S., Walker, S. C., & Hui, F. K. C. (2015). So many variables: joint modeling in community ecology. *Trends in Ecology and Evolution*, *30*(12), 766–779. https://doi.org/10.1016/j.tree.2015.09.007

Webb, C. O., Ackerly, D. D., & Kembel, S. W. (2008). Phylocom: Software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics*, *24*(18), 2098–2100. https://doi.org/10.1093/bioinformatics/btn358

Weiher, E., & Keddy, P. A. (1995). Assembly rules, null models, and trait dispersion: new questions from old patterns. *Oikos*, *74*(1), 159–164.

Wiegand, T., Gunatilleke, S., & Gunatilleke, N. (2007). Species associations in a heterogeneous Sri Lankan dipterocarp forest. *The American Naturalist*, *170*(4), E77–E95. https://doi.org/10.1086/521240

Wiens, J. J., & Donoghue, M. J. (2004). Historical biogeography, ecology and species richness. *Trends in Ecology and Ecolution*, *19*(12), 639–644. https://doi.org/10.1016/j.tree.2004.09.011

Wildlife Conservation Society, & Center for International Earth Science Information Network. (2005). *Global Human Influence Index (Geographic), v2 (1995-2004)*. Palisades: NASA Socioeconomic Data and Applications Center (SEDAC). https://doi.org/10.7927/H4BP00QC

Wilson, J. B., & Stubbs, W. J. (2012). Evidence for assembly rules: limiting similarity within a saltmarsh. *Journal of Ecology*, *100*(1), 210–221. https://doi.org/10.1111/j.1365-

2745.2011.01891.x

Zobel, M. (1997). The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends in Ecology & Evolution*, *12*(7), 266–269. https://doi.org/10.1016/S0169-5347(97)01096-3

Table 1. Percentages of estimated raw and residual positive and negative associations at sampling site and ecoregion scales according to the models fitted to the presence-absence and abundance data.

Data type	**Spatial scale**	**Associations (%)**			
		Positive		Negative	
		Raw	Residual	Raw	Residual
Presence-absence	Site	43.0	51.3	17.1	7.1
	Ecoregion	22.6	12.7	18.7	8.6
Abundance	Site	17.2	10.2	1.0	0.6
	Ecoregion	0.06	0.01	0.03	0.01

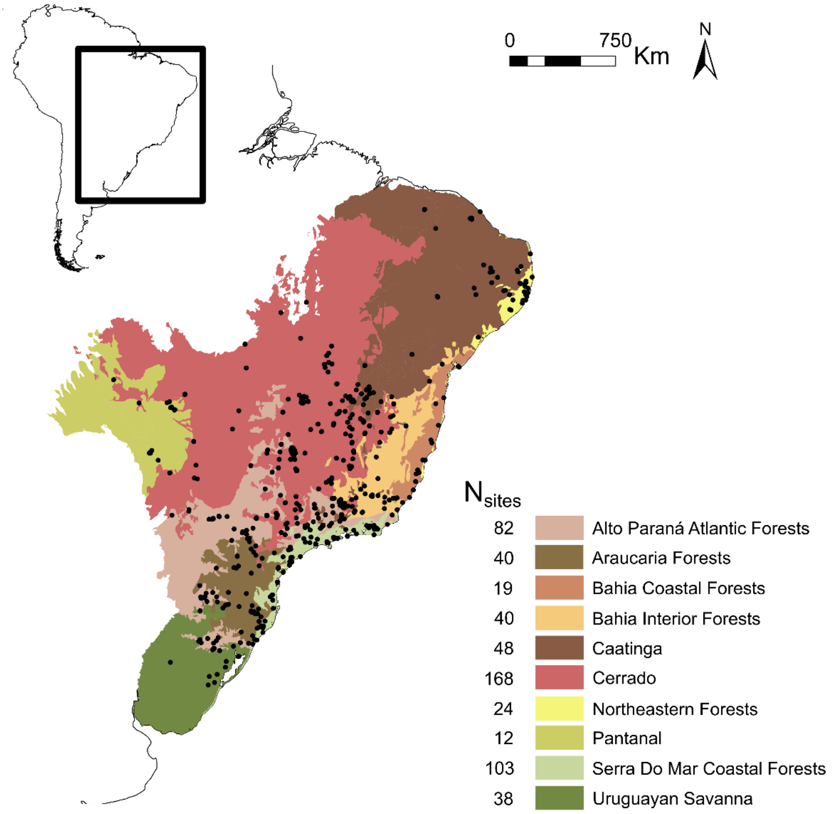


Figure 1. Map of the hierarchically structured sampling design in eastern South America. Included levels are ecoregion (N = 10 (colour); simplified based on Olson et al., 2001) and sampling site (N = 574; black circle). Distribution of sampling sites among ecoregions is indicated next to the legend.

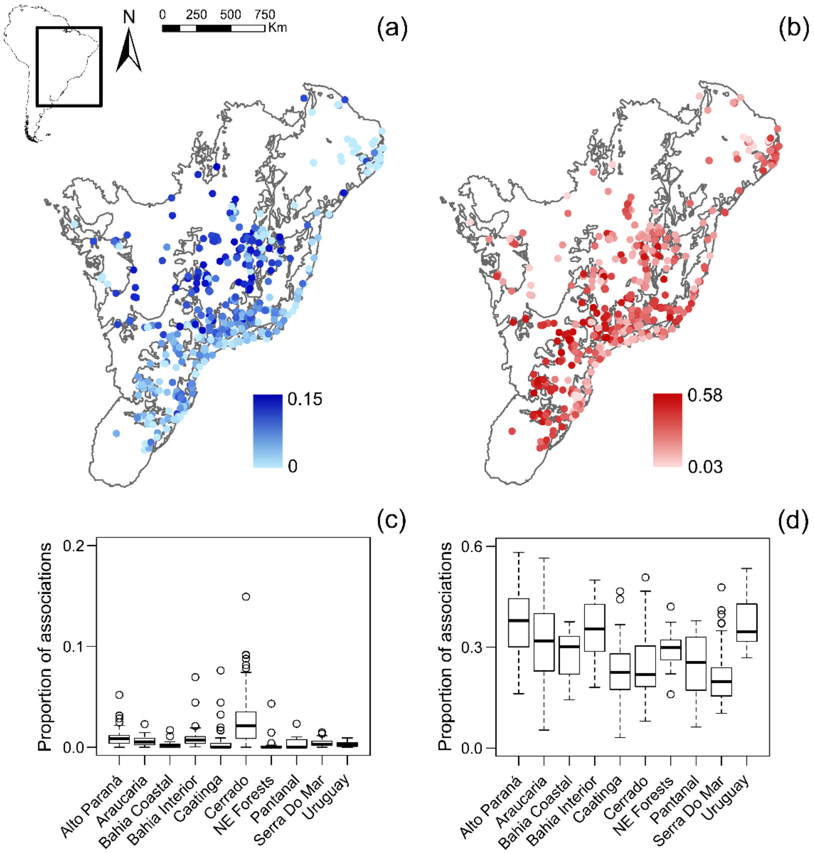


Figure 2. Spatial distribution of proportions of (a) residual negative and (b) residual positive associations over the species pairs present across sampling sites and variation of (c) residual negative and (d) residual positive association proportions in each ecoregion, that are delimited with grey lines in panels (a) and (b) (see Figure 1 for ecoregion names). Note the different y-axis scales in panels (c) and (d).

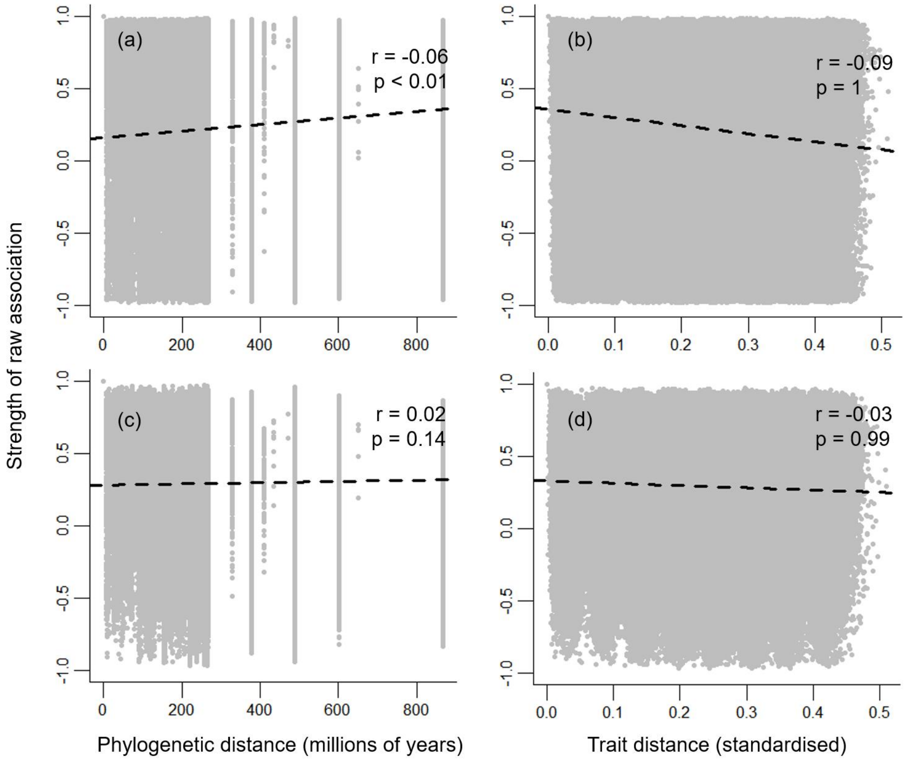


Figure 3. Relationships of pairwise raw association strengths and phylogenetic and trait distances according to the models fitted to the presence-absence data (a)-(b) and abundance data (c)-(d). Panels (a)-(b) represent raw association strength ~ phylogenetic distance and raw association strength ~ trait distance according to the model fitted to the presence-absence data – relationships, respectively. Panels (c)-(d) represent raw association strength ~ phylogenetic distance and raw association strength ~ trait distance –relationships, respectively. Each grey circle represents an estimated pairwise association. Mantel test results (correlation coefficient (r) and significance (p) -values) based on 1000 permutations are shown for each matrix pair correlation.

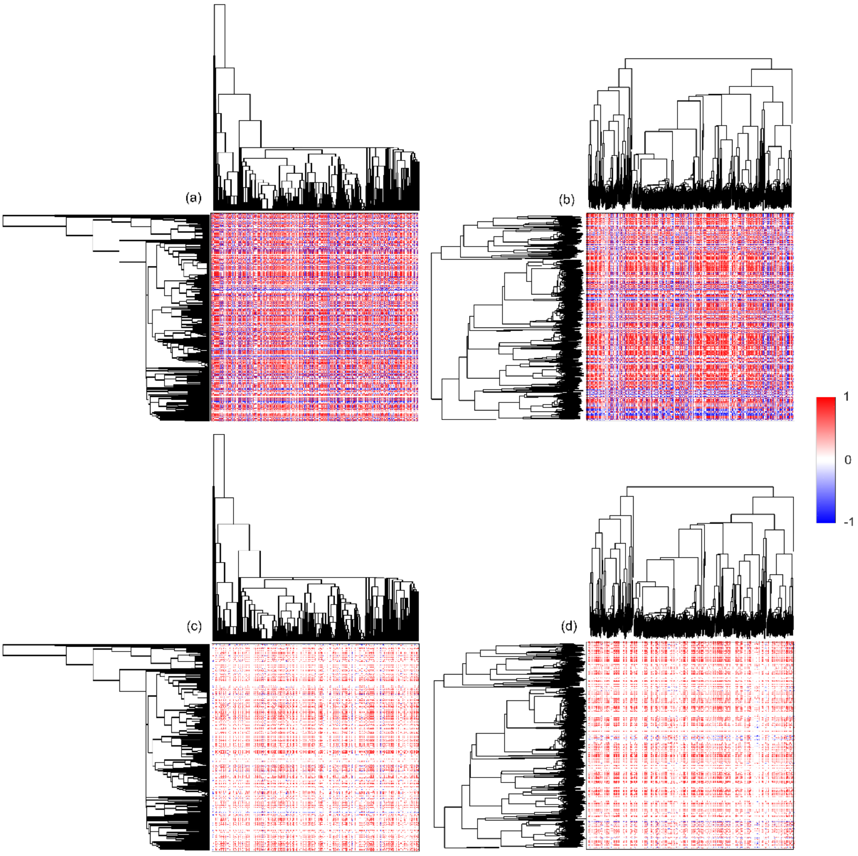


Figure 4. Estimated raw associations at sampling site scale, based on models fitted to the presence-absence data (a)-(b) and abundance data (c)-(d). The illustrated association matrix identifies species pairs showing a positive (red) or negative (blue) association, shown only if association has either sign with at least 95 % posterior probability (the non-significant associations are shown as white). The species have been ordered according to phylogenetic ((a) and (c)) and trait ((b) and (d)) distance dendrograms.

Marjakangas et al.

Co-occurrences of tropical trees: disentangling abiotic and biotic forces

Supporting information Appendix S1.

Additional results

Table S1. Variance partitioning. Percentage of variance explained (%) by each included covariate and spatial random effect in models fitted to the presence-absence and abundance data. For description of the covariates, see Methods.

Category	**Covariate**	**Model**	
		Presence-absence	Abundance
Spatial random effect	Site level	57	37
	Ecoregion level	8	7.3
Sampling	Effort (ha)	1.8	14
	Sampling method	0.59	2.1
Topography	Declivity	1.1	3.4
	Slope	0.47	2.2
Climate	Mean annual precipitation	6.3	4.5
	Mean annual temperature	13	9.9
	Bioclimatic stress	8.9	8.2
Disturbance	Fragment area (ha)	1.5	4.1
	Human influence	0.79	3.3
Soil	Soil quality	1.1	4.1

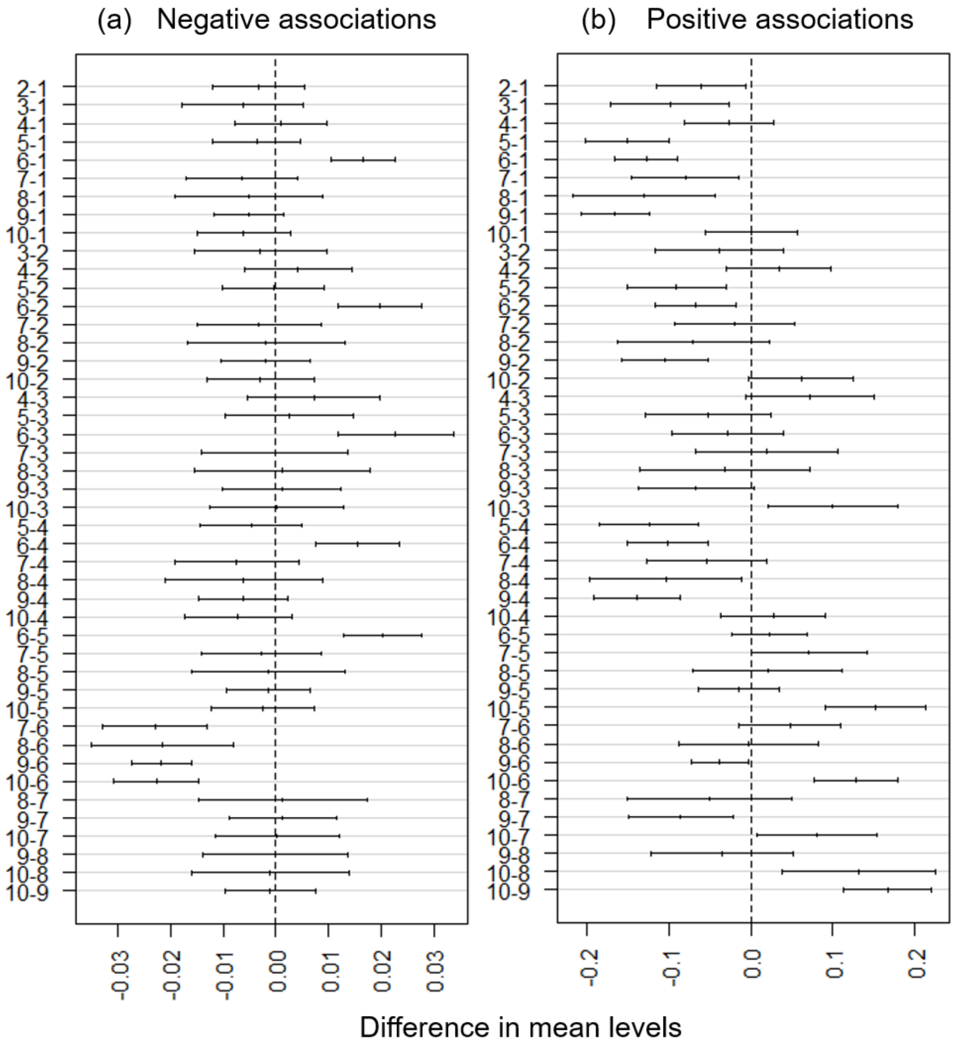


Figure S1. Results of Tukey's HSD test with 95% confidence level on pairwise differences in proportions of residual (a) negative and (b) positive associations among studied ecoregions based on the model fitted to the abundance data. Ecoregions are numbered alphabetically on the y-axis: 1 = Alto Paraná, 2 = Araucaria, 3 = Bahia Coastal, 4 = Bahia Interior, 5 = Caatinga, 6 = Cerrado, 7 = NE Forests, 8 = Pantanal, 9 = Serra Do Mar, 10 = Uruguay. See Figure 1 in main text for ecoregion limits.

Table S2. List of the species with the strongest residual positive and negative associations, i.e. with the absolute mean over the significant residual association belonging to the 98% quantile, according to models fitted to the presence-absence and abundance data.

Presence-absence data			Abundance data		
Species	**Strength$_{association}$**	**Type of association**	**Species**	**Strength$_{association}$**	**Type of association**
Zanthoxylum monogynum	0.880	positive	*Zanthoxylum rhoifolium*	0.863	positive
Zanthoxylum rhoifolium	0.876	positive	*Zeyheria tuberculosa*	0.827	positive
Zollernia ilicifolia	0.871	positive	*Allophylus edulis*	0.817	positive
Zollernia glabra	0.861	positive	*Annona rugulosa*	0.813	positive
Ziziphus glaziovii	0.855	positive	*Zanthoxylum kleinii*	0.812	positive
Cordia sellowiana	0.849	positive	*Cupania vernalis*	0.812	positive
Cinnamomum pseudoglaziovii	0.849	positive	*Guapira opposita*	0.811	positive
Guapira opposita	0.849	positive	*Campomanesia guazumifolia*	0.810	positive
Garcinia gardneriana	0.848	positive	*Casearia sylvestris*	0.810	positive
Hirtella hebeclada	0.848	positive	*Celtis iguanaea*	0.808	positive
Aniba firmula	0.848	positive	*Centrolobium sclerophyllum*	0.806	positive
Hyeronima alchorneoides	0.847	positive	*Campomanesia xanthocarpa*	0.805	positive
Duguetia lanceolata	0.847	positive	*Guazuma ulmifolia*	0.804	positive
Heisteria silvianii	0.846	positive	*Casearia decandra*	0.804	positive
Guatteria australis	0.846	positive	*Lecythis lurida*	0.803	positive
Amaioua guianensis	0.846	positive	*Bauhinia forficata*	0.802	positive
Coussapoa microcarpa	0.845	positive	*Guettarda viburnoides*	0.802	positive
Dendropanax cuneatus	0.845	positive	*Acosmium lentiscifolium*	0.801	positive
Alchornea triplinervia	0.844	positive	*Nectandra oppositifolia*	0.801	positive
Ixora brevifolia	0.844	positive	*Machaerium paraguariense*	0.801	positive
Zanthoxylum petiolare	-0.878	negative	*Guarea guidonia*	-0.831	negative
Zanthoxylum caribaeum	-0.842	negative	*Handroanthus vellosoi*	-0.824	negative
Virola sebifera	-0.831	negative	*Handroanthus heptaphyllus*	-0.822	negative
Vochysia tucanorum	-0.828	negative	*Cassia ferruginea*	-0.820	negative
Vismia guianensis	-0.826	negative	*Faramea multiflora*	-0.818	negative
Xylopia sericea	-0.823	negative	*Hyeronima alchorneoides*	-0.815	negative
Commiphora leptophloeos	-0.811	negative	*Dilodendron bipinnatum*	-0.813	negative
Myrrhinium atropurpureum	-0.804	negative	*Eugenia astringens*	-0.813	negative
Manihot carthagenensis	-0.803	negative	*Guapira opposita*	-0.807	negative
Vochysia magnifica	-0.801	negative	*Guazuma ulmifolia*	-0.804	negative
Maytenus gonoclada	-0.801	negative	*Albizia polycephala*	-0.802	negative
Amburana cearensis	-0.800	negative	*Dalbergia villosa*	-0.801	negative
Zanthoxylum riedelianum	-0.796	negative	*Handroanthus serratifolius*	-0.801	negative
Tachigali denudata	-0.795	negative	*Himatanthus obovatus*	-0.801	negative
Lecythis pisonis	-0.789	negative	*Eugenia florida*	-0.801	negative
Myrceugenia euosma	-0.788	negative	*Cordia trichoclada*	-0.799	negative
Seguieria americana	-0.787	negative	*Ilex theezans*	-0.793	negative
Xylopia langsdorfiana	-0.787	negative	*Myrcia sylvatica*	-0.792	negative
Xylopia aromatica	-0.786	negative	*Guettarda viburnoides*	-0.791	negative
Swartzia apetala	-0.786	negative	*Euplassa cantareirae*	-0.791	negative

Table S3. Trait space differences of the species with the strongest residual positive and negative associations, i.e. with the absolute mean over the significant residual associations belonging to the 98% quantile (for species lists, see Table S1 above). Each row represents a trait in question and each column represents the Welch's two sample t-test parameters. T-test is not calculated for binomial traits without species belonging to the respective trait category (e.g. Climax).

Trait	t	df	p	Mean (top negative)	Mean (top positive)
Maximum height	-0.65	35.29	0.52	19.64	20.87
Leaf area	-0.13	31.83	0.90	1.41	1.44
Dispersal syndrome					
Anemochoric	0.72	37.32	0.48	0.30	0.20
Zoochoric	-0.68	37.65	0.50	0.65	0.75
Autochoric	-	-	-	0	0
Barochoric	-	-	-	0	0
Hydrochoric	-	-	-	0	0
Successional group					
Climax	-	-	-	0	0
Early secondary	0.00	38.00	1.00	0.60	0.60
Late secondary	0.35	37.88	0.73	0.30	0.25
Pioneer	-	-	-	0	0
Geographic distribution					
Central South America	-	-	-	0	0
Eastern South America	0.32	37.97	0.75	0.40	0.35
Local endemic	-	-	-	0	0
Neotropical	-0.35	37.88	0.73	0.25	0.30
Pantropical	-	-	-	0	0
Regional endemic	-0.41	37.52	0.69	0.15	0.20
South America	0.41	37.52	0.69	0.20	0.15
Southern South America	-	-	-	0	0
Exotic	-	-	-	0	0
Northern South America	-	-	-	0	0
Western South America	-	-	-	0	0
Seed length	0.07	37.88	0.94	-0.02	-0.03
Wood density	0.61	31.40	0.55	0.66	0.64
Leaf type	0.31	37.99	0.76	0.45	0.40

PAPER III

Fragmented tropical forests lose mutualistic plant-animal interactions

Emma-Liina Marjakangas[1*], Nerea Abrego[1,2], Vidar Grøtan[1], Renato A. F. de Lima[3], Carolina Bello[4], Ricardo S. Bovendorp[4], Laurence Culot[5], Érica Hasui[6], Fernando Lima[4,7], Renata Lara Muylaert[4], Bernardo Brandão Niebuhr[4], Alexandre A. Oliveira[3], Lucas Augusto Pereira[5], Paulo I. Prado[3], Richard D. Stevens[8,9], Maurício Humberto Vancine[4], Milton Cezar Ribeiro[4], Mauro Galetti[4], Otso Ovaskainen[1,10]

[1] Centre for Biodiversity Dynamics, Norwegian University of Science and Technology, N-7491 Trondheim, Norway
[2] Department of Agricultural Sciences, PO Box 27, FI-00014 University of Helsinki, Finland
[3] Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, 05508-090, São Paulo, Brazil
[4] Departamento de Ecologia, Instituto de Biociências, Universidade Estadual Paulista (UNESP), 13506-900 Rio Claro, Brazil
[5] Departamento de Zoologia e Centro de Aquicultura, Instituto de Biociências, Universidade Estadual Paulista (UNESP), 13506-900 Rio Claro, Brazil
[6] Instituto de Ciências da Natureza, Universidade Federal de Alfenas, Alfenas, Brazil
[7] IPÊ - Instituto de Pesquisas Ecológicas, CP 47 Nazaré Paulista, SP, 12960-000, Brazil
[8] Department of Natural Resources Management, PO Box 42125, Lubbock TX 79409, U.S.A
[9] Museum of Texas Tech University, 3301 4th Street, Lubbock, TX 79415, U.S.A
[10] Faculty of Biological and Environmental Sciences, PO Box 65, FI-00014 University of Helsinki, Finland
[*] Corresponding author, email: emma-liina.marjakangas@ntnu.no, tel. +4746748211, ORCiD ID: 0000-0002-5245-3779, address: Realfagbygget E3-164, Høgskoleringen 5, N-7491 Trondheim, Norway

Keywords: Atlantic Forest, co-occurrence, ecological network, fragmentation, frugivory, Hierarchical Modelling of Species Communities (HMSC), joint species distribution model, keystone species, seed dispersal, zoochory

Abstract

Aim: Forest fragmentation is among the principal causes of global biodiversity loss, yet how it affects mutualistic interactions between plants and animals at large spatial scale is poorly understood. In particular, tropical forest regeneration depends on animal-mediated seed dispersal, but the seed dispersing animals face rapid decline due to forest fragmentation and defaunation. Here, we assess how fragmentation influences the pairwise interactions between 407 seed disperser and 1424 tree species in a highly fragmented biodiversity hotspot.

Location: Atlantic Forest, South America

Methods: We predicted interaction networks in 912 sites covering the entire biome by combining verified interaction data with co-occurrence probabilities obtained from a spatially explicit joint species distribution model. We identified keystone seed dispersers by computing a species-specific keystone index and by selecting those species belonging to the top 5% quantile. **Results:** We show that forest fragmentation affects seed dispersal interactions negatively, and the decreased area of functionally connected forest, rather than increased edge effects, is the main driver behind the loss of interactions. Both the seed disperser availability for the local tree communities and in particular the proportion of interactions provided by keystone seed dispersers decline with increasing degree of fragmentation. Importantly, just 21 keystone species provided >40% of all interactions. The numbers of interactions provided by keystone and non-keystone species, however, were equally negatively affected by fragmentation, suggesting that seed dispersal interactions may not be rewired under strong fragmentation effects. **Conclusions:** We highlight the importance of understanding the fragmentation-induced compositional shifts in seed disperser communities as they may lead to lagged and multiplicative effects on tree communities. Our results illustrate the utility of model-based prediction of interaction networks as well as model-based identification of keystone species as a tool for prioritizing conservation efforts. Similar modelling approaches could be applied to other threatened ecosystems and interaction types globally.

1 Introduction

Deforestation is among the principal causes of global biodiversity loss (Haddad et al., 2015). Alarmingly, deforestation rates are higher in biodiversity-rich areas, such as the tropics (Hansen et al., 2013). Forest loss, edge effects and reduced connectivity among remaining forest patches (for simplicity, hereafter together referred to as forest fragmentation) directly affect biodiversity (Fahrig, 2003, 2017; Pfeifer et al., 2017), for example by driving populations beyond their extinction thresholds (Hanski, 1999). Indirectly, forest fragmentation can reduce biodiversity by disrupting species interactions (Fortuna & Bascompte, 2006; Valiente-Banuet et al., 2015). Mutualistic interaction networks, such as seed dispersal networks, are fundamental in maintaining ecosystem functioning and thus their disruption can lead to profound cascade effects on important ecosystem services (Bello et al., 2015; Schleuning et al., 2015). Therefore, determining how forest fragmentation influences mutualistic interaction networks should be a central goal in biodiversity conservation (Tylianakis et al., 2010).

The integrity of species interaction networks contributes to the stability of ecological communities (Okuyama & Holland, 2008). Yet, the species richness in the landscape alone does not explain the type and number of interactions: not all species are equally important in maintaining community stability (Hagen et al., 2012; Dáttilo et al., 2016; Emer et al., 2018). Interaction networks are more sensitive to the loss of those species that interact with many other species (Morris, 2010). In particular, the so-called keystone species, defined as those “whose impact is disproportionally large relative to their abundance” (Power et al., 1996), are tightly connected to other species and considered critical for the structure of communities. Importantly, keystone species have been found to ensure the resilience of communities in fragmented landscapes (Peterson et al., 1997). Thus, detecting and focusing conservation efforts on keystone species may be a useful strategy for preserving ecosystem functioning.

In forest ecosystems, frugivorous animals, particularly birds and large mammals, are the most important seed dispersers (Fleming & Kress, 2013; Sebastián-González, 2017), but they face rapid decline due to forest fragmentation and defaunation (Galetti et al., 2013; Nagy-Reis et al., 2017; de Assis Bomfim et al., 2018). Large mammals can disperse a magnitude of large seeds over long distances (Vidal et al., 2013), whereas small- and medium-sized birds are limited to small seeds due to trait matching (Bender et al., 2018), but tend to be more abundant and thus interact more frequently and with a higher number of plant species. In general, landscapes with large, continuous forest fragments hold more animal and plant species as well as interaction links between taxa than their more fragmented counterparts (Hanski et al., 2013). Forest fragmentation may disrupt seed dispersal networks, which in turn may profoundly alter patterns of plant reproduction, such as seed size and spatial aggregation of seedlings (Galetti et al., 2013; Kurten, 2013). Species-specific responses to habitat fragmentation, on the other hand, depend on life-history traits (Henle et al., 2004; Hagen et al., 2012). Small, abundant and generalist animals are more likely to be tolerant to fragmentation than large, rare specialists (Henle et al., 2004; Beca et al., 2017). Parallel to animals, the most negatively affected tree species are rare specialists that are animal-pollinated and produce few large seeds (Kolb & Diekmann, 2005; Cramer et al., 2007; Markl et al., 2012).

Forest fragmentation affects frugivory and seed dispersal through various processes, including habitat loss (García & Chacoff, 2007; Valdivia & Simonetti, 2007), fragment isolation and edge effects (Magrach et al., 2014), and changes in within-habitat quality (Lehouck et al., 2009a). The effects of forest loss and fragmentation on biodiversity are often difficult to disentangle without appropriate sampling design as they can occur in synergy (Fahrig, 2003). However, together these processes may cause frugivore population declines or extinctions (Cordeiro & Howe, 2003), and changes in the frugivore community composition (Santos & Tellería, 1994) or in the capacity of functional complementarity among frugivores (Lehouck et al., 2009b). The fragmentation mechanisms affecting seed dispersal interactions have mainly been studied locally (but see Markl et al., 2012; Magrach et al., 2014; Fontúrbel et al., 2015), focusing on patterns of community composition and species richness of frugivores (e.g., García & Martínez, 2012). Furthermore, direct observations on seed disperser interactions are usually reported for few taxonomic groups, and at small temporal and geographical scales. Since the available data on species interactions limit research spatially and taxonomically, community modelling approaches can be used to approximate interaction patterns at large spatial scales (Ovaskainen et al., 2017; Zurell et al., 2018).

Here, we test the hypothesis that increasing fragmentation in the landscape negatively impacts seed dispersal interactions, namely the number of interactions and the proportion of interactions provided by keystone seed dispersers. We expect negative effects on seed dispersal interactions due to loss of seed dispersers in the landscape. However, we also expect some of these negative effects to be counteracted or diluted by seed disperser replacement, i.e. network rewiring. We compiled data on the occurrences of 407 animal and 1424 tree species occurring within the Atlantic Forest of South America, a highly fragmented biodiversity hotspot (Ribeiro et al., 2009). We combined species assemblage and network modelling to evaluate the effects of forest fragmentation on seed dispersal. More specifically, we predicted species occurrences using a spatially explicit joint species distribution model (Ovaskainen et al., 2017), and inferred interactions from co-occurrences by utilizing verified interaction data (Bello et al., 2017).

2 Methods

Data on species communities and environmental covariates

The Atlantic Forest biome provides an excellent model system for studying the effects of forest loss as it presents a full gradient of fragmentation due to the historic land use (Ribeiro et al., 2009). We used the most spatially and taxonomically comprehensive community databases available for the Atlantic Forest in Brazil (the ATLANTIC series data papers: https://github.com/LEEClab/Atlantic_series, and the Neotropical Tree Communities database (TreeCo version 2.0): http://labtrop.ib.usp.br/doku.php?id=projetos:treeco:start). Altogether, we compiled data on 1831 species occurring in 1953 sampling sites, totalling nearly 59,000 species occurrence records (Fig. 1). The data were collected between years 1990 and 2017, during which the geographical coordinates are of required accuracy (de Lima et al., 2015; Bovendorp et al., 2017; Lima et al., 2017; Muylaert et al., 2017; Culot et al., 2018; Hasui et al., 2018). Surveys were selected based on the reported information on the sampling design making sure that sampling was conducted within the Atlantic Forest biome limits *sensu* Ribeiro et al. (2009), and that there was sufficiently detailed information on the sampling site as well as the sampling design. For each of the major taxonomic group (bats, birds, large mammals, primates, small mammals, and trees), we compiled data on: (1) the occurrences of species in the surveys; (2) species' life-history traits; (3) taxonomic relationships among the species; and (4) environmental covariates associated with each sampling site, in addition to geographic coordinates (Table 1).

Species occurrences. We used presence-absence data of 407 seed disperser and 1424 tree species to produce occurrence matrices. As our focus was on seed dispersal networks, we included only animals identified to species-level and reported as frugivores (≥10% of the diet consists of fruits) in the EltonTraits database (Wilman et al., 2014). Furthermore, we included those tree species that were identified as zoochoric (Almeida-Neto et al., 2008; Bello et al., 2017), and had ≥5 occurrences in the original data. We considered as trees those tree and palm species that are reported to grow ≥4 meters high. The four mammal data sets overlapped partially in a sense that one species from the bat data, six species from the primate data, and three species from the small mammal data also occurred in the large mammal data. We included these overlapping species in the joint species distribution models of both data sets with the aim of testing the robustness of the predicted occurrence probabilities for data collected on the same species by different methods.

Species traits. Seed disperser life-history trait data were first obtained from the EltonTraits database (Wilman et al., 2014), and missing values were then completed using various data sources (Table S1.1). The included seed disperser life-history traits were body mass, degrees of frugivory and omnivory, endemism in the Atlantic Forest, foraging strata, and commonness. In rare cases of missing data (n =2), the trait value of a close relative was used. For tree species, we included seed size, wood density, maximum height, and commonness. The life-history traits of trees were obtained from the TreeCo database and completed with genus-level averages in cases of missing values (35 % of species with data available on all four traits), except for the maximum heights of the species for which we only used the species-level data (Díaz et al., 2015).

Taxonomic relationships. Due to the lack of comprehensive quantitative phylogenies, we derived the phylogenetic correlation matrices from the taxonomic trees that included the levels of orders, families, genera, and species (except for bats: subfamilies, genera and species; and for primates families, genera, and species), and that assumed equal branch lengths for the levels. Due to computational limitations, we did not include taxonomic correlations in the bird and tree models.

Environmental covariates. Environmental covariates were obtained from a variety of sources based on the reported geographical coordinates of sampling sites (Hijmans et al., 2005; Ribeiro et al., 2009; Soares-Filho et al., 2013; Fick & Hijmans, 2017; Ribeiro et al., in prep.). These covariates were selected among a larger set of potential environmental covariates based on preliminary analyses that aimed at identifying a set of uncorrelated covariates (for the full correlation matrix of the selected covariates, see Table S2.1). We computed the selected environmental covariates at landscape scale to best account for their effects on occurrences of species with varying sets of traits, such as species-specific range size. As fragmentation-related variables, we included ratio of forest core to forest edge within 10-kilometer window, area of functionally connected forest, and distance to nearest road (data obtained between 2013 and 2015). We set 120 meters as the threshold value for considering separate forest fragments to be part of "a functionally connected forest patch" to allow meaningful comparisons between species with very different gap crossing capabilities (e.g., Lees & Peres, 2009). This value does not match perfectly the movement of some smaller or resident species, but provides a useful proxy for average matrix crossing capability of all species. We note that the impacts of forest loss and fragmentation cannot be discerned without an appropriate sampling design and therefore our fragmentation-related variables may represent synergistic effects of both forest loss and fragmentation. Size of the focal forest fragment was not included in the analyses due to its strong correlation with area of functionally connected forest (Spearman correlation coefficient = 0.78). In addition to the fragmentation-related variables that were of our focal interest, we included climatic, topographic, and land use variables to control for their influence on variation in species occurrences. We used Albers Equal Area Conic projection with SAD69 Datum in all spatial analyses.

Joint species distribution modelling of each taxonomic group

To synthesize data on species occurrences, environmental covariates, spatial context, species traits, and taxonomic relationships within a single modelling framework, we applied Hierarchical Modelling of Species Communities (HMSC; Ovaskainen et al., 2017). HMSC is a joint species distribution model, and it thus models the occurrences of all species simultaneously, allowing both species- and community-level predictions. Joint modelling allows including rare species in the analyses as information can be ‘borrowed’ from more common species through shared traits and evolutionary history, as well as spatial configuration of species co-occurrences. In addition to modelling the species-specific responses to environmental covariates, HMSC examines how these responses are influenced by species traits and phylogenetic relatedness. Separately for each taxonomic group, we fitted a binomial model with probit link to the presence-absence data. In all models, we included spatially structured latent variables to account for spatial autocorrelation in the species occurrence data (Ovaskainen et al., 2016, 2017). We fitted the models in Bayesian inference framework using the Matlab implementation of HMSC provided by Ovaskainen et al. (2017) with default prior distributions.

To evaluate the predictive power of the HMSC models, we applied a cross-validation procedure. Cross-validation is a useful tool to measure the predictive performance of a model without extensive and often unfeasible field work. We partitioned the sites randomly into five sets, fitted the model using four of the five sets as training data, and predicted the validation data on the remaining fifth set of sites. We repeated this analysis five times, thus generating an independent prediction for each site. We evaluated the predictive performances of the HMSC models by computing Tjur's R^2 (Tjur, 2009) and area under curve (AUC) using ‘PresenceAbsence’ package in R software version 3.5.0 (Freeman & Moisen, 2008) for the match between model prediction and the validation data.

We examined the roles of the fragmentation-related covariates (core-edge ratio, area of functionally connected forest, and distance to road) by partitioning the explained variation among the predictors, and by assessing how the responses to the environmental predictors were mediated by species traits.

Generating predicted communities

To overcome the problem of low spatial overlap among survey locations across taxonomic groups, we used HMSC to generate predicted communities for the entire Atlantic Forest in Brazil. We created a regular grid of 40,000 sites spanning the Atlantic Forest limits in ArcGIS software (version 10.3). Then, we selected those 912 sites that overlapped with the Atlantic

Forest remnants, and used the fitted models to predict species communities of all taxonomic groups. These predictions utilize all information in the data, as they are based on the measured values of the environmental covariates in the grid cells (through the fixed effect part of the HMSC), as well as on the occurrences of the species in nearby sampling sites (through the spatially structured latent variable part, see Ovaskainen et al. 2016). By sampling the model parameters from the full joint posterior distribution, we accounted for parameter uncertainty while generating 500 replicates of predicted communities for each of the 912 prediction sites.

Modelling interactions between seed dispersers and zoochoric trees

Two conditions need to be simultaneously satisfied to enable a particular animal species to act as a seed disperser for a particular plant species in a particular site. First, the animal species and the plant species need to have the potential for interaction, i.e. the animal uses the plant as a resource. Second, the animal and plant species need to co-occur at the particular site. We modelled these two components separately, so that the predicted probability of the two species interacting at a particular site is the probability that they potentially interact (which is independent of the site), multiplied by the probability that the two species co-occur at the particular site. We examined these associations between seed dispersers and trees based on the predicted communities. For each prediction site and each replicate of predicted community, we calculated the co-occurrence probability for each seed disperser-tree pair as the product of their species-specific occurrence probabilities. Similarly to Marjakangas et al. (2018), we used the ATLANTIC-FRUGIVORY database (Bello et al., 2017) to assign all seed disperser-tree pairs a semi-quantitative probability of potential for an interaction. The database presents occurrences of fruit consumption events, excluding pulp consumption and seed predation. We considered potential for an interaction to be very likely (probability 1) if it was recorded by more than one study in different locations, and likely (probability 0.75) if it was recorded by one study in one location. Due to low taxonomic coverage of the interaction database (84% of seed disperser and 30% of tree species), we completed the data by considering potential for an interaction plausible (probability 0.5) if the seed disperser interacts with another tree species within the focal tree species' genus, and unlikely (probability 0) if the seed disperser has no recorded interactions with any tree species within the focal tree species' genus. We set the probabilities of interactions recorded by only one study to be <1 to account for uncertainty in their spatial prevalence and to obtain conservative estimates on pairwise interactions in local communities. Finally, we calculated predicted site- and replicate-specific seed disperser-tree interaction probabilities as the product of their co-occurrence probabilities and their potential for interaction probabilities. Essentially, we assume an interaction if the two species co-occur in a site, and have the potential to interact, the latter in the sense that they have been observed to interact at least in some location. To support this analytical approach, we tested for the phylogenetic signal of interaction partner sharing among plant species, and found that plant species within a genus shared more interaction partners (on average 2.6 shared interaction partners) than plant species that belonged to different genera (on average 0.7 shared interaction partners) (Appendix S3).

We used the predicted interaction probabilities to compute for each site the interaction link connectance (CON), defined as the proportion of seed disperser-tree pairs that interact out of all pairs that are present in the site, with value ranging between 0 and 1 (Jordano, 1987). We also computed for each site a measure of seed disperser availability for the local tree community (SA), defined as the mean number (over tree species) of seed disperser species with which a tree species interacts.

To identify community-level keystone seed dispersers, we utilized two alternative methods. As a model-based approach, we computed for each seed disperser a keystone index, defined as the expected number of tree species with which it interacts, averaged over the sites where the seed disperser is predicted to occur (Eq. S4.1). Following the definition by Power et al. (1996), we identified as keystone species those seed dispersers that had a disproportionally large impact on the community in relation to their abundance, their keystone index value belonging to the top 5% quantile (Table S4.1). Due to the lack of abundance data for all seed disperser species, we use species' commonness as a proxy for their abundances. As a traditional approach, we selected 5% of the species as keystone seed dispersers based on species' contributions to interaction network structure, relative abundances and vulnerability, as these characteristics have been found important by previous studies (Table S4.2; Vidal et al., 2014; Domínguez-García & Muñoz, 2015). Finally, we computed for each site the proportion of interactions that were provided by the keystone seed dispersers identified by the model-based approach (KEY) and by the traditional approach. We chose these three interaction metrics (CON, SA, KEY) because they represent key characteristics of the seed dispersal network structure and can offer complementary information on fragmentation effects on the interactions that tropical trees heavily depend on.

To investigate how seed dispersal interactions depend on fragmentation, we derived for each prediction site values of core-edge ratio, area of functionally connected forest, and distance to nearest road. We then examined how the connectance (CON), seed disperser availability (SA), and proportion of interactions provided by keystone seed dispersers (KEY), co-varied with these three fragmentation covariates. To do so, we fitted for each pair of interaction metric (the response variable) and fragmentation-related covariate (the explanatory variable) 500 linear regressions, i.e. one for each posterior replicate of the predicted community. We computed the posterior probability for the association being positive (i.e. fragmentation reducing seed dispersal interactions; note that all our fragmentation-related covariates decrease with increased degree of fragmentation) as the fraction of positive slopes among the 500 slopes, and quantified effect size as the mean R^2-value over the predictions. We note that these regression models do not account for possibly spatially autocorrelated residuals, and thus they should be considered to examine realized patterns of co-variation between fragmentation and seed dispersal rather than causal links between these.

In addition to overall analysis involving the entire Atlantic Forest biome, we conducted the above described analyses separately for each of the seven biogeographical sub-regions of the biome (Fig. S5.1; Ribeiro et al., 2009). This was done to examine the robustness of the results with respect to uneven sampling effort and other variation possibly not controlled for in our analyses. Furthermore, to account for possible bias, we repeated the analyses without completing the interaction matrix and instead used the original data on pairwise interactions in binary format as basis for *post hoc* calculations (Appendix S3).

3 Results

Spatial and taxonomic variation in species occurrences

Using Tjur's R^2 as measure for predictive performance, the fitted models explained 19–54% (and predicted 14–36% based on the cross-validation) of the variation in species' occurrences across the Atlantic Forest (Table 2). Among the studied taxa, primates showed the most predictable patterns in their occurrences (explanatory R^2=54%), followed by large mammals (R^2=33%), birds (R^2=32%), bats (R^2=30%), small mammals (R^2=28%), and trees (R^2=19%). AUC as a measure for predictive performance yielded parallel, but slightly higher model performance estimates compared to those by Tjur's R^2 (Table 2). Some of the species were included in two models (see Methods), and we found that their mean predicted occurrence probabilities did not differ notably between the two separate analyses (Table S6.1).

Overall, climate was the most important environmental predictor of species occurrences. Averaged over the taxonomic groups, the three climatic variables explained 26% of the total variation (Table 2). Land use around the sampling site explained 24%, and fragmentation 11% of the total variation. Fragmentation explained larger proportion of the total variation for seed dispersers than for trees (12.7% and 2.6%, respectively).

Averaged over the groups, traits explained 59.3% of the variation in species responses to environmental variables (Table 2). The influence of traits in explaining species responses was particularly high in the case of primates (77%) and low for trees (36%). Among the considered traits, commonness and endemism to Atlantic Forest had the strongest effects in explaining variation in species responses to environmental variables (Fig. S7.1).

Influence of fragmentation on interactions between seed dispersers and trees

Our results demonstrate that fragmented parts of the Atlantic Forest harbour much simpler interaction networks than its more continuous parts (Fig. 1). We found that link connectance (CON), seed disperser availability (SA) and proportion of interactions provided by keystone seed dispersers (KEY) were influenced by the area of functionally connected forest, but not by core-to-edge ratio or distance to nearest road (Fig. 2). Link connectance of interactions between seed dispersers and trees was generally higher in the southern parts of the Atlantic Forest and lower in the northern parts (Fig. 3). When computed separately for each taxonomic group, connectance values were higher for primates (mean=0.126, SD=0.055) and birds (mean=0.082, SD=0.025), than for other seed disperser groups (mean value for bats=0.028, for large mammals=0.021, and for small mammals=0.003). Seed disperser availability varied between 1.3–8.8 seed disperser species per tree species, the highest values found in southern coastal areas (Fig. 3). The model-based approach for identifying keystone seed dispersers pinpointed 21 species (Table S4.1), and on average across the biome, they provided 42% of all seed dispersal interactions. Numbers of interactions by both the keystone and the non-keystone species increased similarly with increasing area of functionally connected forest (Fig. 4). One third of the identified keystone and non-keystone seed dispersers are endemic to Atlantic Forest (38% and 32%, respectively). On average, the keystone seed dispersers had a higher proportion of fruits in their diet than the non-keystone frugivores (t=2.65, p=0.014, mean difference=14.1%), but there was no difference in average body size between keystone and non-keystone species (t=1.33, p=0.20, mean difference=-230.6g). Results based on the traditional approach for identifying keystone seed dispersers were parallel, albeit the selected species provided a smaller proportion of all seed dispersal interactions (17.3%) compared to those identified by the model-based approach (Table S4.3, Fig. S4.1 and Fig. S4.2). Seven species were identified as keystone species by both selection methods (Tables S4.1 and S4.2).

The influence of fragmentation on the interaction metrics was qualitatively similar, but non-significant within each biogeographical sub-region, compared to the results obtained for the entire biome (Table S5.1). Furthermore, the results were parallel when using the known interactions data in binary format instead of semi-quantitative interaction probabilities (Fig. S3.2, S3.3 and S3.4).

4 Discussion

Tree community composition, and thereby forest regeneration, is dependent on seed dispersal provided by frugivores (Asquith et al., 1997; Cramer et al., 2007). Consequently, several ecosystem functions and services may be at risk when the seed dispersal network is subjected to a fragmentation scenario. We demonstrated that forest loss and fragmentation affect seed dispersal interactions negatively: we found not only the overall connectance and seed disperser availability, but also the proportion of interactions provided by keystone seed dispersers to decline with increasing degree of fragmentation. Importantly, we identified the area of functionally connected forest, rather than increased edge effects, to be the main driver behind the loss of seed dispersal interactions. This result is in line with the fact that individual species have been found to show varying responses to edge effects (Oliveira et al., 2004; Ries et al., 2004), whereas the occurrence and persistence of most species generally depends positively on the area of available habitat (Bender et al., 1998). Furthermore, the Atlantic Forest is extremely fragmented with almost half of the forest cover within <100 meters from the nearest edge (Ribeiro et al., 2009), thus most species that persist in the area are necessarily at least to some extent tolerant to edge effects (Beca et al., 2017). Furthermore, functional connectivity correlated with mean annual temperature and precipitation as well as with precipitation seasonality across the biome, suggesting that some of the fragmentation-induced effects on seed dispersal networks may be masked by the climatic effects in the model fitting. Yet, fragmentation and climate covariates were recorded at different spatial resolutions, thereby hampering the interpretation of their actual relationship. Moreover, fragmentation is a result of local and regional land use practices, leading to inevitable interplay of the factors. Hence, forest fragmentation may act in concert with climate and land use practices, and it should therefore be considered together with climate change and land use intensification when planning conservation and management actions.

Earlier studies have illustrated that individual interactions within networks can be gained or lost as a response to habitat alterations (de Assis Bomfim et al., 2018), even when changes in the species composition remain indistinguishable (Nielsen & Totland, 2014). Therefore, structural changes in the network, namely rewiring, could mitigate some direct and short-term effects of fragmentation on tree seed dispersal by the replacement of extinct interaction links. Our results, however, showed that the number of interactions provided both by keystone and non-keystone species were equally negatively affected by fragmentation, suggesting that the loss of interactions provided by keystone seed dispersers are not replaced by those provided by other species in the seed dispersal network. Donatti et al. (2011) found that keystone species replacement is unlikely to occur in highly fragmented landscapes because of network clustering and the nested nature of existing interactions. That is, interactions are more frequent within than among subsets of species (modules) (Olesen et al., 2007), and therefore, the number of functionally compensatory species is limited to the species within each module. This in turn explains the extinct interactions in the local communities under strong fragmentation effects. The keystone seed dispersers that were identified with our model-based approach represent two ecologically distinct groups: old-growth forest habitat specialists, and secondary forest diet generalists that are common throughout the Atlantic Forest. These two groups are unlikely to have mutually interchangeable compensation capacity for rewiring and should therefore be considered separately in conservation and management. On the other hand, Timóteo et al. (2016) revealed extensive structural plasticity through rewiring in a seed dispersal network following experimental removal of the dominant seed disperser. This indicates that when fruit resources are made available for other species, rewiring could be observed given the temporal extent of the study design. Nevertheless, sharing some sampling and prediction sites with Emer et al. (2018), our results align to support the view that the effects of losing community-level keystone species and related interactions can be detrimental for ecosystems, for which the conservation of keystone species is a viable solution.

Regardless of the comprehensive data used in this study, the uncertainty of the results pose limitations for several reasons. Firstly, we treat the data as a snapshot despite the underlying temporal aspect, which introduces additional noise to the obtained results. In particular, the data of rare species occurrences are still sparse, making it difficult to accurately predict their distributional ranges. There is also a temporal difference in collection of species occurrence and fragmentation data, further adding to the noise in the results. Secondly, robust quantification of fragmentation effects is especially difficult in the northern Atlantic Forest, where anthropogenic defaunation is more severe and sampling effort lower than in the southern parts (Canale et al., 2012). To test the robustness of the results with respect to these uncertainties, we computed interaction-fragmentation relationships for each biogeographical sub-region separately and found the patterns to be similar. Finally, the data on known interactions are biased towards well-studied species and areas, which we partly accounted for by completing the interaction data with genus-level generalizations (after generalization, we cover 84% of seed disperser and 80% of tree species). Since we accounted only for recorded interactions, our measure of seed disperser availability presents a conservative estimate, and consequently the true numbers of interactions and interacting species are likely to be far larger. However, due to the large scale of the study area, some interactions may only be realized in parts of the study area, leading to overestimation of interactions in others (Fründ et al., 2013). In particular, functional traits related to mutualistic interactions tend to vary spatially among populations, leading to possible local deviances from the recorded interaction patterns (González-Varo & Traveset, 2016). In addition to the loss of species, forest fragmentation may have additional negative effects on seed dispersal interactions through changes in these functional traits, such as seed disperser foraging behaviour and plant phenology, which we did not consider in the present work. Therefore, we urge future research to improve the spatial and taxonomic extent of the interaction matrix by implementing trait matching models (Bartomeus et al., 2016; Sebastián-González et al., 2017), and by using DNA metabarcoding methods to directly observe the consumed plant species in the animal faeces (Hibert et al., 2013).

Generally, collection of ecological data is costly, which leads seed dispersal research, among other fields, to focus on well-studied bird taxa and small spatial scales (e.g. García et al., 2013). Here, we used the best available data to approximate structural changes in seed dispersal interactions at unprecedentedly large spatial scale and at the entire network level. Our results illustrate the utility of model-based prediction of interaction networks, as well as objective model-based identification of keystone species as a tool for prioritizing conservation efforts. Similar modelling approach could be applied to other threatened ecosystems and interaction types globally. To provide an even more synthesized view, we hope future work to include also other multi-layer networks relevant to plant recruitment beyond seed dispersal, such as seed predation and herbivory (García-Callejas et al., 2018).

Understanding species interaction dynamics of biodiversity hotspots, such as the Atlantic Forest, under imminent anthropogenic threats is essential for reversing the global biodiversity loss. Since land use intensification and consequent forest fragmentation in the Atlantic Forest are recent in ecological and evolutionary time scales, it is likely that species communities have not had time to respond to the changes (Metzger et al., 2009, but see Galetti et al., 2013). Potentially, there is unpaid extinction debt in communities, and interaction networks might undergo fundamental transformations in the future (Metzger et al., 2009). In particular, this might be the case in the tree communities since their interaction partners are currently declining and thereby the future seedling recruitment could be left impaired. Therefore, compositional shifts in the seed disperser communities can serve as early warning signs for lagged and multiplicative fragmentation effects on the tree communities.

Acknowledgements

We thank all those researchers that collected the community data and Mathias Pires for his ideas for completing the interaction matrix. This work was partly supported by the Research Council of Norway through its Centres of Excellence Funding Scheme (223257) to ELM, NA, VG & OO via Centre for Biodiversity Dynamics, and by the Academy of Finland grants to OO (1273253, 250444 and 284601). Data compilation was supported by FAPESP grants #2013/08722-5 to RAFL, #2013/25441-0 and #2014/18800-6 to RSB, #2014/14739-0 to LC, #2015/17739-4 and #2017/21816-0 to RLM, #2017/08440-0 to LAP, #2017/09676-8 to MHV, #2013/50421-2 to MCR, and #2014/01986-0 to MG. In addition, FL, BBSN, MHV and MCR were supported by CAPES, and MCR and MG by CNPq.

References

Almeida-Neto, M., Campassi, F., Galetti, M., Jordano, P., & Oliveira-Filho, A. (2008) Vertebrate dispersal syndromes along the Atlantic forest: broad-scale patterns and macroecological correlates. *Global Ecology and Biogeography*, **17**, 503–513.

Asquith, N.M., Wright, S.J., & Clauss., M.J. (1997) Does mammal community composition control recruitment in neotropical forest? Evidence from Panama. *Ecology*, **78**, 941–946.

de Assis Bomfim, J., Guimarães, P.R., Peres, C.A., Carvalho, G., & Cazetta, E. (2018) Local extinctions of obligate frugivores and patch size reduction disrupt the structure of seed dispersal networks. *Ecography*, **41**, 1–11.

Beca, G., Vancine, M.H., Carvalho, C.S., Pedrosa, F., Alves, R.S.C., Buscariol, D., Peres, C.A., Ribeiro, M.C., & Galetti, M. (2017) High mammal species turnover in forest patches immersed in biofuel plantations. *Biological Conservation*, **210**, 352–359.

Bello, C., Galetti, M., Montan, D., Pizo, M.A., Mariguela, T.C., Culot, L., Bufalo, F.S., Labecca, F., Pedrosa, F., Constantini, R., Emer, C., Silva, W.R., da Silva, F.R., Ovaskainen, O., & Jordano, P. (2017) ATLANTIC-FRUGIVORY: a plant-frugivore interaction dataset for the Atlantic Forest. *Ecology*, **98**, 1729.

Bello, C., Galetti, M., Pizo, M.A., Magnago, L.F.S., Rocha, M.F., de Lima, R.A.F., Peres, C.A., Ovaskainen, O., & Jordano, P. (2015) Defaunation affects carbon storage in tropical forests. *Science Advances*, **1**, e1501105.

Bender, D.J., Contreras, T.A., & Fahrig, L. (1998) Habitat loss and population decline: a meta-analysis of the patch size effect. *Ecology*, **79**, 517–533.

Bender, I.M.A., Kissling, W.D., Blendinger, P.G., Böhning-Gaese, K., Hensen, I., Kühn, I., Muñoz, M.C., Neuschulz, E.L., Nowak, L., Quitián, M., Saavedra, F., Santillán, V., Töpfer, T., Wiegand, T., Matthias Dehling, D., & Schleuning, M. (2018) Morphological trait matching shapes plant-frugivore networks across the Andes. *Ecography*, **41**, 1–10.

Bovendorp, R.S., Villar, N., Abreu-Junior, E.F. de, Bello, C., Regolin, A.L., Percequillo, A.R., & Galetti, M. (2017) Atlantic small-mammal: A dataset of communities of rodents and marsupials of the Atlantic forests of South America. *Ecology*, **98**, 2226.

Canale, G.R., Peres, C.A., Guidorizzi, C.E., Gatto, C.A.F.R., & Kierulff, M.C.M. (2012) Pervasive defaunation of forest remnants in a tropical biodiversity hotspot. *PLoS ONE*, **7**, e41671.

Cordeiro, N.J. & Howe, H.F. (2003) Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. *Proceedings of the National Academy of Sciences*, **100**, 14052–14056.

Cramer, J.M., Mesquita, R.C.G., & Bruce Williamson, G. (2007) Forest fragmentation differentially affects seed dispersal of large and small-seeded tropical trees. *Biological Conservation*, **137**, 415–423.

Culot, L., Pereira, L.A., Agostini, I., et al. (2018) ATLANTIC-PRIMATES: a dataset of communities and occurrences of primates in the Atlantic Forests of South America. *Ecology*, 1.

Dáttilo, W., Lara-Rodríguez, N., Jordano, P., Guimarães, P.R., Thompson, J.N., Marquis, R.J., Medeiros, L.P., Ortiz-Pulido, R., Marcos-García, M.A., & Rico-Gray, V. (2016) Unravelling Darwin’s entangled bank: architecture and robustness of mutualistic networks with multiple interaction types. *Proceedings of the Royal Society B: Biological Sciences*, **283**, 20161564.

Díaz, S., Kattge, J., Cornelissen, J.H.C., et al. (2015) The global spectrum of plant form and function. *Nature*, **529**, 167–171.

Domínguez-García, V. & Muñoz, M.A. (2015) Ranking species in mutualistic networks. *Scientific Reports*, **5**, 8182.

Donatti, C.I., Guimarães, P.R., Galetti, M., Pizo, M.A., Marquitti, F.M.D., & Dirzo, R. (2011) Analysis of a hyper-diverse seed dispersal network: modularity and underlying mechanisms. *Ecology Letters*, **14**, 773–781.

Emer, C., Galetti, M., Pizo, M.A., Guimarães, P.R., Moraes, S., Piratelli, A., & Jordano, P. (2018) Seed-dispersal interactions in fragmented landscapes - a metanetwork approach. *Ecology Letters*, **21**, 484–493.

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, & Systematics*, **34**, 487–515.

Fahrig, L. (2017) Ecological responses to habitat fragmentation per se. *Annual Review of Ecology, Evolution, and Systematics*, **48**, 1–23.

Fick, S.E. & Hijmans, R.J. (2017) WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, **37**, 4302–4315.

Fleming, T.H. & Kress, W.J. (2013) *The ornaments of life: coevolution and conservation in the tropics.* University of Chicago Press, Chicago.

Fontúrbel, F.E., Candia, A.B., Malebrán, J., Salazar, D.A., González-Browne, C., & Medel, R.

(2015) Meta-analysis of anthropogenic habitat disturbance effects on animal-mediated seed dispersal. *Global Change Biology*, **21**, 3951–3960.

Fortuna, M.A. & Bascompte, J. (2006) Habitat loss and the structure of plant-animal mutualistic networks. *Ecology Letters*, **9**, 278–283.

Freeman, E.A. & Moisen, G. (2008) PresenceAbsence: An R Package for Presence-Absence Model Analysis. *Journal of Statistical Software*, **23**, 1–31.

Fründ, J., Dormann, C.F., Holzschuh, A., & Tscharntke, T. (2013) Bee diversity effects on pollination depend on functional complementarity and niche shifts. *Ecology*, **94**, 2042–2054.

Galetti, M., Guevara, R., Cortes, M., Fadini, R., Von Matter, S., Leite, A.B., Labecca, F., Ribeiro, T., Carvalho, C.S., Collevatti, R.G., Pires, M.M., Guimarães, P.R., Brancalion, P.H., Ribeiro, M.C., & Jordano, P. (2013) Functional extinctions of birds drives rapid evolutionary changes in seed size. *Science*, **340**, 1086–1091.

García-Callejas, D., Molowny-Horas, R., & Araújo, M.B. (2018) Multiple interactions networks: towards more realistic descriptions of the web of life. *Oikos*, **127**, 5–22.

García, D. & Chacoff, N.P. (2007) Scale-dependent effects of habitat fragmentation on hawthorn pollination, frugivory, and seed predation. *Conservation Biology*, **21**, 400–411.

García, D. & Martínez, D. (2012) Species richness matters for the quality of ecosystem services: A test using seed dispersal by frugivorous birds. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 3106–3113.

García, D., Martínez, D., Herrera, J.M., & Morales, J.M. (2013) Functional heterogeneity in a plant-frugivore assemblage enhances seed dispersal resilience to habitat loss. *Ecography*, **36**, 197–208.

González-Varo, J.P. & Traveset, A. (2016) The labile limits of forbidden interactions. *Trends in Ecology and Evolution*, **31**, 700–710.

Haddad, N.M., Brudvig, L.A., Clobert, J., et al. (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, **1**, e1500052.

Hagen, M., Kissling, W.D., Rasmussen, C., et al. (2012) Biodiversity, species interactions and ecological networks in a fragmented world. *Advances in Ecological Research*, **46**, 89–120.

Hansen, M.C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., & Townshend, J.R.G. (2013) High-resolution global maps of 21st-century forest cover change. *Science*, **342**, 850–854.

Hanski, I. (1999) *Metapopulation ecology.* Oxford University Press Inc., New York.

Hanski, I., Zurita, G.A., Bellocq, I.M., & Rybicki, J. (2013) Species-fragmented area relationship. *Proceedings of the National Academy of Sciences of the United States of America*, **110**, 12715–20.

Hasui, É., Metzger, J.P., Pimentel, R.G., et al. (2018) ATLANTIC BIRDS: a dataset of bird species from the Brazilian Atlantic Forest. *Ecology*, **99**, 497.

Henle, K., Davies, K.F., Kleyer, M., Margules, C.R., & Settele, J. (2004) Predictors of species sensitivity to fragmentation. *Biodiversity and Conservation*, **13**, 207–251.

Hibert, F., Taberlet, P., Chave, J., Scotti-Saintagne, C., Sabatier, D., & Richard-Hansen, C. (2013) Unveiling the diet of elusive rainforest herbivores in next generation sequencing era? The tapir as a case study. *PLoS ONE*, **8**, .

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Jordano, P. (1987) Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. *American Naturalist*, **129**, 657–677.

Kolb, A. & Diekmann, M. (2005) Effects of life-history traits on responses of plant species to forest fragmentation. *Conservation Biology*, **19**, 929–938.

Kurten, E.L. (2013) Cascading effects of contemporaneous defaunation on tropical forest communities. *Biological Conservation*, **163**, 22–32.

Lees, A.C. & Peres, C.A. (2009) Gap-crossing movements predict species occupancy in Amazonian forest fragments. *Oikos*, **118**, 280–290.

Lehouck, V., Spanhove, T., Colson, L., Adringa-Davis, A., Cordeiro, N.J., & Lens, L. (2009a) Habitat disturbance reduces seed dispersal of a forest interior tree in a fragmented African cloud forest. *Oikos*, **118**, 1023–1034.

Lehouck, V., Spanhove, T., Demeter, S., Groot, N.E., & Lens, L. (2009b) Complementary seed dispersal by three avian frugivores in a fragmented Afromontane forest. *Journal of Vegetation Science*, **20**, 1110–1120.

Lima, F., Beca, G., Muylaert, R.L., et al. (2017) ATLANTIC-CAMTRAPS: a dataset of medium and large terrestrial mammal communities in the Atlantic Forest of South America. *Ecology*, **98**, 2979.

de Lima, R.A.F., Mori, D.P., Pitta, G., Melito, M.O., Bello, C., Magnago, L.F.S., Zwiener, V.P., Saraiva, D.D., Marques, M.C.M., de Oliveira, A.A., & Prado, P.I. (2015) How much do we know about the endangered Atlantic Forest? Reviewing nearly 70 years of information on tree community surveys. *Biodiversity and Conservation*, **24**, 2135–2148.

Magrach, A., Laurance, W.F., Larrinaga, A.R., & Santamaria, L. (2014) Meta-analysis of the effects of forest fragmentation on interspecific interactions. *Conservation Biology*, **28**, 1342–1348.

Marjakangas, E.-L., Genes, L., Pires, M.M., Fernandez, F.A.S., de Lima, R.A.F., de Oliveira, A.A., Ovaskainen, O., Pires, A.S., Prado, P.I., & Galetti, M. (2018) Estimating interaction credit for trophic rewilding in tropical forests. *Philosophical Transactions of the Royal Society B*, **373**, 20170435.

Markl, J.S., Schleuning, M., Forget, P.M., Jordano, P., Lambert, J.E., Traveset, A., Wright, S.J., & Böhning-Gaese, K. (2012) Meta-analysis of the effects of human disturbance on seed dispersal by animals. *Conservation Biology*, **26**, 1072–1081.

Metzger, J.P., Martensen, A.C., Dixo, M., Bernacci, L.C., Ribeiro, M.C., Teixeira, A.M.G., &

Pardini, R. (2009) Time-lag in biological responses to landscape changes in a highly dynamic Atlantic forest region. *Biological Conservation*, **142**, 1166–1177.

Morris, R.J. (2010) Anthropogenic impacts on tropical forest biodiversity: a network structure and ecosystem functioning perspective. *Philosophical Transactions of the Royal Society B*, **365**, 3709–3718.

Muylaert, R.L., Stevens, R.D., Esbérard, C.E.L., et al. (2017) ATLANTIC BATS: a dataset of bat communities from the Atlantic Forests of South America. *Ecology*, **98**, 3227.

Nagy-Reis, M.B., Estevo, C.A., Setz, E.Z.F., Ribeiro, M.C., Chiarello, A.G., & Nichols, J.D. (2017) Relative importance of anthropogenic landscape characteristics for Neotropical frugivores at multiple scales. *Animal Conservation*, **20**, 520–531.

Nielsen, A. & Totland, Ø. (2014) Structural properties of mutualistic networks withstand habitat degradation while species functional roles might change. *Oikos*, **123**, 323–333.

Okuyama, T. & Holland, J.N. (2008) Network structural properties mediate the stability of mutualistic communities. *Ecology Letters*, **11**, 208–216.

Olesen, J.M., Bascompte, J., Dupont, Y.L., & Jordano, P. (2007) The modularity of pollination networks. *Proceedings of the National Academy of Sciences*, **104**, 19891–19896.

Oliveira, M.A., Grillo, A.S., & Tabarelli, M. (2004) Forest edge in the Brazilian Atlantic forest: drastic changes in tree species assemblages. *Oryx*, **38**, 389–394.

Ovaskainen, O., Roy, D.B., Fox, R., & Anderson, B.J. (2016) Uncovering hidden spatial structure in species communities with spatially explicit joint species distribution models. *Methods in Ecology and Evolution*, **7**, 428–436.

Ovaskainen, O., Tikhonov, G., Norberg, A., Blanchet, F.G., Duan, L., Dunson, D., Roslin, T., & Abrego, N. (2017) How to make more out of community data? A conceptual framework and its implementation as models and software. *Ecology Letters*, **20**, 561–576.

Peterson, G., Allen, C.R., & Holling, C.S. (1997) Ecological Resilience, Biodiversity, and Scale. *Ecosystems*, **1**, 6–18.

Pfeifer, M., Lefebvre, V., Peres, C.A., et al. (2017) Creation of forest edges has a global impact on forest vertebrates. *Nature*, **551**, 187–191.

Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G.C., Castilla, J.C., Lubchenco, J., & Paine, R.T. (1996) Challenges in the quest for keystones. *BioScience*, **46**, 609–620.

Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J., & Hirota, M.M. (2009) The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation*, **142**, 1141–1153.

Ribeiro, M.C., Vancine, M. H., Niebuhr, B. B., Bernardo, R., Tonetti, V. R., Giovanelli, J., … Sobral-Souza, T. (in preparation). ATLANTIC SPATIAL: A dataset of spatial and climate variables for the Atlantic Forests of South America.

Ries, L., Fletcher, R.J., Battin, J., & Sisk, T.D. (2004) Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annual Review of Ecology, Evolution, and Systematics*, **35**, 491–522.

Santos, T. & Tellería, J.L. (1994) Influence of forest fragmentation on seed consumption and dispersal of Spanish juniper Juniperus thurifera. *Biological conservation*, **70**, 129–134.

Schleuning, M., Fründ, J., & García, D. (2015) Predicting ecosystem functions from biodiversity and mutualistic networks: an extension of trait-based concepts to plant-animal interactions. *Ecography*, **38**, 380–392.

Sebastián-González, E. (2017) Drivers of species' role in avian seed-dispersal mutualistic networks. *Journal of Animal Ecology*, **86**, 878–887.

Soares-Filho, B.S., Lima, L.S., Hissa, L.B., Costa, W.L.S., Rodrigues, H.O., Ferreira, B.M., Machado, R.F., Campos, A.R., Lima, T.C., & Gomes, W.W. (2013) *OTIMIZAGRO: Uma plataforma integrada de modelagem de uso e mudanças no uso da terra para o Brasil.* IGC/UFMG, Brasilia.

Timóteo, S., Ramos, J.A., Vaughan, I.P., & Memmott, J. (2016) High resilience of seed dispersal webs highlighted by the experimental removal of the dominant disperser. *Current Biology*, **26**, 910–915.

Tjur, T. (2009) Coefficients of determination in logistic regression models - a new proposal: The coefficient of discrimination. *American Statistician*, **63**, 366–372.

Tylianakis, J.M., Laliberté, E., Nielsen, A., & Bascompte, J. (2010) Conservation of species interaction networks. *Biological Conservation*, **143**, 2270–2279.

Valdivia, C.E. & Simonetti, J.A. (2007) Decreased frugivory and seed germination rate do not reduce seedling recruitment rates of Aristotelia chilensis in a fragmented forest. *Biodiversity and Conservation*, **16**, 1593–1602.

Valiente-Banuet, A., Aizen, M.A., Alcántara, J.M., Arroyo, J., Cocucci, A., Galetti, M., García, M.B., García, D., Gómez, J.M., Jordano, P., Medel, R., Navarro, L., Obeso, J.R., Oviedo, R., Ramírez, N., Rey, P.J., Traveset, A., Verdú, M., & Zamora, R. (2015) Beyond species loss: the extinction of ecological interactions in a changing world. *Functional Ecology*, **29**, 299–307.

Vidal, M.M., Hasui, É., Pizo, M.A., Tamashiro, J.Y., Silva, W.R., & Guimarães, P.R. (2014) Frugivores at higher risk of extinction are the key elements of a mutualistic network. *Ecology*, **95**, 3440–3447.

Vidal, M.M., Pires, M.M., & Guimarães, P.R. (2013) Large vertebrates as the missing components of seed-dispersal networks. *Biological Conservation*, **163**, 42–48.

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M., & Jetz, W. (2014) EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, **95**, 2027–2027.

Zurell, D., Pollock, L.J., & Thuiller, W. (2018) Do joint species distribution models reliably detect interspecific interactions from co-occurrence data in homogenous environments? *Ecography*, 1–8.

Table 1. Description of data compiled on (A) species occurrence data, (B) species life-history traits, (C) taxonomic levels used to build the taxonomic correlations, and (D) data on environmental covariates. Each environmental covariate is classified as fragmentation-related, land use-related, climate-related or topography-related. There are no missing values for any of the environmental variables and traits mentioned in the table.

A. Species occurrences

Taxonomic group	$N_{species}$	N_{sites}	Sampling method(s)	Total effort (occurrence records)
Bats	48	186	Mist nets	1753
Birds	251	456	Mist nets, point counts	11674
Large mammals	36	133	Camera traps	930
Primates	22	325	Transect lines, camera traps, visualizations, vocalizations, surveys	558
Small mammals	60	275	Live traps, pitfall traps	1369
Trees	1424	578	Plots	42666

B. Life-history traits

Trait	Description	Bats	Birds	L. mammals	Primates	S. mammals	Trees
Commonness	Total number of occurrences in database.	x	x	x	x	x	x
Body mass	Body mass (log10 g).	x	x	x	x	x	
Frugivory	Proportion of fruits in diet (%).	x	x	x	x	x	
Omnivory	Proportion of total number of food sources listed as dietary categories in source data (%).	x	x	x	x	x	
Foraging strata	In case of mammals, main foraging stratum of the species. Levels: ground, scansorial, arboreal, aerial. In case of birds, proportion of time spent in each foraging stratum (%). Levels: water, ground, understory, midheight, canopy, aerial.	x	x	x	x	x	
Endemism	Endemic to Atlantic forest. Levels: endemic, non-endemic.	x	x	x	x	x	
Wood density	Wood density (g/cm^3).						x
Seed size	Seed length (cm).						x
Height	Maximum growth height (m).						x

C. Taxonomic levels

Class	Bats	Birds	Large mammals	Primates	Small mammals	Trees
Order	-	15	7	-	2	29
Family	-	36	19	4	4	97
Subfamily	4	-	-	-	-	-
Genus	25	145	31	7	30	328
Species	48	251	36	22	60	1424

D. Environmental covariates

Covariate	Description	Category	Reference
Core-edge ratio	Each 60m x 60m forest pixel was classified to belong to edge (respectively, core) if the distance to nearest forest edge was at most (respectively, at least) 120m from the nearest edge. We computed the core-edge ratio as the ratio between the percentage of core and edge forest within a square window of side length 10000m, centered on the sampling site.	Fragmentation	Appendix S11
Area of functionally connected forest	Area of functionally connected forest (ha), i.e. forest that could be reached from the sampling site without crossing gaps larger than 120m. Sampling sites up to 120 m from the forest edge obtain the value as if located inside the fragment. Log10 transformed, at 30m resolution.	Fragmentation	Appendix S11

Distance to road	Euclidean distance to nearest road (m), at 30m resolution.	Fragmentation	Appendix S11
Matrix composition	The proportion of different matrix types within 10200m diameter of the sampling site (%), at 500m resolution. Levels: water, urban, pasture, savanna, annual agriculture, perennial agriculture.	Land use	Soares-Filho et al. (2013)
Temperature seasonality	Temperature seasonality measured by standard deviation, at 982m resolution.	Climate	Fick and Hijmans (2017)
Precipitation	Mean annual precipitation (mm), at 982m resolution.	Climate	Fick & Hijmans (2017)
Precipitation seasonality	Precipitation seasonality measured by coefficient of variation, at 982m resolution.	Climate	Fick & Hijmans (2017)
Altitude	Height above sea level (m), at 982m resolution.	Topography	Hijmans et al. (2005)
Declivity	Inclination of the surface in relation to the horizontal (%).	Topography	Hijmans et al. (2005)

Table 2. Summary of the results of taxon-specific joint species distribution models. The explanatory and predictive powers are based on model fit to the data used to parameterize the model (explanatory power) and independent validation data (predictive power). In addition, we calculated the area under the curve (AUC) for each model based on the cross-validated estimates. We obtained these values by partitioning the sites randomly into five sets, fitting the model using four of the five sets as training data, and predicting the validation data on the remaining fifth set of sites. We repeated this analysis five times, thus generating an independent prediction for each site. The phylogenetic signal, ρ, measures how largely the species' responses to the environment are structured by their relatedness (based on the taxonomical correlations matrix), with 0 being the minimal and 1 the maximal value. The variable γ measures the proportion of the species' responses to the environmental covariates that can be attributed to the life-history traits included in the model. The mean posterior estimates of ρ and γ are presented. The percentages of explained variance attributed to fixed and random effects are shown as averages over species.

Output parameter	**Taxonomic group**					
	Bats	Birds	Large mammals	Primates	Small mammals	Trees
Explanatory R^2	0.30	0.32	0.33	0.54	0.28	0.19
Predictive R^2	0.16	0.20	0.14	0.36	0.17	0.15
AUC	0.73	0.76	0.70	0.86	0.76	0.71
Phylogenetic signal ρ	0.95	-	0.49	0.06	0.59	-
Variation due to traits γ (%)	64	61	75	77	43	36
Variance partitioning						
Fragmentation (%)	13.7	6.7	16.5	10.5	16	2.6
Land use (%)	25.3	11.6	37.7	35.3	28	8.6
Topography (%)	13.5	8.6	8.1	6.5	10.1	7.9
Climate (%)	32.8	13	21.3	31.5	36.2	22
Spatial random effect	14	60	13	15	9.2	59

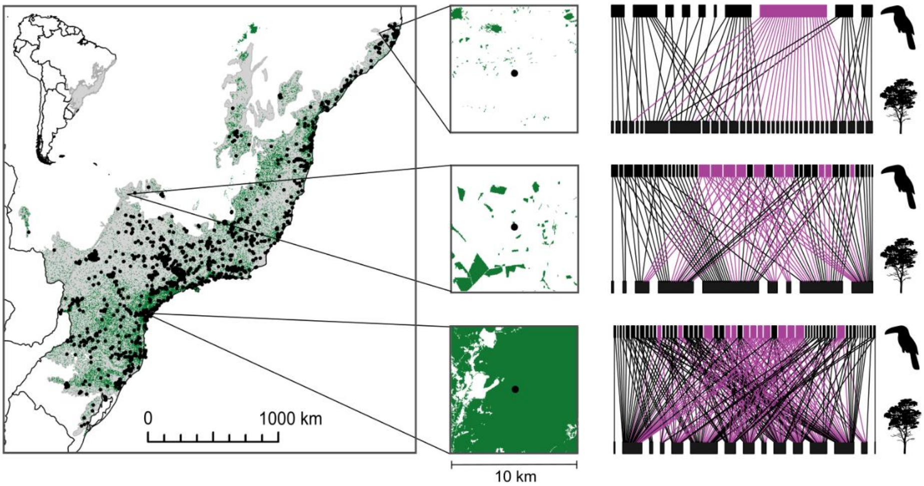


Fig. 1. The study design and schematic illustration of the key results. In the left-most panel, the black dots represent the sampling sites (N = 1953) from which occurrence data on seed dispersers and trees were acquired. The grey colour delineates the original extent of the Atlantic Forest biome, and green colour shows remaining forest fragments. The three locations highlighted in the middle panel have been selected to represent a gradient in forest fragmentation, with decreasing degree of fragmentation from top to bottom. The right-most panel shows predicted interaction networks as bipartite graphs, where the upper and lower boxes correspond respectively to the seed dispersers and trees, and purple colour indicates keystone seed dispersers and their respective interactions. For illustrative purposes, species are ordered to minimize the overlap of the shown interactions.

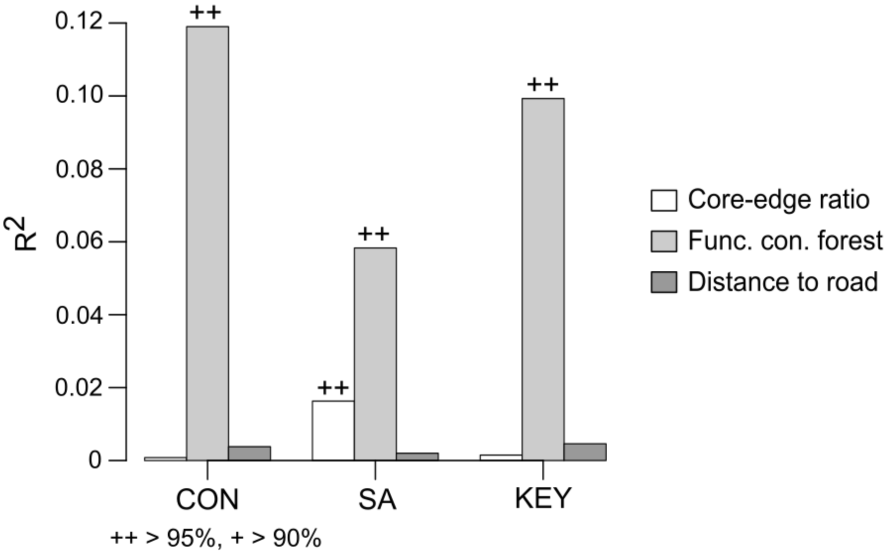


Fig. 2. Effect of fragmentation-related covariates on metrics of seed dispersal interactions. Height of each bar represents the mean R^2-value over 500 linear regressions, where each interaction metric is considered as response variable and each fragmentation-related covariate as explanatory variable. The statistical support for fragmentation affecting seed dispersal interactions negatively is measured by posterior probability for the slope being positive (i.e. fragmentation reducing seed dispersal interactions; note that all our fragmentation-related covariates decrease with increased degree of fragmentation), and is indicated by the + or ++ symbols. CON = link connectance, SA = seed disperser availability, KEY = proportion of interactions provided by keystone seed dispersers according to the model-based approach.

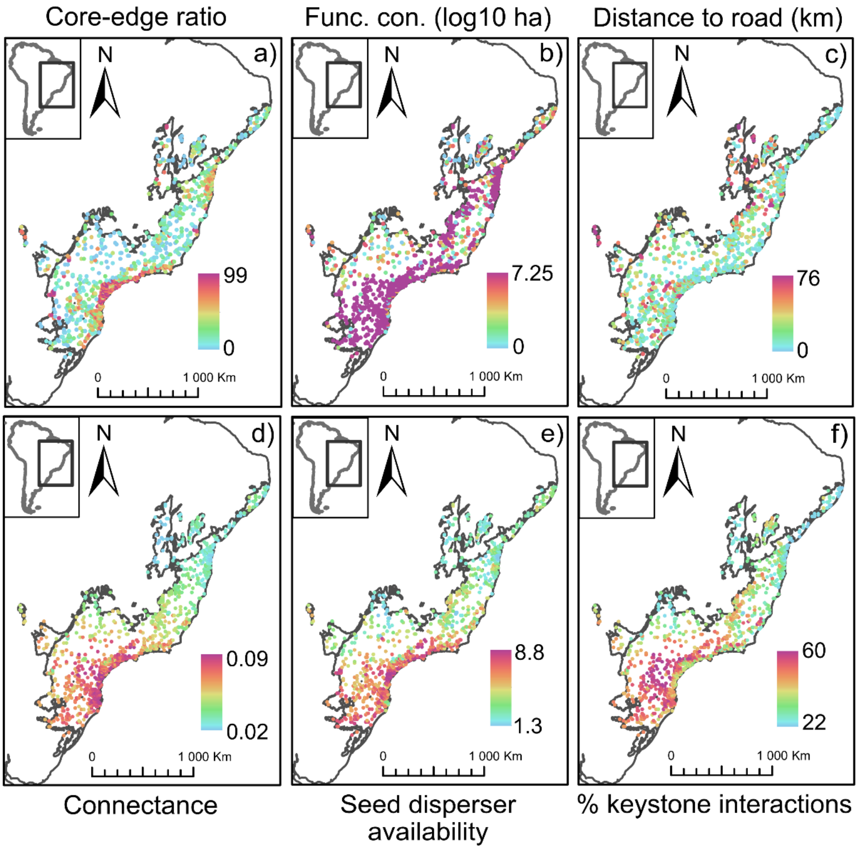


Fig. 3. Spatial distribution of fragmentation- related variables and interaction metrics across the Brazilian Atlantic Forest. Panels a)-c) represent the fragmentation-related covariates of core-to-edge ratio, area of functionally connected forest, and distance to nearest road, respectively. Panels d)–f) represent the interaction metrics of connectance (CON), seed disperser availability (SA), and proportion of interactions provided by the keystone seed dispersers according to the model-based approach (KEY), respectively. The values of the variables in each prediction site are illustrated by a colour gradient.

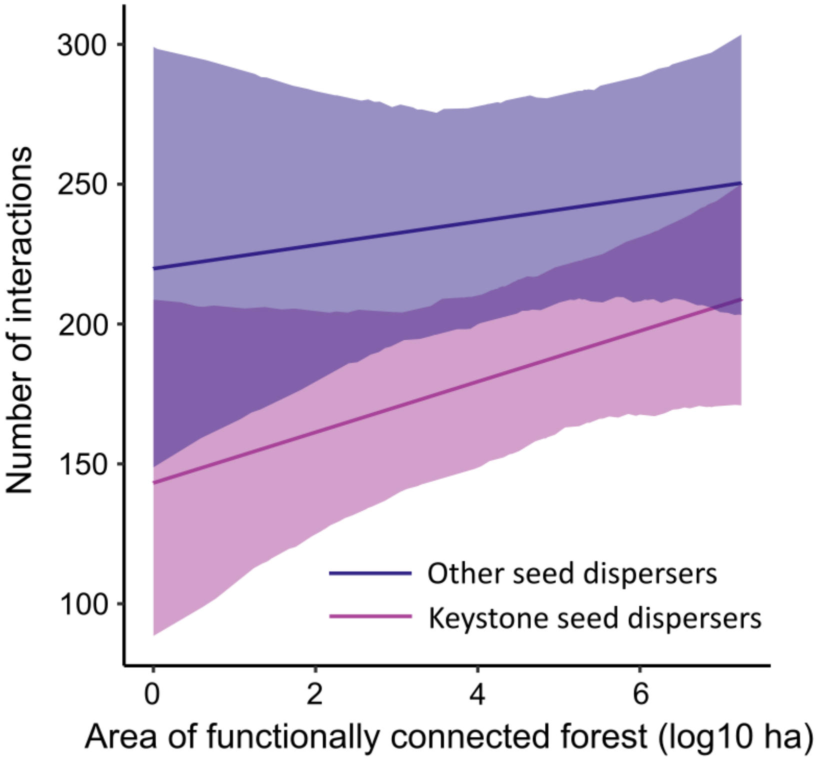


Fig. 4. Relationship between the area of functionally connected forest and the number of seed dispersal interactions. The purple line and ribbon show the number of interactions provided by keystone species whereas the blue line and ribbon show the number of interactions provided by non-keystone species. Keystone seed dispersers were identified with the model-based approach. The lines (respectively, ribbons) show the 50% (respectively, 95%) quantiles of the slope of the linear regression between number of interactions and area of functionally connected forests.

Marjakangas E., Abrego N., Grøtan V., de Lima R.A.F., Bello C., Bovendorp R.S.,

Culot L., Hasui É., Lima F., Muylaert R.L., Niebuhr B.B., Oliveira A.A., Pereira L.A.,

Prado P.I., Stevens R.D., Vancine M.H., Ribeiro M.C., Galetti M., Ovaskainen O.

Fragmented tropical forests lose mutualistic plant-animal interactions

Supporting information Appendix S1

Table S1.1. Full list of literature sources consulted for species life-history traits.

Taxa	Trait	Reference
Primates	Level of frugivory	Aguiar, L. M. et al. 2003. Dieta, Área de Vida, Vocalizações e Estimativas Populacionais de *Alouatta guariba* em um Remanescente Florestal no Norte do Estado do Paraná.
Primates	Level of frugivory	Amora, T. A. et al. 2013. Use of Alternative Plant Resources by Common Marmosets (*Callithric jacchus*) in the Semi-Arid Caatinga Scrub Forests of Northeastern Brazil.
Primates	Level of frugivory	Bicca-Marques, J. C., and Calegaro-Marques, C. 1993. Feeding Postures in the Black Howler Monkey, *Alouatta caraya*.
Primates	Level of frugivory	Bravo, S. P., and Sallenave, A. 2003. Faranging Behavior and Activity Patterns of Alouatta caraya in the Northeastern Argentinean Flooded Forest.
Primates	Level of frugivory	Carvalho Jr, O., et al. 2004. Diet of a Muriqui Group (*Brachyteles arachnoides*) in Continuous Primary Forest.
Primates	Level of frugivory	Caselli, C. B. 2008. Ecologia Alimentar, Padrão de Atividade e Uso do Espaço por *Callicebus nigrifrons* (Primates: Pitheciidae).
Primates	Level of frugivory	Caselli, C. B., and Setz, E. Z. F. 2011. Feeding Ecology and Activity Pattern of Black-Fronted Titi Monkeys (*Callicebus nigrifrons*) in a Semideciduous Tropical Forest of Southern Brazil.
Primates	Level of frugivory	Corrêa, H. K. M. 1995. Ecologia e Comportamento Alimentar de um Grupo de Saguis-da-Serra-Escuros (*Callithrix aurita* E. Geoffroy 1812) no Parque Estadual da Serra do Mar, Núcleo Cunha, São Paulo, Brasil.
Primates	Level of frugivory	Corrêa, H. K. M. et al. 2000. Between-Year Differences in the Feeding Ecology of Highland Marmosets (*Callithrix aurita* and *Callithrix flaviceps*) in Southeastern Brazil.
Primates	Level of frugivory	da Silva, Z. L. 2012. Fatores Determinantes no Uso do Espaço por *Callithrix penicillata* (E. Geoffroy, 1812) Introduzidos em Fragmento Urbano.
Primates	Level of frugivory	David, V. A. 2005. Padrão de Atividades, Ecologia Alimentar e Área de Vida em um Grupo de *Callithrix pinicillata* (Humboldt, 1812) (Primates, Callitrichidae) (Sagui-de-Tufos-Pretos).
Primates	Level of frugivory	de Castro, C. S. S. 2003. Tamanho da Área de Vida e Padrão de Uso do Espaço em Grupos de Saguis, *Callithrix jacchus* (Linnaeus) (Primates, Callitrichidae).
Primates	Level of frugivory	di Bitetti, M. S. 2001. Home-Range Use by the Tufted Capuchin Monkey (*Cebus apella nigritus*) in a Subtropical Rainforest of Argentina.
Primates	Level of frugivory	Dias, L. G., and Strier K. B. 2003. Effects of Group Size on Ranging Patterns in *Brachyteles arachnoides hypoxanthus*.
Primates	Level of frugivory	dos Santos, G. P. 2008. Padrão de Atividades, Dieta e Área de Vida de *Callicebus nigrifrons* (Spix, 1823).
Primates	Level of frugivory	dos Santos, G. P. et al. 2012. The Diet of Wild Black-Fronted Titi Monkeys *Callicebus nigrifrons* During a Bamboo Masting Year.
Primates	Level of frugivory	Fernandes, C. C. 2013. Padrão de Atividade, Dieta e Uso do Espaço por *Callicebus personatus* (Primates, Pitheciidade) em uma Área de Parque Urbano, Município de Santa Teresa, ES.
Primates	Level of frugivory	Fernández, V. A. et al. 2013. Who is Coordinating Collective Movements in Black and Gold Howler Monkeys?
Primates	Level of frugivory	Fontes, I, P. 2011. Variação de Curto e Longo Prazo na Ecologia de *Callicebus coimbrai* Kobayashi & Langguth, 1999: Implicações para a Conservação de Populações na Paisagem Fragmentada da Mata Atlântica de Sergipe.
Primates	Level of frugivory	Fortes, V. B. 2008. Ecologia e Comportamento do Bugio-Ruivo (*Alouatta guariba clamitans* Cabrera 1940) em Fragmentos Florestais na Depressão Central do Rio Grande do Sul, Brasil.
Bats	Body mass	Gardner, A. L. 2007. Mammals of South America. Marsupials, Xenarthrans, Shrews, and Bats 1. The University of Chicago Press. 690 p.
Primates	Level of frugivory	Guzzo, G. B. 2009. Ecologia e Comportamento de *Alouatta guariba clamitans* Cabrera, 1940, em um Fragmento de Mata de Araucária na Serra Gaúcha.
Primates	Level of frugivory	Heiduck, S. 1997. Food Choice in Masked Titi Monkeys (*Callicebus personatus melanochir*): Selectivity or Opportunism?

Primates	Level of frugivory	Hubrecht, R. C. 1985. Home Range Size and Use and Territorial Behavior in the Common Marmoset, *Callithrix jacchus jacchus*, at the Tapacura Field Station, Recife, Brazil.
All seed dispersers	Endemism	IUCN 2017. The IUCN Red List of Threatened Species. Version 2017-3. <http://www.iucnredlist.org>. Downloaded on 18 December 2017.
Primates	Level of frugivory	Kinzey, W. G., and Becker, M. 1983. Activity Patterns of the Masked Titi Monkey, *Callicebus personatus*.
Primates	Level of frugivory	Koch, F. 2008. Dieta e Comportamento de um Grupo *de Aloutta guariba clamitans* Cabrera, 1940: Uma Relação de Causa e Efeito?
Trees	Seed size, maximum height, wood density	Lima, R. A. F. the Neotropical Tree Communities database (TreeCo version 2.0): http://labtrop.ib.usp.br/doku.php?id=projetos:treeco:start
Primates	Level of frugivory	Ludwig, G.; et al. 2005. Uma Avaliação da Dieta, da Área de Vida e das Estimativas Populacionais de *Cebus nigritus* (Goldfuss, 1809) em um Fragmento Florestal no Norte do Estado do Paraná.
Primates	Level of frugivory	Martins, I. G. 2007. Padrão de Atividades do Sagui *Callithrix jacchus* Numa Área de Caatinga.
Primates	Level of frugivory	Martins, M. M. 2005. The Southern Muriqui *Brachyteles arachnoides*: Ecology of a Population in a Semideciduous Forest Fragment.
Primates	Level of frugivory	Martins, M. M. 2008. Fruit Diet of *Alouatta guariba* and *Brachyteles arachnoides* in Southeastern Brazil: Comparison of Fruit Type, Color, and Seed Size.
Primates	Level of frugivory	Martins, M. M., and Setz, E. Z. 2000. Diet of BuffyTufted-Eared Marmosets (*Callithrix aurita*) in a Forest Fragment in Southeastern Brazil.
Primates	Level of frugivory	Martins, W. P. 2010. Densidade Populacional e Ecologia de um Grupo de Macaco-Prego-de-Crista (*Cebus robustus*; Kuhl, 1820) na Reserva Natural Vale.
Primates	Level of frugivory	Milton, K. 1984. Habitat, Diet, and Activity Patterns of Free-Ranging Wolly Spider Monkeys (*Brachyteles arachnoides* E. Geoffroy 1806).
Primates	Level of frugivory	Miranda, G. H. B., and Faria, D. S. 2001. Ecological Aspects of Black-Pincelled Marmoset (*Callithrix penicillata*) in the Cerradão and Dense Cerrado of the Brazilian Central Plateau.
Primates	Level of frugivory	Miranda, J. M. D., and Passos, F. C. 2004. Hábito Alimentar de *Alouatta guariba* (Humboldt) (Primates, Atelidae) em Floresta de Araucária, Paraná, Brasil.
Primates	Body size, level of frugivory	Mittermeier, R. A. et al. 2013. Handbook of the Mammals of the world - Volume 3 - Primates.
Bats	Body mass	Nogueira, M. R., Lima I. P., Peracchi A. L., and Simmons N. B.. 2012. New Genus and Species of nectar-feeding bat from the Atlantic Forest of Southeastern Brazil (Chiroptera: Phyllostomidae: Glossophaginae). American Museum Novitates 3747:1–32.
Primates	Level of frugivory	Passamani, M. 1996. Ecologia e Comportamento de um Grupo de Sagui-da-Cara-Branca (*Callithrix geoffroyi*) em um Fragmento de Mata Atlântica no Espírito Santo.
Primates	Level of frugivory	Passamani, M., and Rylands, A. B. 2000. Home Range of a Geoffroy's Marmoset Group, *Callithrix geoffroyi* (Primates, Callitrichidae) in Southeastern Brazil.
Primates	Level of frugivory	Pontes, A. R. M., and da Cruz, M. A. O. M. 1995. Home Range, Intergroup Transfers, and Reproductive Status of Common Marmosets *Callithrix jacchus* in a Forest Fragment in Northeastern Brazil.
Primates	Level of frugivory	Prates, H. M., and Bicca-Marques, J. C. 2011. Vivendo no Limite? Dieta de um Grupo de Bugios-Pretos (*Alouatta caraya*) Habitante de um Pomar.
Primates	Level of frugivory	Price, E. C., and Piedade, H. M. 2001. Ranging Behavior and Intraspecific Relationships of Masked Titi Monkeys (*Callicebus personatus personatus*).
Primates	Level of frugivory	Raboy, B. E. et al. 2008. Ecology of *Callithrix kuhlli* and a Review of Eastern Brazilian Marmosets.
Primates	Level of frugivory	Reis, M. N. G. 2012. Ecologia Alimentar e Comportamento de *Callicebus nigrifrons* em um Fragmento florestal de Mata Atlântica em Campinas, SP.
Primates	Level of frugivory	Rímoli, A. O. et al. 2008. Behavior Patterns of a Group of Black Howler Monkeys *Alouatta caraya* (Humboldt, 1812) in a Forest Fragment in Terenos, Mato Grosso do Sul: A Seasonal Analysis.
Primates	Level of frugivory	Rímoli, J. et al. 2008. Seasonal and Longitudinal Variation in the Behavior of Free-Ranging Black tufted Capuchins *Cebus nigritus* (Goldfuss,1809) in a Fragment Forest in Southeastern Brazil.
Primates	Level of frugivory	Rímoli, J. et al. 2012. Diet and Activity Patterns of Black Howler Monkeys *Alouatta caraya* (Humboldt, 1812, Primates, Atelidae) in Ecotone Cerrado-Pantanal in the Left Bank of Aquidauana River, Mato Grosso do Sul, Brazil.
Primates	Level of frugivory	Rocha, M. F., and Passamani, M. 2009. Uso do Espaço por um Grupo de Saguis-da-Cara-Branca (*Callithrix geoffroyi*) no Sudeste do Brasil.
Primates	Level of frugivory	Rylands, A. B. 1989. Sympatric Brazilian Callitrichids: The Black Tufted-Ear Marmoset, *Callithrix kuhlli*, and the Golden-Headed Lion Tamarin, *Leontopithecus chrysomelas*.
Primates	Level of frugivory	Santana, M. M. 2012. Comportamento, Dieta e Uso do Espaço em um Grupo de Guigó-de-Coimbra (*Callicebus coimbrai* Kobayashi & Langguth, 1999) no RVS Mata do Junco Capela – SE.
Primates	Level of frugivory	Scanlon, C. E. et al. 1989. Home Range Use and the Exploitation of Gum in the Marmoset *Callithrix jacchus jacchus*.

Primates	Level of frugivory	Souza-Alves, J. P. 2010. Ecologia Alimentar de um Grupo de Guigó-de-Coimbra-Filho (*Callicebus coimbrai* Kobayashi & Langguth, 1999): Perspectivas para a Conservação da Espécie na Paisagem Fragmentada do Sul de Sergipe.
Primates	Level of frugivory	Souza-Alves, J. P. 2013. Ecology and Life-History of Coimbra-Filho's titi monkeys (*Callicebus coimbrai*) in the Brazilian Atlantic Forest.
Primates	Level of frugivory	Souza-Alves, J. P. et al. 2011. Seasonal Versatility in the Feeding Ecology of a Group of Titis (*Callicebus coimbrai*) in the Northern Brazilian Atlantic Forest.
Bats	Body mass	Stevens, R. D., and Willig, M. R. 2000. Density compensation in New World bat communities. Oikos 89: 367-377.
Primates	Level of frugivory	Talebi, M. et al. 2005. Diet of Southern Muriquis in Continuous Brazilian Atlantic Forest.
Primates	Level of frugivory	Thompson, C. L. et al. 2013. Spatial Distribution and Exploitation of Trees Gouged by Common Marmosets (*Callithrix jacchus*).
Primates	Level of frugivory	Vilela, A. A., and Del-Claro, K. 2011. Feeding Behavior of the Black-Tufted-ear Marmoset (*Callithrix penicillata*) (Primata, Callitrichidae) in a Tropical Cerrado Savanna.
All seed dispersers	Dietary traits, body mass, foraging strata	Wilman, H., Belmaker J., Simpson J., de la Rosa C., Rivadeneira M. M., and Jetz W. 2014. EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. Ecology 95:2027–2027.
Primates	Level of frugivory	Zago, L. et al. 2013. Dieta de *Callithrix penicillata* (E. Geoffroy, 1812) (Primates, Callitrichidae) introduzidos na Ilha de Santa Catarina.

Marjakangas E., Abrego N., Grøtan V., de Lima R.A.F., Bello C., Bovendorp R.S., Culot L., Hasui É., Lima F., Muylaert R.L., Niebuhr B.B., Oliveira A.A., Pereira L.A., Prado P.I., Stevens R.D., Vancine M.H., Ribeiro M.C., Galetti M., Ovaskainen O.

Fragmented tropical forests lose mutualistic plant-animal interactions

Supporting information Appendix S2

Table S2.1. Spearman correlation coefficients of pairwise correlations between the selected environmental covariates used in the model fitting. Pairwise correlations stronger than ±0.30 are bolded. Water, Urban, Pasture, Savanna, Ann. agr. and Per. agr. refer to the matrix composition categories (Table 1 in main text). For more detailed information on the environmental covariates, see Table 1 in main text.

	Water	**Urban**	**Pasture**	**Savanna**	**Ann. agr.**	**Per. agr.**	**Road**	**Core /edge**	**Func. con.**	**Declivity**	**Altitude**	**Temp. seas.**	**Mean prec.**	**Prec. seas.**
Water	1	0.041	-0.118	-0.051	-0.073	-0.075	0.011	-0.023	-0.138	-0.087	-0.225	-0.003	0.017	0.013
Urban		1	-0.167	-0.085	-0.071	-0.076	-0.200	-0.045	0.041	0.053	-0.078	-0.007	0.087	0.033
Pasture			1	-0.050	-0.119	-0.021	-0.068	-0.298	**-0.342**	-0.052	0.107	**-0.330**	**-0.406**	**0.314**
Savanna				1	-0.019	-0.098	0.145	-0.076	-0.206	-0.108	0.158	-0.119	-0.124	0.063
Ann. agr.					1	-0.077	-0.108	-0.116	-0.124	-0.233	0.004	0.282	0.061	-0.144
Per. agr.						1	-0.124	-0.095	0.055	-0.048	-0.097	-0.175	-0.028	-0.244
Road							1	0.128	-0.021	-0.046	0.115	-0.019	-0.119	0.061
Core/edge								1	0.156	0.025	-0.036	0.135	0.182	-0.072
Func. con.									1	**0.304**	0.160	**0.476**	**0.507**	**-0.400**
Declivity										1	0.187	0.121	0.153	0.024
Altitude											1	0.117	0.122	0.213
Temp. seas.												1	**0.536**	**-0.496**
Mean prec.													1	**-0.410**
Prec. seas.														1

Marjakangas E., Abrego N., Grøtan V., de Lima R.A.F., Bello C., Bovendorp R.S., Culot L., Hasui É., Lima F., Muylaert R.L., Niebuhr B.B., Oliveira A.A., Pereira L.A., Prado P.I., Stevens R.D., Vancine M.H., Ribeiro M.C., Galetti M., Ovaskainen O.

Fragmented tropical forests lose mutualistic plant-animal interactions

Supporting information Appendix S3

1 Phylogenetic signal of interaction partner sharing

In order to test whether plant species within a particular genus were more likely to share a seed dispersal partner, we compared the average number of shared seed dispersal partners within each plant genus to the average number of shared seed dispersal partners among plant species in different genera in the subset data.

We included those plant species that fulfilled two criteria: 1) they had a recorded interaction with at least one seed disperser species in Bello et al. (2017) interaction database, and 2) there were more than one plant species within each genus. This left us with 71 plant genera, divided into 334 species. After this initial filtering of plant species, we also removed those seed disperser species that no longer had any interactions with any of the included plant species and were left with 207 seed disperser species.

We found the average number of shared interaction partners among plant genera to be 0.69. The plant species sharing the most interaction partners (n = 40) were *Alchornea glandulosa* and *Myrsine coriacea*. The average number of shared interaction partners within plant genera varied between 0 and 38, the mean across all genera being 2.6 shared partners (Figure S3.1). The number of plant species per genus varied between 2 (several genera) and 36 (*Miconia*) after filtering the data. This indicates that it is more common for plant species within a genus to share seed dispersal partners than it is for plant species on average.

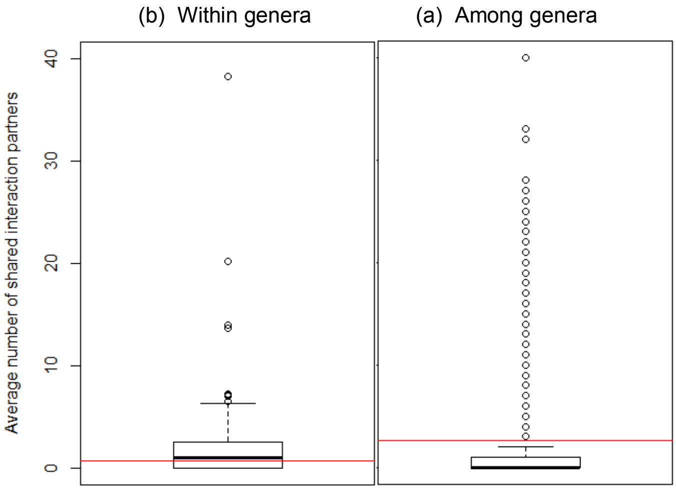
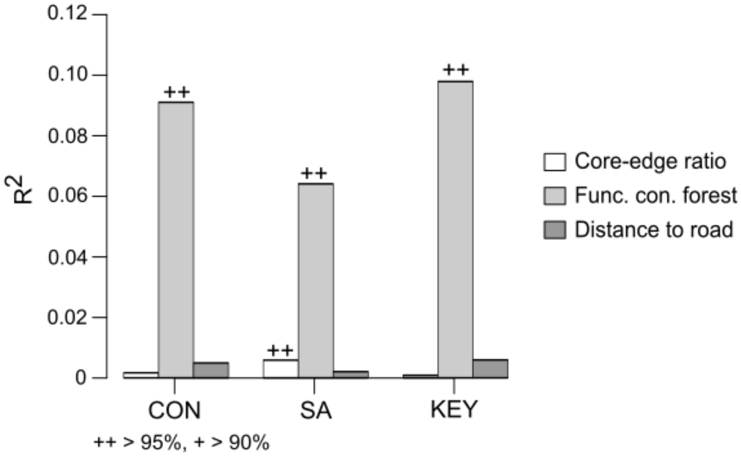


Figure S3.1. The average number of shared interaction partners (a) within plant genera and (b) among plant genera. Red lines represents the average number of shared interaction partners in the other scenario: among plant genera, i.e. all species pairs excluding those belonging to the same genus (in panel (a)), and the average number of shared interaction partners within genera (in panel (b)). Note the imbalanced sample sizes: 71 genera and 54006 species pairs.

2 Interaction metric-fragmentation covariate relationships with original interaction data

To confirm our results, we repeated the key analyses without completing the interaction matrix and used the original binary data on pairwise interactions (Bello et al., 2017) as basis for post hoc calculations. More specifically, we estimated the three interaction variables with the original interaction data and then tested their relationships with the fragmentation covariates, as described in Methods (see main text).

We found that area of functionally connected forest had the strongest effect on interaction metrics (Figure S3.2). Furthermore, all interaction metrics had higher values in southern parts of the Atlantic Forest compared to the northern parts (S3.3). These results are parallel to those obtained with semi-quantitative interaction probabilities (see main text), only the absolute values were lower as expected when modelling the phenomena without completing the interaction matrix. When evaluating the effect of functionally connected forest area to number of interactions provided by keystone and non-keystone species, we found that the number interactions declined with decreasing forest area (Figure S3.4). The result is again quantitatively similar, but absolute values lower compared to those obtained with semi-quantitative interaction probabilities. We observed slightly different slopes between the interactions provided by keystone and non-keystone species, indicating that interactions by keystone species may be more strongly affected by fragmentation than those by non-keystone species. The 95% quantiles, however, overlap so much that a true difference is not possible to conclude.



++ > 95%, + > 90%

Figure S3.2. Effect of fragmentation-related covariates on metrics of seed dispersal interactions. Height of each bar represents the mean R2-value over 500 linear regressions, where each interaction metric is considered as response variable and each fragmentation-related covariate as explanatory variable. The statistical support for fragmentation affecting seed dispersal interactions negatively is measured by posterior probability for the slope being positive (i.e. fragmentation reducing seed dispersal interactions; note that all our fragmentation-related covariates decrease with increased degree of fragmentation), and is indicated by the + or ++ symbols. CON = link connectance, SA = seed disperser availability, KEY = proportion of interactions provided by keystone seed dispersers according to the model-based approach.

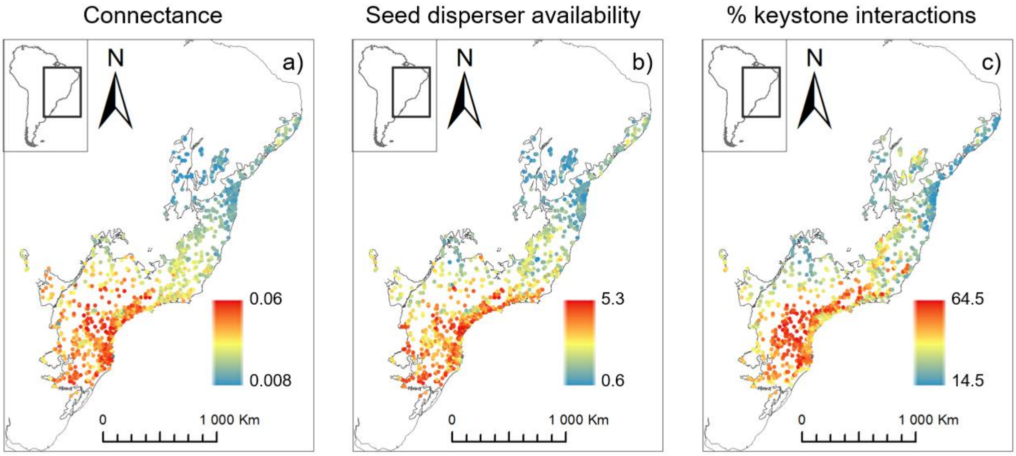


Figure S3.3. Spatial distribution of interaction metrics across the Brazilian Atlantic Forest. Panels a)-c) represent the interaction metrics of connectance (CON), seed disperser availability (SA), and proportion of interactions provided by the keystone seed dispersers according to the model-based approach (KEY), respectively. The values of the variables in each prediction site are illustrated by a color gradient.

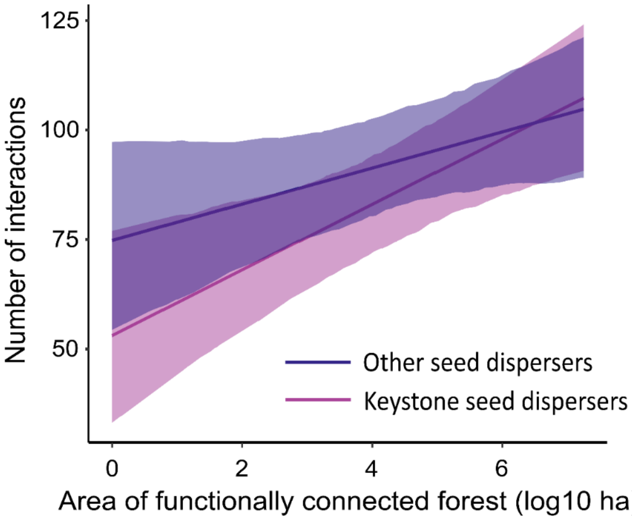


Figure S3.4. Relationship between the area of functionally connected forest and the number of seed dispersal interactions. The purple line and ribbon show the number of interactions provided by keystone species whereas the blue line and ribbon show the number of interactions provided by non-keystone species. Keystone seed dispersers were identified with the model-based approach. The lines (respectively, ribbons) show the 50% (respectively, 95%) quantiles of the slope of the linear regression between number of interactions and area of functionally connected forests.

Marjakangas E., Abrego N., Grøtan V., de Lima R.A.F., Bello C., Bovendorp R.S., Culot L., Hasui É., Lima F., Muylaert R.L., Niebuhr B.B., Oliveira A.A., Pereira L.A., Prado P.I., Stevens R.D., Vancine M.H., Ribeiro M.C., Galetti M., Ovaskainen O.

Fragmented tropical forests lose mutualistic plant-animal interactions

Supporting information Appendix S4

Eq. S4.1. Calculation the keystone index for each seed disperser species.

$$E\,[N_i] = \frac{\sum_k (p_{ik} * (\sum_j p_{jk} * y_{ij}))}{\sum_k p_{ik}}$$

Where,

$N_i = \mathit{mean\ number\ of\ known\ interactions\ with\ tree\ species\ that\ seed\ disperser\ i\ has\ in\ the\ sites\ where\ it\ occurs}$

$p_{ik} = \mathit{occurrence\ probability\ of\ seed\ disperser\ i\ in\ prediction\ location\ k}$

$p_{jk} = \mathit{occurrence\ probability\ of\ tree\ j\ in\ prediction\ location\ k}$

$y_{ij} \in \{0, 0.5, 0.75, 1\}, \mathit{interaction\ matrix\ value\ between\ seed\ disperser\ i\ and\ tree\ j}$

Table S4.1. List of identified keystone species based on the calculated species-specific keystone index values. The average keystone index among all seed disperser species was 4.25, and we chose the top 5% quantile of species with keystone index value >21.5. The conservation status of the species is categorized *sensu* International Union for Conservation of Nature (IUCN 2017. The IUCN Red List of Threatened Species. Version 2017-3. <http://www.iucnredlist.org>. Accessed 05.01.2018). Forest use of the species is categorized based on information from IUCN database; species associated with secondary forests may also inhabit old-growth forests, but not vice versa.

Data set	Species	Keystone index	IUCN classification	Endemic	Forest use	Total occurrence
Primates	*Brachyteles arachnoides*	52.18	Endangered	Yes	Old-growth	2
Birds	*Turdus albicollis*	38.12	Least Concern	No	Secondary forest	188
Birds	*Turdus rufiventris*	36.59	Least Concern	No	Secondary forest	232
Birds	*Penelope superciliaris*	36.54	Least Concern	No	Secondary forest	84
Birds	*Tangara sayaca*	31.40	Least Concern	No	Secondary forest	150
Birds	*Chiroxiphia caudata*	30.41	Least Concern	Yes	Secondary forest	225
Birds	*Turdus leucomelas*	29.98	Least Concern	No	Secondary forest	207
Birds	*Pitangus sulphuratus*	29.92	Least Concern	No	Secondary forest	207
Primates	*Alouatta guariba*	29.06	Least Concern	Yes	Secondary forest	85
Birds	*Turdus flavipes*	26.13	Least Concern	No	Secondary forest	78
Birds	*Turdus amaurochalinus*	25.98	Least Concern	No	Secondary forest	141
Birds	*Selenidera maculirostris*	25.89	Least Concern	Yes	Old-growth	32
Birds	*Saltator similis*	25.84	Least Concern	No	Secondary forest	166
Birds	*Tachyphonus coronatus*	25.44	Least Concern	Yes	Secondary forest	185
Birds	*Carpornis cucullata*	24.95	Near Threatened	Yes	Old-growth	9
Birds	*Ramphastos dicolorus*	24.91	Least Concern	No	Old-growth	38
Birds	*Aburria jacutinga*	23.27	Endangered	Yes	Old-growth	4
Birds	*Elaenia flavogaster*	22.82	Least Concern	No	Secondary forest	72
Birds	*Tangara cayana*	22.03	Least Concern	No	Secondary forest	89
Primates	*Leonthopithecus chrysomelas*	21.66	Endangered	Yes	Secondary forest	21
Birds	*Myiodynastes maculatus*	21.53	Least Concern	No	Secondary forest	149

Table S4.2. Alphabetically ordered list of selected keystone species based on existing literature and expert evaluation (see Methods). The conservation status of the species is categorized *sensu* International Union for Conservation of Nature (IUCN 2017. The IUCN Red List of Threatened Species. Version 2017-3. <http://www.iucnredlist.org>. Accessed 05.01.2018). Forest use of the species is categorized based on information from IUCN database; species associated with secondary forests may also inhabit old-growth forests, but not vice versa.

Data set	Species	IUCN classification	Endemic	Forest use	Total occurrence
Primates	*Alouatta caraya*	Least Concern	No	Secondary forest	10
Primates	*Brachyteles hypoxanthus*	Critically Endangered	Yes	Old-growth	4
Birds	*Carpornis cucullata*	Near Threatened	Yes	Old-growth	9
Birds	*Euphonia pectoralis*	Least Concern	No	Old-growth	47
Birds	*Habia rubica*	Least Concern	No	Secondary forest	143
Birds	*Ilicura militaris*	Least Concern	Yes	Old-growth	31
Primates	*Leontopithecus chrysomelas*	Endangered	Yes	Secondary forest	21
Birds	*Lipaugus lanioides*	Near Threatened	Yes	Old-growth	5
Mammals	*Nasua nasua*	Least Concern	No	Secondary forest	9
Birds	*Pteroglossus bailloni*	Near Threatened	Yes	Old-growth	12
Birds	*Ramphastos dicolorus*	Least Concern	No	Old-growth	38
Birds	*Selenidera maculirostris*	Least Concern	Yes	Old-growth	32
Birds	*Tangara cyanocephala*	Least Concern	Yes	Secondary forest	12
Birds	*Tangara cyanoptera*	Near Threatened	Yes	Secondary forest	17
Birds	*Tangara desmaresti*	Least Concern	Yes	Old-growth	15
Birds	*Tangara ornata*	Least Concern	Yes	Secondary forest	32
Birds	*Tangara seledon*	Least Concern	Yes	Secondary forest	28
Birds	*Tityra cayana*	Least Concern	No	Secondary forest	79
Birds	*Trichothraupis melanops*	Least Concern	No	Secondary forest	191
Birds	*Turdus albicollis*	Least Concern	No	Secondary forest	188
Birds	*Turdus flavipes*	Least Concern	No	Secondary forest	78

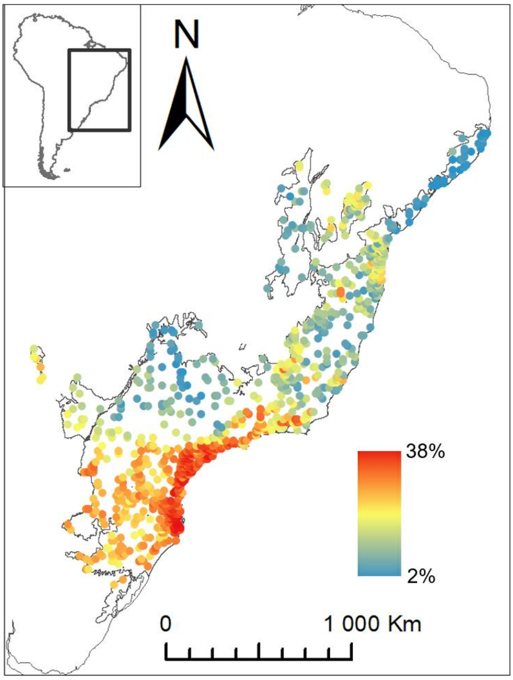


Fig. S4.1. Spatial distribution of proportion of seed dispersal interaction provided by the keystone seed dispersers across the Brazilian Atlantic Forest. Keystone species were selected according to the traditional approach (see Methods). The values of the variables in each prediction site are illustrated by a colour gradient.

Table S4.3. Effect of fragmentation-related covariates on proportion of interactions provided by keystone seed dispersers. R^2-column represents the mean R^2-value over 500 linear regressions, where each interaction metric is considered as response variable and fragmentation covariate as explanatory variable. The statistical support for fragmentation affecting seed dispersal interactions negatively is measured by posterior probability for the slope being positive (i.e. fragmentation reducing seed dispersal interactions; note that all our fragmentation-related covariates decrease with increased degree of fragmentation). Keystone seed dispersers were selected according to the traditional approach (see Methods).

Fragmentation covariate	R^2	Statistical support
Core-edge ratio	0.044	1
Area of functionally connected forest	0.249	1
Distance to nearest road	0.009	0.93

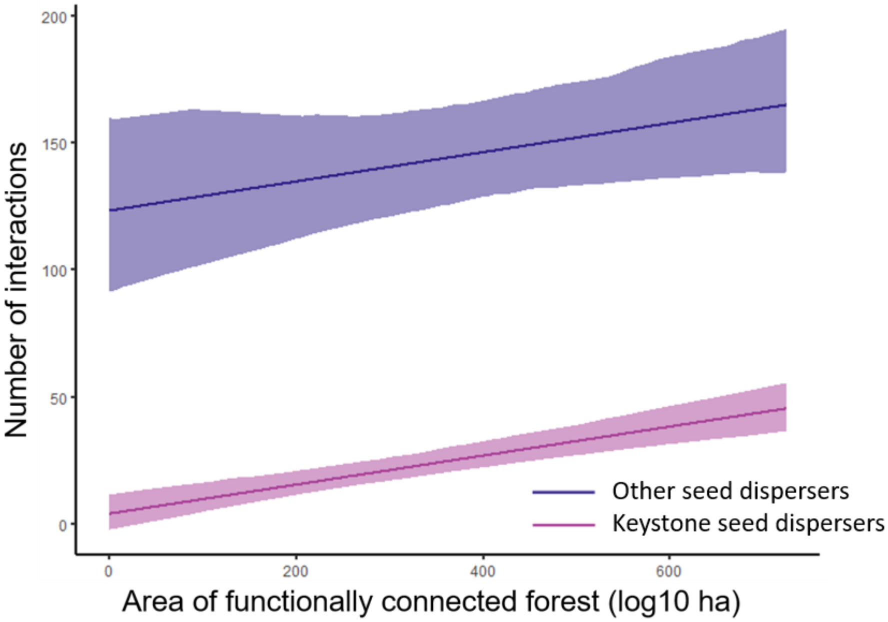


Fig. S4.2. Relationship between the area of functionally connected forest and the number of seed dispersal interactions. The purple line and ribbon show the number of interactions provided by keystone species whereas the blue line and ribbon show the number of interactions provided by non-keystone species. Keystone seed dispersers were identified by the traditional approach (see Methods). The lines (respectively, ribbons) show the 50% (respectively, 95%) quantiles of the slope of the linear regression between number of interactions and area of functionally connected forests.

Marjakangas E., Abrego N., Grøtan V., de Lima R.A.F., Bello C., Bovendorp R.S., Culot L., Hasui É., Lima F., Muylaert R.L., Niebuhr B.B., Oliveira A.A., Pereira L.A., Prado P.I., Stevens R.D., Vancine M.H., Ribeiro M.C., Galetti M., Ovaskainen O.

Fragmented tropical forests lose mutualistic plant-animal interactions

Supporting information Appendix S5

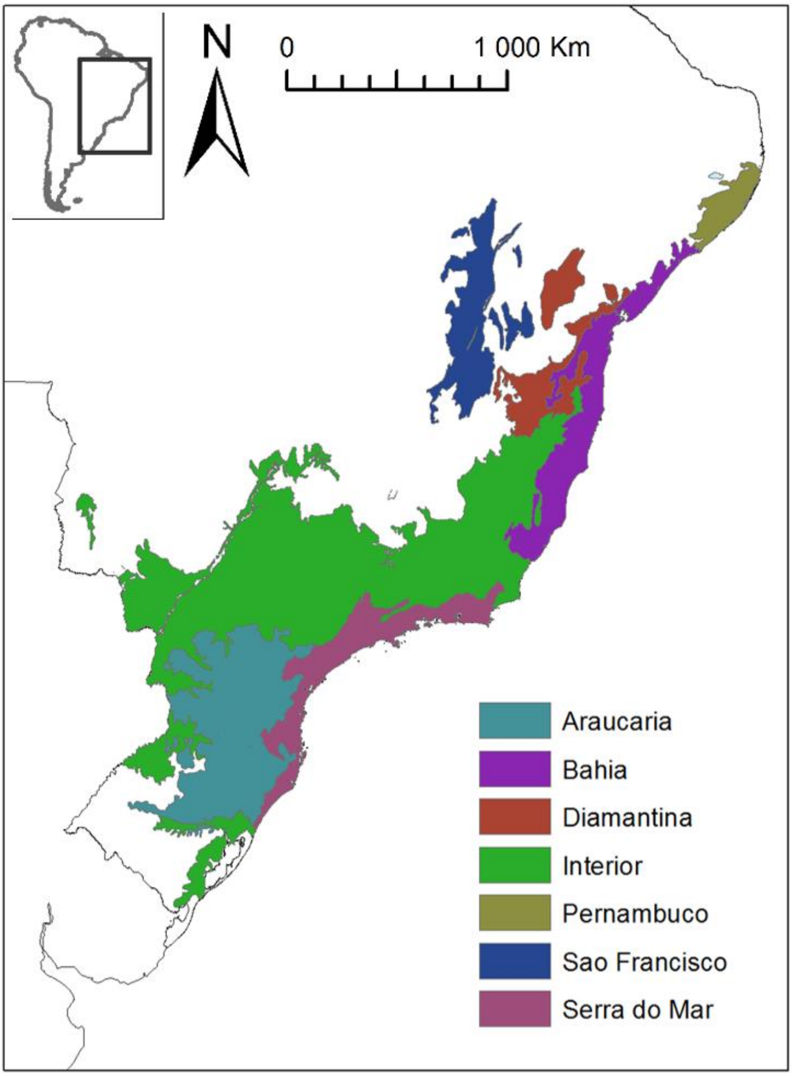


Fig. S5.1. Spatial distribution of biogeographical sub-regions in the Brazilian Atlantic Forest. Note that in this study we did not consider Brejos Nordestinos sub-region. Modified from Ribeiro et al. (2009).

Table S5.1. Results on the relationships between interaction metrics and fragmentation-related covariates in each biogeographical sub-region. Value in each cell represents the mean R^2-value over 500 linear regression fitted to the prediction site specific data, where each interaction metric is considered as response variable and each fragmentation-related covariate (ratio = core-edge ratio, funcon = area of functionally connected forest, road = distance to nearest road) as explanatory variable. The statistical support for fragmentation decreasing the different measures of seed dispersal interactions is shown in parentheses after the respective R^2-value. The statistical support is measured by posterior probability for the slope being positive (i.e. fragmentation reducing seed dispersal interactions; note that all our fragmentation-related covariates decrease with increased degree of fragmentation). CON = link connectance, SA = seed disperser availability (seed dispersal interactions per tree species), and KEY = proportion of interactions provided by keystone species according to the model-based approach.

		Biogeographical sub-region						
		Araucaria	Bahia	Diamantina	Interior	Pernambuco	Sao Francisco	Serra do Mar
CON	R^2_{ratio} (% positive slopes)	0.008 (0.61)	0.007 (0.08)	0.028 (0.64)	0.008 (0.02)	0.038 (0.52)	0.031 (0.47)	0.041 (0)
	R^2_{funcon}(% positive slopes)	0.007 (0.48)	0.016 (0.27)	0.055 (0.79)	0.006 (0.56)	0.044 (0.57)	0.033 (0.48)	0.005 (0.50)
	R^2_{road} (% positive slopes)	0.010 (0.57)	0.023 (0.76)	0.057 (0.92)	0.006 (0.36)	0.045 (0.55)	0.061 (0.81)	0.009 (0.28)
SA	R^2_{ratio} (% positive slopes)	0.016 (0.83)	0.012 (0.77)	0.027 (0.57)	0.019 (0.98)	0.041 (0.50)	0.055 (0.67)	0.010 (0.92)
	R^2_{funcon}(% positive slopes)	0.010 (0.86)	0.017 (0.52)	0.038 (0.68)	0.035 (0.99)	0.053 (0.60)	0.044 (0.65)	0.008 (0.78)
	R^2_{road} (% positive slopes)	0.007 (0.41)	0.017 (0.46)	0.019 (0.53)	0.006 (0.51)	0.057 (0.44)	0.060 (0.68)	0.016 (0.81)
KEY	R^2_{ratio} (% positive slopes)	0.009 (0.27)	0.002 (0.46)	0.021 (0.40)	0.002 (0.34)	0.037 (0.51)	0.080 (0.91)	0.005 (0.38)
	R^2_{funcon}(% positive slopes)	0.010 (0.36)	0.045 (0.94)	0.037 (0.73)	0.029 (0.97)	0.085 (0.25)	0.035 (0.58)	0.030 (0.99)
	R^2_{road} (% positive slopes)	0.009 (0.58)	0.022 (0.71)	0.055 (0.93)	0.007 (0.66)	0.045 (0.63)	0.214 (1)	0.040 (0.99)

Marjakangas E., Abrego N., Grøtan V., de Lima R.A.F., Bello C., Bovendorp R.S., Culot L., Hasui É., Lima F., Muylaert R.L., Niebuhr B.B., Oliveira A.A., Pereira L.A., Prado P.I., Stevens R.D., Vancine M.H., Ribeiro M.C., Galetti M., Ovaskainen O.

Fragmented tropical forests lose mutualistic plant-animal interactions

Supporting information Appendix S6

Table S6.1. Comparison of model outputs of the overlapping mammal species. The total occurrences in the focal data set (bat, primate or small mammal) and in the secondary data set (large mammals) were compiled from the original data. We calculated the differences between the predicted occurrence probabilities in each of the 912 prediction sites in the two separate models, and took the mean over the locations to obtain a robust estimate of the difference of occurrence probability predictions (Δp). Finally, we listed the keystone index of the species in the focal data.

Data set	**Species**	**$N_{\text{occurrence}}$ (focal data)**	**$N_{\text{occurrence}}$ (secondary data)**	**Δp**	**Keystone index (focal data)**
Bats	*Sturnira lilium*	137	70	0.24	5.82
Primates	*Alouatta caraya*	10	52	-0.39	13.10
Primates	*Callithrix kuhlii*	58	3	0.09	2.34
Primates	*Callithrix penicillata*	45	3	0.01	0.99
Primates	*Leonthopithecus chrysomelas*	21	3	0.02	21.66
Primates	*Sapajus nigritus*	92	21	-0.11	16.86
Primates	*Sapajus xanthosternos*	29	3	0.04	16.34
S. mammals	*Gracilianus agilis*	10	61	-0.50	0
S. mammals	*Juliomys pictipes*	36	2	0.12	0
S. mammals	*Monodelphis scalops*	21	8	-0.05	0

Marjakangas E., Abrego N., Grøtan V., de Lima R.A.F., Bello C., Bovendorp R.S., Culot L., Hasui É., Lima F., Muylaert R.L., Niebuhr B.B., Oliveira A.A., Pereira L.A., Prado P.I., Stevens R.D., Vancine M.H., Ribeiro M.C., Galetti M., Ovaskainen O.

Fragmented tropical forests lose mutualistic plant-animal interactions

Supporting information Appendix S7

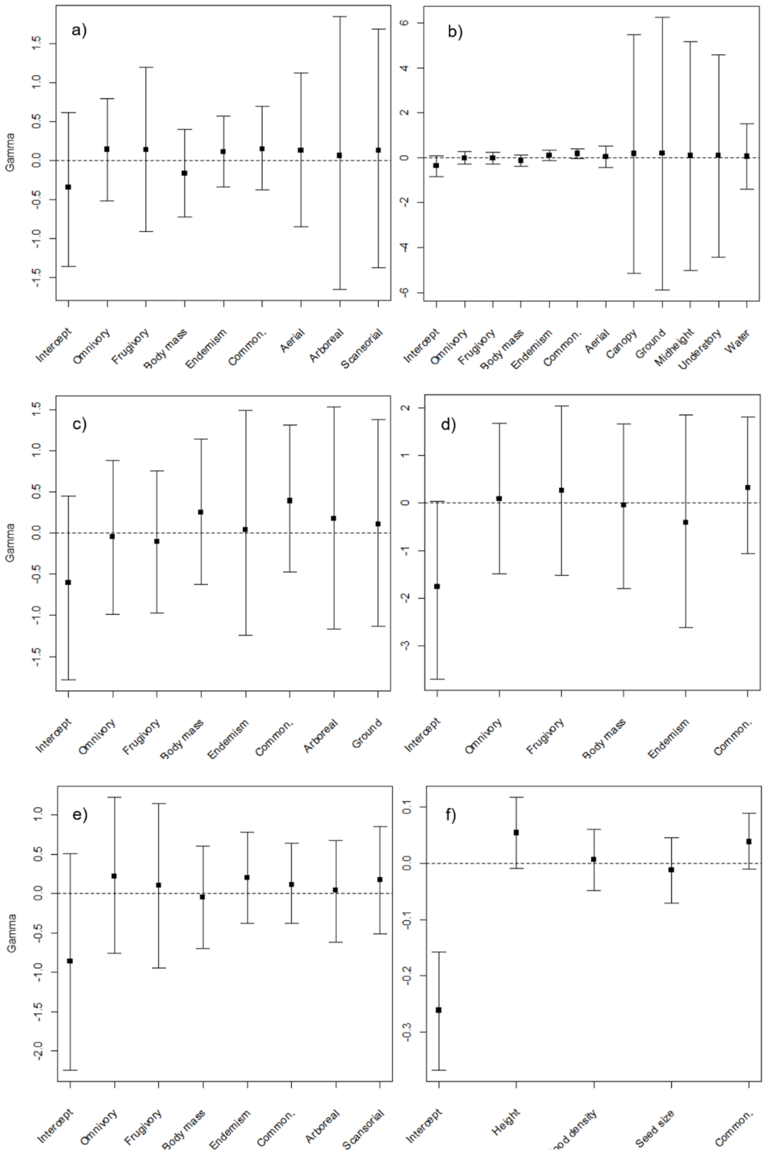


Fig. S7.1. Effect of life-history traits on species responses to the environment. The variable γ (gamma) measures the proportion of the species' responses to the environmental covariates can be attributed to the life-history traits included in the model. Panels a)-f) represent the taxonomic groups (bats, birds, large mammals, primates, small mammals and trees, respectively). The boxplots represent the mean response to all environmental covariates, whereas the error bars represent the 2.5% and 97.5% quantiles of the reponses to all environmental covariates. For detailed description of included traits and environmental covariates, see Table 1 in the main text.

PAPER IV

Not included due to copyright restrictions

Electronic Supplementary Material

Appendix C

Marjakangas et al. 2018 Philosophical Transactions of the Royal Society B

Detailed description of used data, joint species distribution modelling, and the explanatory power of the models.

Data on species communities and environmental covariates

We used the most spatially and taxonomically comprehensive community databases available for the Atlantic Forest (the ATLANTIC series data papers: https://github.com/LEEClab/Atlantic_series, and the Neotropical Tree Communities database (TreeCo version 2.0): http://labtrop.ib.usp.br/doku.php?id=projetos:treeco:start). Altogether, we compiled data on 211 frugivore and 1426 plant species (Culot et al. (In press); Lima *et al.* 2015; Lima *et al.* 2017; Hasui *et al.* 2018). See electronic supplementary material, appendices A and B for species lists. We selected the surveys conducted between 1990 and 2017 based on the published information on the sampling design, including precise geographical coordinates, sufficiently detailed information on the sampling site as well as the sampling itself. For the major seed disperser groups, birds, large and medium sized mammals and primates, we compiled data on: (1) the occurrences of species in the surveys; (2) species life-history traits; (3) taxonomic correlations among the species; and (4) environmental covariates associated with each sampling site, in addition to the geographical coordinates (table S1).

Species occurrences. We used presence-absence data to produce occurrence matrices. We used data on all seed disperser genera with interactions recorded in the Atlantic Forest (Bello et al. 2017), excluding species known to behave more as seed predators than dispersers as well as bats and small mammals due to incomplete data on distribution or interaction patterns (which could impair the assessment of a spatial credit at broad scale) and to taxonomic inconsistency in some genera (which could impair the prediction of pairwise interactions. In addition, we only included plant species that were identified as zoochoric (Almeida-Neto et al. 2008, Bello et al. 2017), reported to grow ≥4 meters high, and had ≥5 observations in the plant occurrence dataset.

Species traits. We obtained frugivore life-history traits from the EltonTraits database (Wilman et al. 2014), and completed the missing values with various data sources (Table S2). Included frugivore traits were body mass, levels of frugivory and omnivory, endemism in Atlantic Forest, foraging strata, and commonness. As plant life-history traits we included seed size, wood density, and maximum height that were obtained from the TreeCo database. Plant trait data were completed with genus level averages in cases of missing values, with the exception of maximum height for which we only used the species-level data (Díaz et al. 2015).

Taxonomic correlations. Due to the lack of comprehensive quantitative phylogenies, we derived the phylogenetic correlation matrices from the taxonomic trees that included the levels of orders, families, genera and species (except for primates: families, genera and species), and that assumed equal branch lengths for the levels. The correlation measure between species within a taxonomic group varies from 0 to 1, value 0 indicating no shared taxonomic levels. Due to computational limitations, we did not include taxonomic correlation in the bird and plant models.

Environmental covariates. We obtained environmental covariates from a variety of sources based on the reported geographical coordinates of sampling sites in the database (Hijmans *et al.* 2005; Ribeiro *et al.* 2009; Soares-Filho *et al.* 2013; Karger *et al.* 2016; Environmental Systems Research Institute (ESRI) 2017; Fick & Hijmans 2017). We included climatic, topographic and fragmentation-related variables to control for their variation in the species occurrence data. We used Albers' projected coordinate system with SAD69 datum in all spatial analyses.

Joint species distribution modelling of each taxonomic group

To synthesize data on species occurrences, environmental covariates, species traits and taxonomic relationships within a single modelling framework, we applied hierarchical modelling of species communities (HMSC) (Ovaskainen et al. 2017). HMSC is a joint species distribution model that models the occurrences of all species simultaneously, with the objective of obtaining community-level predictions. We used HMSC to model each major taxonomic group (birds, large and medium-sized mammals, primates and plants) separately. For each group, we fitted a binomial model with probit link to the presence-absence data. In addition to modelling the species-specific responses to environmental covariates, HMSC examines how these responses are influenced by shared species traits and phylogenetic relatedness. In all analyses, we included spatially structured latent variables to account for spatial autocorrelation in the species occurrence data as well as to model co-occurrence patterns (Ovaskainen et al. 2016, 2017). We fitted the models using a Bayesian inference framework written in Matlab (Ovaskainen et al. 2017), using the default prior distributions.

To evaluate the predictive power of the HMSC models, we applied a cross-validation procedure. To do so, we randomly selected 4/5 of the sampling sites as training sites for model fitting, and then used the fitted models to predict the occurrence data on the remaining validation sites. We repeated this procedure five times so that in each time we iterated the training and validation sites, thus generating an independent prediction for each sampling site. We compared the goodness of fit of predictions to the validation data by calculating Tjur's (2009) R^2.

The fitted HMSC models explained 19–54% (14–36% based on the cross-validation) of the variation in species' occurrences across the Brazilian Atlantic Forest. Among the studied taxa, primates showed the most predictable patterns in their occurrences (R^2=0.54), followed by large mammals (R^2=0.34), birds (R^2=0.33), and plants R^2=0.20).

Table S1. Description of data compiled regarding (A) species occurrence data, (B) species life-history traits, (C) taxonomic levels used to build the taxonomic correlations, and (D) data on environmental covariates. Each environmental covariate is classified as fragmentation-related, land use-related, climate-related or topography-related. There are no missing values for any of the environmental variables and traits mentioned in the table.

A. Species occurrences

Taxonomic group	$N_{species}$	N_{sites}	Sampling method(s)	Total effort (occurrence records)
Birds	251	456	Mist nets, point counts	11674
Large mammals	36	133	Camera traps	930
Primates	22	325	Transect lines, camera traps, visualizations, vocalizations, surveys	558
Plants	1426	578	Plots	42666

B. Life-history traits

Trait	Description	Birds	L. mammals	Primates	Plants
Commonness	Total number of occurrences in database.	x	x	x	x
Body mass	Body mass (log10 g).	x	x	x	
Frugivory	Proportion of fruits in diet (%).	x	x	x	
Omnivory	Proportion of total number of food sources listed as dietary categories in source data (%).	x	x	x	
Foraging strata	In case of mammals, main foraging stratum of the species. Levels: ground, scansorial, arboreal, aerial. In case of birds, proportion of time spent in each foraging stratum (%). Levels: water, ground, understory, midheight, canopy, aerial.	x	x	x	
Endemism	Endemic to Atlantic forest. Levels: endemic, non-endemic.	x	x	x	
Wood density	Wood density (g/cm^3).				x
Seed size	Seed length (cm).				x
Height	Maximum growth height (m).				x

C. Taxonomic levels

Class	Birds	L. mammals	Primates	Plants
Order	15	7	-	29
Family	36	19	4	97
Subfamily	-	-	-	-
Genus	145	31	7	328
Species	251	36	22	1426

D. Environmental covariates

Covariate	Description	Category	Reference
Core-edge ratio	Each 60m x 60m forest pixel was classified to belong to edge (respectively, core) if the distance to nearest forest edge was at most (respectively, at least) 120m from the nearest edge. We computed the core-edge ratio as the ratio between the percentage of core and edge forest within a square window of side length 10000m, centered on the sampling site.	Fragmentation	Ribeiro *et al.* (2009)
Area of functionally connected forest	Area of functionally connected forest (ha), i.e. forest that could be reached from the sampling site without crossing gaps larger than 120m. Sampling sites up to 120 m from the forest edge obtain the value as if located inside the fragment. Log10 transformed, at 30m resolution.	Fragmentation	Ribeiro *et al.* (2009)
Distance to road	Euclidean distance to nearest road (m), at 30m resolution.	Fragmentation	Ribeiro *et al.* (2009)

Matrix composition	The proportion of different matrix types within 5100m radius of the sampling site (%), at 500m resolution. Levels: water, urban, pasture, savannah, annual agriculture, perennial agriculture.	Fragmentation	Soares-Filho *et al.* (2013)
Temperature seasonality	Temperature seasonality (standard deviation * 100), at 982m resolution.	Climate	Fick & Hijmans (2017)
Precipitation	Mean annual precipitation (mm), at 982m resolution.	Climate	Fick & Hijmans (2017)
Precipitation seasonality	Precipitation seasonality (coefficient of variation), at 982m resolution.	Climate	Fick & Hijmans (2017)
Altitude	Height above sea level (m), at 982m resolution.	Topography	Hijmans *et al.* (2005)
Declivity	Inclination of the surface in relation to the horizontal (%).	Topography	Hijmans *et al.* (2005)

Table S2. Full list of literature sources consulted for species life-history traits.

Reference	Taxa	Trait
Wilman, H., Belmaker J., Simpson J., de la Rosa C., Rivadeneira M. M., and Jetz W. 2014. EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. Ecology 95:2027–2027.	All frugivores	Dietary traits, body mass, foraging strata
IUCN 2017. The IUCN Red List of Threatened Species. Version 2017-3. <http://www.iucnredlist.org>. Downloaded on 18 December 2017.	All frugivores	Endemism
Lima, R. A. F. the Neotropical Tree Communities database (TreeCo version 2.0): http://labtrop.ib.usp.br/doku.php?id=projetos:treeco:start	Plants	Seed size, maximum height, wood density
Mittermeier, R. A. et al. 2013. Handbook of the Mammals of the world - Volume 3 - Primates.	Primates	Body size, level of frugivory
Bicca-Marques, J. C., and Calegaro-Marques, C. 1993. Feeding Postures in the Black Howler Monkey, *Alouatta caraya*.	Primates	Level of frugivory
Prates, H. M., and Bicca-Marques, J. C. 2011. Vivendo no Limite? Dieta de um Grupo de Bugios-Pretos (*Alouatta caraya*) Habitante de um Pomar.	Primates	Level of frugivory
Rímoli, J. et al. 2012. Diet and Activity Patterns of Black Howler Monkeys *Alouatta caraya* (Humboldt, 1812, Primates, Atelidae) in Ecotone Cerrado-Pantanal in the Left Bank of Aquidauana River, Mato Grosso do Sul, Brazil.	Primates	Level of frugivory
Rímoli, A. O. et al. 2008. Behavior Patterns of a Group of Black Howler Monkeys *Alouatta caraya* (Humboldt, 1812) in a Forest Fragment in Terenos, Mato Grosso do Sul: A Seasonal Analysis.	Primates	Level of frugivory
Bravo, S. P., and Sallenave, A. 2003. Faranging Behavior and Activity Patterns of Alouatta caraya in the Northeastern Argentinean Flooded Forest.	Primates	Level of frugivory
Fernández, V. A. et al. 2013. Who is Coordinating Collective Movements in Black and Gold Howler Monkeys?	Primates	Level of frugivory
Miranda, J. M. D., and Passos, F. C. 2004. Hábito Alimentar de *Alouatta guariba* (Humboldt) (Primates, Atelidae) em Floresta de Araucária, Paraná, Brasil.	Primates	Level of frugivory
Martins, M. M. 2008. Fruit Diet of *Alouatta guariba* and *Brachyteles arachnoides* in Southeastern Brazil: Comparison of Fruit Type, Color, and Seed Size.	Primates	Level of frugivory
Guzzo, G. B. 2009. Ecologia e Comportamento de *Alouatta guariba clamitans* Cabrera, 1940, em um Fragmento de Mata de Araucária na Serra Gaúcha.	Primates	Level of frugivory
Aguiar, L. M. et al. 2003. Dieta, Área de Vida, Vocalizações e Estimativas Populacionais de *Alouatta guariba* em um Remanescente Florestal no Norte do Estado do Paraná.	Primates	Level of frugivory
Koch, F. 2008. Dieta e Comportamento de um Grupo *de Aloutta guariba clamitans* Cabrera, 1940: Uma Relação de Causa e Efeito?	Primates	Level of frugivory
Fortes, V. B. 2008. Ecologia e Comportamento do Bugio-Ruivo (*Alouatta guariba clamitans* Cabrera 1940) em Fragmentos Florestais na Depressão Central do Rio Grande do Sul, Brasil.	Primates	Level of frugivory
Carvalho Jr, O., et al. 2004. Diet of a Muriqui Group (*Brachyteles arachnoides*) in Continuous Primary Forest.	Primates	Level of frugivory
Milton, K. 1984. Habitat, Diet, and Activity Patterns of Free-Ranging Wolly Spider Monkeys (*Brachyteles arachnoides* E. Geoffroy 1806).	Primates	Level of frugivory

Talebi, M. et al. 2005. Diet of Southern Muriquis in Continuous Brazilian Atlantic Forest.	Primates	Level of frugivory
Martins, M. M. 2005. The Southern Muriqui *Brachyteles arachnoides*: Ecology of a Population in a Semideciduous Forest Fragment.	Primates	Level of frugivory
Dias, L. G., and Strier K. B. 2003. Effects of Group Size on Ranging Patterns in *Brachyteles arachnoides hypoxanthus*.	Primates	Level of frugivory
Souza-Alves, J. P. et al. 2011. Seasonal Versatility in the Feeding Ecology of a Group of Titis (*Callicebus coimbrai*) in the Northern Brazilian Atlantic Forest.	Primates	Level of frugivory
Souza-Alves, J. P. 2010. Ecologia Alimentar de um Grupo de Guigó-de-Coimbra-Filho (*Callicebus coimbrai* Kobayashi & Langguth, 1999): Perspectivas para a Conservação da Espécie na Paisagem Fragmentada do Sul de Sergipe.	Primates	Level of frugivory
Souza-Alves, J. P. 2013. Ecology and Life-History of Coimbra-Filho's titi monkeys (*Callicebus coimbrai*) in the Brazilian Atlantic Forest.	Primates	Level of frugivory
Santana, M. M. 2012. Comportamento, Dieta e Uso do Espaço em um Grupo de Guigó-de-Coimbra (*Callicebus coimbrai* Kobayashi & Langguth, 1999) no RVS Mata do Junco Capela – SE.	Primates	Level of frugivory
Fontes, I, P. 2011. Variação de Curto e Longo Prazo na Ecologia de *Callicebus coimbrai* Kobayashi & Langguth, 1999: Implicações para a Conservação de Populações na Paisagem Fragmentada da Mata Atlântica de Sergipe.	Primates	Level of frugivory
Heiduck, S. 1997. Food Choice in Masked Titi Monkeys (*Callicebus personatus melanochir*): Selectivity or Opportunism?	Primates	Level of frugivory
Caselli, C. B., and Setz, E. Z. F. 2011. Feeding Ecology and Activity Pattern of Black-Fronted Titi Monkeys (*Callicebus nigrifrons*) in a Semideciduous Tropical Forest of Southern Brazil.	Primates	Level of frugivory
dos Santos, G. P. et al. 2012. The Diet of Wild Black-Fronted Titi Monkeys *Callicebus nigrifrons* During a Bamboo Masting Year.	Primates	Level of frugivory
Reis, M. N. G. 2012. Ecologia Alimentar e Comportamento de *Callicebus nigrifrons* em um Fragmento florestal de Mata Atlântica em Campinas, SP.	Primates	Level of frugivory
Caselli, C. B. 2008. Ecologia Alimentar, Padrão de Atividade e Uso do Espaço por *Callicebus nigrifrons* (Primates: Pitheciidae).	Primates	Level of frugivory
dos Santos, G. P. 2008. Padrão de Atividades, Dieta e Área de Vida de *Callicebus nigrifrons* (Spix, 1823).	Primates	Level of frugivory
Fernandes, C. C. 2013. Padrão de Atividade, Dieta e Uso do Espaço por *Callicebus personatus* (Primates, Pitheciidade) em uma Área de Parque Urbano, Município de Santa Teresa, ES.	Primates	Level of frugivory
Kinzey, W. G., and Becker, M. 1983. Activity Patterns of the Masked Titi Monkey, *Callicebus personatus*.	Primates	Level of frugivory
Price, E. C., and Piedade, H. M. 2001. Ranging Behavior and Intraspecific Relationships of Masked Titi Monkeys (*Callicebus personatus personatus*).	Primates	Level of frugivory
Zago, L. et al. 2013. Dieta de *Callithrix penicillata* (E. Geoffroy, 1812) (Primates, Callitrichidae) introduzidos na Ilha de Santa Catarina.	Primates	Level of frugivory
Miranda, G. H. B., and Faria, D. S. 2001. Ecological Aspects of Black-Pincelled Marmoset (*Callithrix penicillata*) in the Cerradão and Dense Cerrado of the Brazilian Central Plateau.	Primates	Level of frugivory
da Silva, Z. L. 2012. Fatores Determinantes no Uso do Espaço por *Callithrix penicillata* (E. Geoffroy, 1812) Introduzidos em Fragmento Urbano.	Primates	Level of frugivory
Vilela, A. A., and Del-Claro, K. 2011. Feeding Behavior of the Black-Tufted-ear Marmoset (*Callithrix penicillata*) (Primata, Callitrichidae) in a Tropical Cerrado Savanna.	Primates	Level of frugivory
David, V. A. 2005. Padrão de Atividades, Ecologia Alimentar e Área de Vida em um Grupo de *Callithrix pinicillata* (Humboldt, 1812) (Primates, Callitrichidae) (Sagui-de-Tufos-Pretos).	Primates	Level of frugivory
Martins, M. M., and Setz, E. Z. 2000. Diet of BuffyTufted-Eared Marmosets (*Callithrix aurita*) in a Forest Fragment in Southeastern Brazil.	Primates	Level of frugivory
Corrêa, H. K. M. et al. 2000. Between-Year Differences in the Feeding Ecology of Highland Marmosets (*Callithrix aurita* and *Callithrix flaviceps*) in Southeastern Brazil.	Primates	Level of frugivory
Corrêa, H. K. M. 1995. Ecologia e Comportamento Alimentar de um Grupo de Saguis-da-Serra-Escuros (*Callithrix aurita* E. Geoffroy 1812) no Parque Estadual da Serra do Mar, Núcleo Cunha, São Paulo, Brasil.	Primates	Level of frugivory
Passamani, M., and Rylands, A. B. 2000. Home Range of a Geoffroy's Marmoset Group, *Callithrix geoffroyi* (Primates, Callitrichidae) in Southeastern Brazil.	Primates	Level of frugivory

Rocha, M. F., and Passamani, M. 2009. Uso do Espaço por um Grupo de Saguis-da-Cara-Branca (*Callithrix geoffroyi*) no Sudeste do Brasil.	Primates	Level of frugivory
Passamani, M. 1996. Ecologia e Comportamento de um Grupo de Sagui-da-Cara-Branca (*Callithrix geoffroyi*) em um Fragmento de Mata Atlântica no Espírito Santo.	Primates	Level of frugivory
de Castro, C. S. S. 2003. Tamanho da Área de Vida e Padrão de Uso do Espaço em Grupos de Saguis, *Callithrix jacchus* (Linnaeus) (Primates, Callitrichidae).	Primates	Level of frugivory
Martins, I. G. 2007. Padrão de Atividades do Sagui *Callithrix jacchus* Numa Área de Caatinga.	Primates	Level of frugivory
Scanlon, C. E. et al. 1989. Home Range Use and the Exploitation of Gum in the Marmoset *Callithrix jacchus jacchus*.	Primates	Level of frugivory
Thompson, C. L. et al. 2013. Spatial Distribution and Exploitation of Trees Gouged by Common Marmosets (*Callithrix jacchus*).	Primates	Level of frugivory
Hubrecht, R. C. 1985. Home Range Size and Use and Territorial Behavior in the Common Marmoset, *Callithrix jacchus jacchus*, at the Tapacura Field Station, Recife, Brazil.	Primates	Level of frugivory
Pontes, A. R. M., and da Cruz, M. A. O. M. 1995. Home Range, Intergroup Transfers, and Reproductive Status of Common Marmosets *Callithrix jacchus* in a Forest Fragment in Northeastern Brazil.	Primates	Level of frugivory
Amora, T. A. et al. 2013. Use of Alternative Plant Resources by Common Marmosets (*Callithric jacchus*) in the Semi-Arid Caatinga Scrub Forests of Northeastern Brazil.	Primates	Level of frugivory
Raboy, B. E. et al. 2008. Ecology of *Callithrix kuhlli* and a Review of Eastern Brazilian Marmosets.	Primates	Level of frugivory
Rylands, A. B. 1989. Sympatric Brazilian Callitrichids: The Black Tufted-Ear Marmoset, *Callithrix kuhlli*, and the Golden-Headed Lion Tamarin, *Leontopithecus chrysomelas*.	Primates	Level of frugivory
Ludwig, G.; et al. 2005. Uma Avaliação da Dieta, da Área de Vida e das Estimativas Populacionais de *Cebus nigritus* (Goldfuss, 1809) em um Fragmento Florestal no Norte do Estado do Paraná.	Primates	Level of frugivory
di Bitetti, M. S. 2001. Home-Range Use by the Tufted Capuchin Monkey (*Cebus apella nigritus*) in a Subtropical Rainforest of Argentina.	Primates	Level of frugivory
Rímoli, J. et al. 2008. Seasonal and Longitudinal Variation in the Behavior of Free-Ranging Black tufted Capuchins *Cebus nigritus* (Goldfuss,1809) in a Fragment Forest in Southeastern Brazil.	Primates	Level of frugivory
Martins, W. P. 2010. Densidade Populacional e Ecologia de um Grupo de Macaco-Prego-de-Crista (*Cebus robustus*; Kuhl, 1820) na Reserva Natural Vale.	Primates	Level of frugivory

References

Almeida-Neto, M., F. Campassi, M. Galetti, P. Jordano, and A. Oliveira-Filho. 2008. Vertebrate dispersal syndromes along the Atlantic forest: Broad-scale patterns and macroecological correlates. Global Ecology and Biogeography 17:503–513.

Bello, C., M. Galetti, D. Montan, M. A. Pizo, T. C. Mariguela, L. Culot, F. Bufalo, F. Labecca, F. Pedrosa, R. Constantini, C. Emer, W. R. Silva, F. R. da Silva, O. Ovaskainen, and P. Jordano. 2017. ATLANTIC-FRUGIVORY: a plant-frugivore interaction dataset for the Atlantic Forest. Ecology 98:1729.

Culot, L., L. A. Pereira, I. Agostini, M. A. B. Almeida, R. S. C. Alves, I. Aximoff, A. Bager, M. C. Baldovino, T. R. Bella, J. C. Bicca-Marques *et al.* (unpublished). ATLANTIC-PRIMATES: a dataset of communities and occurrences of primates in the Atlantic Forests of South America.

Díaz, S., J. Kattge, J. H. C. Cornelissen, I. J. Wright, S. Lavorel, S. Dray, B. Reu, M. Kleyer, C. Wirth, I. Colin Prentice *et al.* 2015. The global spectrum of plant form and function. Nature 529:167–171.

Environmental Systems Research Institute (ESRI). 2017. ArcGIS Base of World: Continent and country borders.

Fick, S. E., and R. J. Hijmans. 2017. WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37:4302–4315.

Hasui, É., J. P. Metzger, R. G. Pimentel, L. F. Silveira, A. A. de Abreu Bovo, A. C. Martensen, A. Uezu, A. L. Regolin, A. Â. B. de Oliveira, C. A. F. R. Gatto *et al.* 2018. ATLANTIC BIRDS: a dataset of bird species from the Brazilian Atlantic Forest. Ecology 99:497.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25:1965–1978.

Karger, D. N., O. Conrad, J. Böhner, T. Kawohl, H. Kreft, R. W. Soria-Auza, N. E. Zimmermann, H. P. Linder, and M. Kessler. 2016. Climatologies at high resolution for the Earth's land surface areas. Scientific Data 4:170122.

Lima, F., G. Beca, R. L. Muylaert, C. N. Jenkins, M. L. L. Perilli, A. M. de O. Paschoal, R. L. Massara, A. P. Paglia, A. G. Chiarello, M. E. Graipel *et al.* 2017. ATLANTIC-CAMTRAPS: a dataset of medium and large terrestrial mammal communities in the Atlantic Forest of South America. Ecology 98:2979.

Lima, R. A. F., D. P. Mori, G. Pitta, M. O. Melito, C. Bello, L. F. Magnago, V. P. Zwiener, D. D. Saraiva, M. C. M. Marques, A. A. de Oliveira *et al.* 2015. How much do we know about the endangered Atlantic Forest? Reviewing nearly 70 years of information on tree community surveys. Biodiversity and Conservation 24:2135–2148.

Ovaskainen, O., D. B. Roy, R. Fox, and B. J. Anderson. 2016. Uncovering hidden spatial structure in species communities with spatially explicit joint species distribution models. Methods in Ecology and Evolution 7:428–436.

Ovaskainen, O., G. Tikhonov, A. Norberg, F. G. Blanchet, L. Duan, D. Dunson, T. Roslin, and N. Abrego. 2017. How to make more out of community data? A conceptual framework and its implementation as models and software. Ecology Letters 20:561–576.

Ribeiro, M. C., J. P. Metzger, A. C. Martensen, F. J. Ponzoni, and M. M. Hirota. 2009. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biological Conservation 142:1141–1153.

Soares-Filho, B. S., L. S. Lima, L. B. Hissa, W. L. S. Costa, H. O. Rodrigues, B. M. Ferreira, R. F. Machado, A. R. Campos, T. C. Lima, and W. W. Gomes. 2013. OTIMIZAGRO: Uma plataforma integrada de modelagem de uso e mudanças no uso da terra para o Brasil. 1st edition. IGC/UFMG, Brasilia.

Tjur, T. 2009. Coefficients of determination in logistic regression models - a new proposal: The coefficient of discrimination. American Statistician 63:366–372.

Wilman, H., J. Belmaker, J. Simpson, C. de la Rosa, M. M. Rivadeneira, and W. Jetz. 2014. EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. Ecology 95:2027–2027.

Electronic Supplementary Material

Appendix D

Marjakangas et al. 2018 Philosophical Transactions of the Royal Society B

Spatial credit of ecological interactions in the Atlantic Forest sub-regions

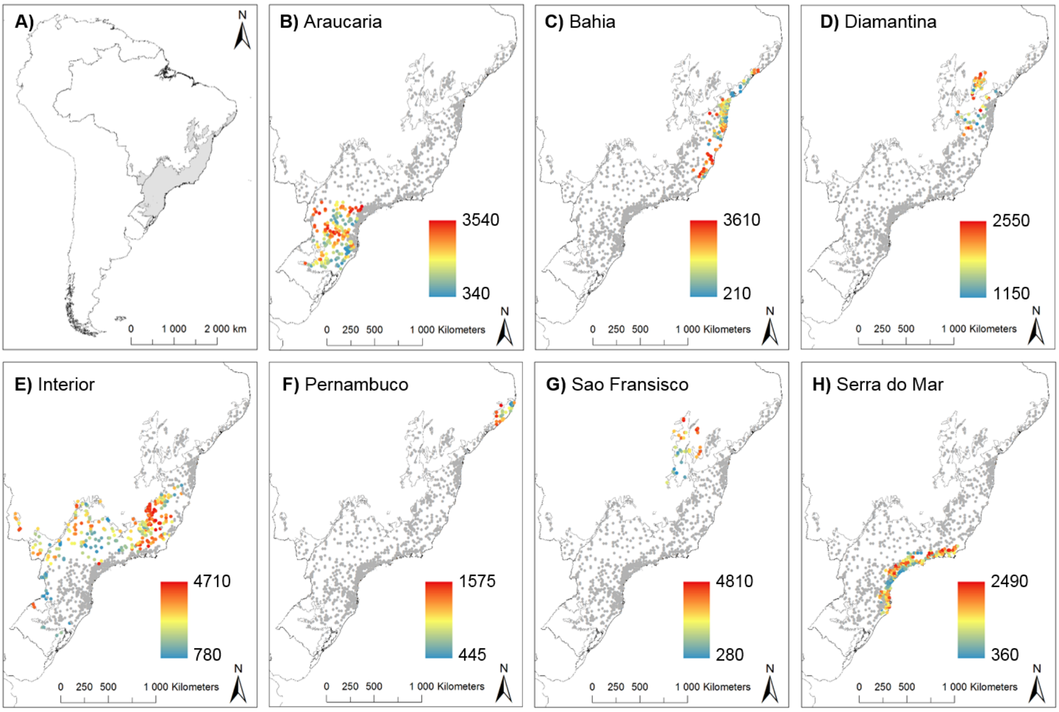


Figure S1. Spatial credit of ecological interactions in the Atlantic Forest sub-regions *sensu* Ribeiro *et al.* (2009). Panel A indicates Atlantic Forest region in grey. Panels B-H indicate the sub-region-specific credit (sub-regions: Araucaria, Bahia, Diamantina, Interior, Pernambuco, Sao Fransisco, and Serra do Mar, respectively). Warmest colors represent highest local credit to be cashed in by rewilding.

Table S3. Species with the highest credit contributions in each of the Atlantic Forest sub-regions. The 12 highest scoring species are ordered in decreasing order of contribution within each sub-region.

Araucaria	Bahia	Diamantina	Interior	Pernambuco	Sao Fransisco	Serra do Mar
Penelope superciliaris	*Selenidera maculirostris*	*Selenidera maculirostris*	*Penelope superciliaris*	*Turdus albicollis*	*Penelope superciliaris*	*Brachyteles arachnoides*
Turdus leucomelas	*Turdus albicollis*	*Penelope superciliaris*	*Aburria jacutinga*	*Penelope superciliaris*	*Tangara sayaca*	*Penelope superciliaris*
Aburria jacutinga	*Aburria jacutinga*	*Turdus albicollis*	*Selenidera maculirostris*	*Pteroglassus bailloni*	*Turdus rufiventris*	*Aburria jacutinga*
Elaenia flavogaster	*Pteroglassus bailloni*	*Tangara cyanoptera*	*Ramphastos dicolorus*	*Procnias nudicollis*	*Elaenia flavogaster*	*Carpornis cucullata*
Tangara sayaca	*Lipaugus lanioides*	*Tangara sayaca*	*Lipaugus lanioides*	*Tityra cayana*	*Turdus amaurochalinus*	*Pitangus sulphuratus*
Pitangus sulphuratus	*Chiroxiphia caudata*	*Turdus amaurochalinus*	*Pteroglassus bailloni*	*Tangara sayaca*	*Pitangus sulphuratus*	*Turdus leucomelas*
Pteroglassus bailloni	*Penelope superciliaris*	*Elaenia flavogaster*	*Turdus flavipes*	*Turdus rufiventris*	*Celeus flavescens*	*Tangara sayaca*
Myiozetetes similis	*Sapajus nigritus*	*Tangara cayana*	*Tangara sayaca*	*Tangara cyanocephala*	*Thlypopsis sordida*	*Pteroglassus bailloni*
Tangara palmarum	*Tangara cyanoptera*	*Myiozetetes similis*	*Brachyteles hypoxanthus*	*Thlypopsis sordida*	*Myiodynastes maculatus*	*Lipaugus lanioides*
Tityra cayana	*Turdus flavipes*	*Ramphocelus carbo*	*Elaenia flavogaster*	*Cacicus haemorrhous*	*Tangara cayana*	*Elaenia flavogaster*
Turdus flavipes	*Tangara sayaca*	*Thlypopsis sordida*	*Tityra cayana*	*Ramphocelus bresilius*	*Myiozetetes similis*	*Selenidera maculirostris*
Tangara cyanocephala	*Sapajus xanthosternos*	*Turdus leucomelas*	*Pitangus sulphuratus*	*Oxyruncus cristatus*	*Empidonomus varius*	*Leontopithecus rosalia*

Relationship between credit of ecological interactions and species richness

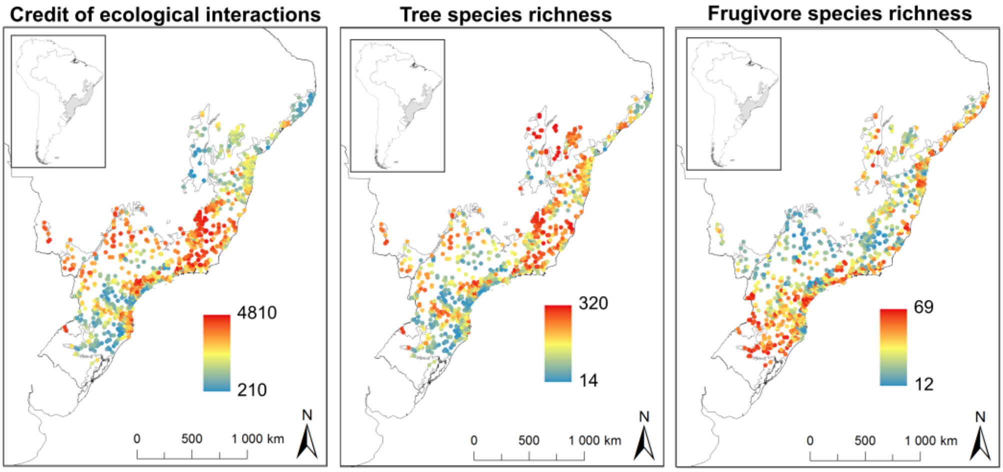


Figure S2. Distribution of credit of ecological interactions, plant species richness and frugivore species across the Atlantic Forest.

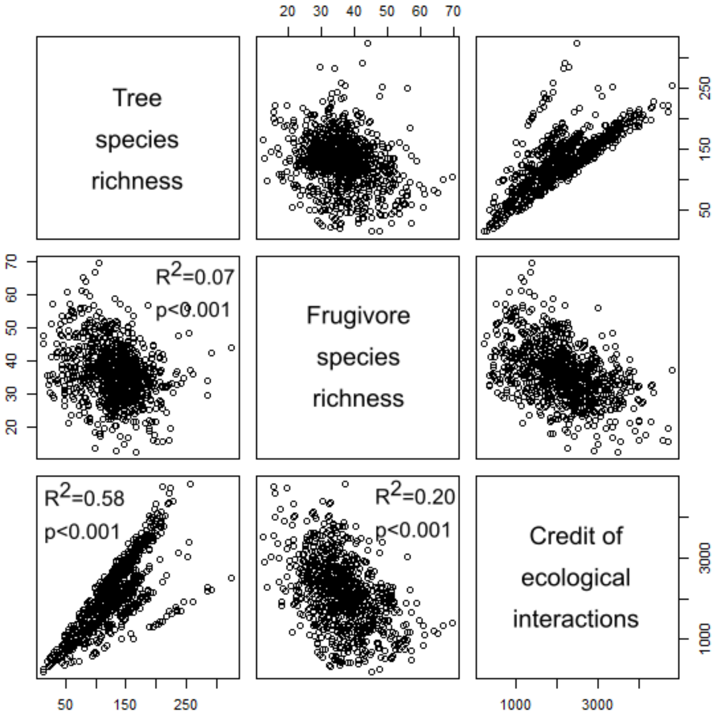


Figure S3. Relationship between plant species richness, frugivore species richness and credit of ecological interactions across the Atlantic Forest. Plots correspond to the spatial relationship among the three variables. R^2- and p-values correspond to the computed pairwise linear regressions among the variables.

Benchmark scenario sensitivity test

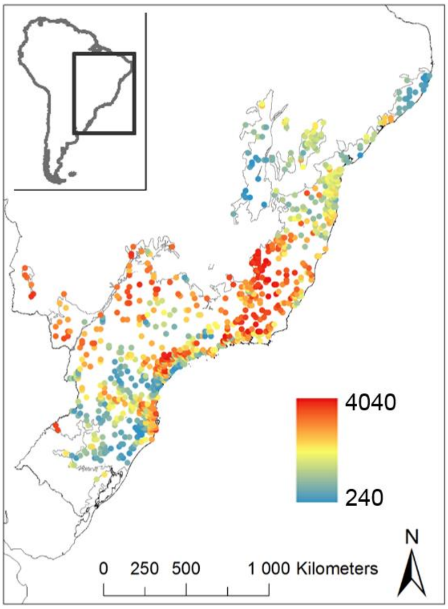


Figure S4 Spatial credit of ecological interactions to be cashed in through rewilding across prediction sites in the Atlantic Forest when assuming an alternative benchmark scenario. We calculated the interaction credit as the difference between an historical benchmark of species occurrence and their current predicted occurrence. The occurrence probability for the frugivores in the benchmark scenario was set as the maximum of posterior mean occurrence probability of each species in the Atlantic Forest. The number of interactions expected to be restored by rewilding are illustrated by a color gradient.

Table S4. The interaction credit contributions of the 12 highest scoring frugivore species across the Atlantic Forest when assuming an alternative benchmark scenario. We measured the interaction credit contribution as the mean expected number of interactions across prediction sites where the frugivore is expected to occur according to the benchmark scenario. We also recorded the total credit as the sum for all sites, the minimum and maximum of local ranks across all prediction sites and the standard deviation of the ranks. The last column represents the IUCN threat categories each species is assigned to: LC = Least concern, NT = Near threatened, VU = vulnerable, EN = Endangered, CR = Critically endangered (IUCN 2018).

Species	Mean credit	Sum credit	Rank Range	Rank SD	IUCN class
Brachyteles arachnoides	36.94	9730.82	11-138	40.48	EN
Selenidera maculirostris	25.75	9637.45	10-153	37.67	LC
Carpornis cucullata	25.22	481.36	65-159	21.44	NT
Lipaugus lanioides	24.48	5248.98	19-155	42.72	NT
Brachyteles hypoxanthus	23.84	13735.11	4-150	25.26	CR
Tangara cyanoptera	23.22	21158.68	1-142	20	NT
Turdus leucomelas	23.2	1357.74	11-160	36.43	LC
Turdus flavipes	22.62	5318.54	19-158	47.48	LC
Penelope superciliaris	22.43	7890.44	14-151	35.46	LC
Pitangus sulphuratus	21.53	881.92	38-160	29.77	LC
Pteroglassus bailloni	20.87	3355.35	57-150	21.35	NT
Leontopithecus chrysomelas	20.06	10173.26	13-138	24.71	EN

Interaction probability sensitivity test

Table S5. Sensitivity analysis on the effect of assigned probabilities of unlikely interactions on species local and regional ranks across the Atlantic Forest. Each species' regional rank is listed for three analyses with different interaction probabilities: $a = 0.001$, $a = 0.05$, and $a = 0.10$, of which the last was used to produce the results in the main text. The 12 regionally highest ranking species from each of the three analyses are included, totaling 14 species. We measured the interaction credit contribution as the mean expected number of interactions across prediction sites where the frugivore is predicted to occur according to the benchmark scenario (Mean credit), ranked the species according to their mean contribution (Regional rank), and present the standard deviation of the local ranks across all prediction sites (SD local rank). The last column represents the IUCN threat categories each species is assigned to: LC = Least concern, NT = Near threatened, VU = vulnerable, EN = Endangered, CR = Critically endangered [36].

Class	**Species**	**Regional rank (SD local rank)**			**Mean credit**			**IUCN class**
		[*a* = 0.001]	**[*a* = 0.05]**	**[*a* = 0.1]**	**[*a* = 0.001]**	**[*a* = 0.05]**	**[*a* = 0.1]**	
Aves	*Aburria jacutinga*	3 (24.69)	3 (28.86)	3 (28.93)	22.47	26.46	30.45	EN
Mammalia	*Brachyteles arachnoides*	1 (55.75)	1 (62.67)	1 (62.66)	43.47	45.73	47.99	EN
Mammalia	*Brachyteles hypoxanthus*	16 (52.27)	14 (59.62)	9 (59.99)	15.81	20.89	25.95	CR
Aves	*Carpornis cucullata*	4 (53.33)	4 (60.09)	4 (59.91)	22.22	25.45	28.68	NT
Aves	*Elaenia flavogaster*	12 (5.63)	13 (8.37)	11 (14.20)	17.83	21.63	24.89	LC
Aves	*Lipaugus lanioides*	10 (43.41)	7 (49.99)	6 (50.57)	18.35	23.06	27.76	NT
Aves	*Penelope superciliaris*	2 (2.61)	2 (4.03)	2 (6.85)	28.93	31.49	34.04	LC
Aves	*Pitangus sulphuratus*	8 (9.11)	12 (15.74)	15 (24.73)	19.05	21.41	23.77	LC
Aves	*Pteroglassus bailloni*	11 (20.89)	8 (24.84)	7 (25.50)	18.28	22.42	26.55	NT
Aves	*Ramphastos dicolorus*	9 (41.72)	10 (47.72)	12 (47.69)	18.71	21.74	24.77	LC
Aves	*Selenidera maculirostris*	5 (18.28)	5 (24.21)	5 (28.97)	21.63	24.98	28.33	LC
Aves	*Tangara cyanoptera*	13 (58.38)	11 (65.94)	10 (65.47)	17.79	21.56	25.33	NT
Aves	*Tangara sayaca*	6 (4.48)	6 (6.47)	8 (10.78)	21.17	23.71	26.26	LC
Aves	*Turdus leucomelas*	7 (10.56)	9 (18.33)	13 (29.26)	19.49	21.92	24.36	LC

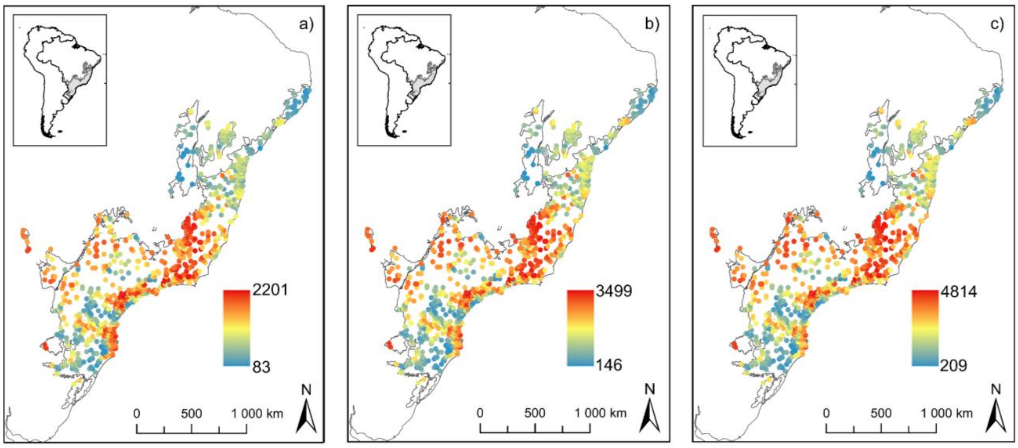


Figure S5. Spatial credit of ecological interactions to be cashed through rewilding with different probabilities for unlikely interactions: *a* = 0.001, *a* = 0.05, and *a* = 0.10, panels a)-c) represent the probabilities, respectively. We calculated the interaction credit as the difference between an historical benchmark of species occurrence and their current predicted occurrence. The number of interactions expected to be rewired by rewilding is depicted by a colour gradient. The warmest colours represent credit hotspots, whereas coldest colours represent sites where there are fewer seed dispersal interactions to be restored through reintroductions. When interaction probability value is set to 0.1 for unlikely interactions, there is a proportional increase in the credit for all areas as compared to results with 0.001 and 0.05 interaction probabilities. Setting unlikely probabilities to 0 would be unrealistic because the absence of observation of an interaction cannot guarantee it does not exist.

Doctoral theses in Biology
Norwegian University of Science and Technology
Department of Biology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos Zoology	Breeding events of birds in relation to spring temperature and environmental phenology
1978	Egil Sakshaug	Dr. philos Botany	The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton
1980	Arnfinn Langeland	Dr. philos Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*
1982	Dag Dolmen	Dr. philos Zoology	Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation
1984	Eivin Røskaft	Dr. philos Zoology	Sociobiological studies of the rook *Corvus frugilegus*
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exposed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos Zoology	Biochemical genetic studies in fish
1985	John Solem	Dr. philos Zoology	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains
1985	Randi E. Reinertsen	Dr. philos Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds
1986	Bernt-Erik Sæther	Dr. philos Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach
1986	Torleif Holthe	Dr. philos Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna
1987	Helene Lampe	Dr. scient Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires
1987	Olav Hogstad	Dr. philos Zoology	Winter survival strategies of the Willow tit *Parus montanus*
1987	Jarle Inge Holten	Dr. philos Botany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway

1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*
1987	Bjørn Åge Tømmerås	Dr. scient Zoology	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction
1988	Hans Christian Pedersen	Dr. philos Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care
1988	Tor G. Heggberget	Dr. philos Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure
1988	Marianne V. Nielsen	Dr. scient Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*)
1988	Ole Kristian Berg	Dr. scient Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.)
1989	John W. Jensen	Dr. philos Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth
1989	Helga J. Vivås	Dr. scient Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*
1989	Reidar Andersen	Dr. scient Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture
1990	Bengt Finstad	Dr. scient Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season
1990	Hege Johannesen	Dr. scient Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams
1990	Tor Jørgen Almaas	Dr. scient Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues
1990	Magne Husby	Dr. scient Zoology	Breeding strategies in birds: Experiments with the Magpie *Pica pica*
1991	Tor Kvam	Dr. scient Zoology	Population biology of the European lynx (*Lynx lynx*) in Norway
1991	Jan Henning L'Abêe Lund	Dr. philos Zoology	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular
1991	Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991	Trond Nordtug	Dr. scient Zoology	Reflectometric studies of photomechanical adaptation in superposition eyes of arthropods
1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway

1991	Odd Terje Sandlund	Dr. philos Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism
1991	Nina Jonsson	Dr. philos Zoology	Aspects of migration and spawning in salmonids
1991	Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992	Torgrim Breiehagen	Dr. scient Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher
1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.)
1992	Tycho Anker-Nilssen	Dr. scient Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
1992	Bjørn Munro Jenssen	Dr. philos Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks
1992	Arne Vollan Aarset	Dr. philos Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells
1993	Tor Fredrik Næsje	Dr. scient Zoology	Habitat shifts in coregonids.
1993	Yngvar Asbjørn Olsen	Dr. scient Zoology	Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels and some secondary effects.
1993	Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993	Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993	Thrine L. M. Heggberget	Dr. scient Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993	Kjetil Bevanger	Dr. scient Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient Botany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994	Peder Fiske	Dr. scient Zoology	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek
1994	Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994	Nils Røv	Dr. scient Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*
1994	Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.)
1994	Inga Elise Bruteig	Dr. scient Botany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994	Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses

1994	Morten Bakken	Dr. scient Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*
1994	Arne Moksnes	Dr. philos Zoology	Host adaptations towards brood parasitism by the Cockoo
1994	Solveig Bakken	Dr. scient Botany	Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply
1994	Torbjørn Forseth	Dr. scient Zoology	Bioenergetics in ecological and life history studies of fishes.
1995	Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions
1995	Hanne Christensen	Dr. scient Zoology	Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*
1995	Svein Håkon Lorentsen	Dr. scient Zoology	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition
1995	Chris Jørgen Jensen	Dr. scient Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995	Martha Kold Bakkevig	Dr. scient Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport
1995	Vidar Moen	Dr. scient Zoology	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations
1995	Hans Haavardsholm Blom	Dr. philos Botany	A revision of the *Schistidium apocarpum* complex in Norway and Sweden
1996	Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae
1996	Ola Ugedal	Dr. scient Zoology	Radiocesium turnover in freshwater fishes
1996	Ingibjørg Einarsdottir	Dr. scient Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines
1996	Christina M. S. Pereira	Dr. scient Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation
1996	Jan Fredrik Børseth	Dr. scient Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics
1996	Gunnar Henriksen	Dr. scient Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region
1997	Gunvor Øie	Dr. scient Botany	Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae
1997	Håkon Holien	Dr. scient Botany	Studies of lichens in spruce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters
1997	Ole Reitan	Dr. scient Zoology	Responses of birds to habitat disturbance due to damming
1997	Jon Arne Grøttum	Dr. scient Zoology	Physiological effects of reduced water quality on fish in aquaculture

1997	Per Gustav Thingstad	Dr. scient Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher
1997	Torgeir Nygård	Dr. scient Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as
1997	Signe Nybø	Dr. scient Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway
1997	Atle Wibe	Dr. scient Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry
1997	Rolv Lundheim	Dr. scient Zoology	Adaptive and incidental biological ice nucleators
1997	Arild Magne Landa	Dr. scient Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation
1997	Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*
1997	Jarle Tufto	Dr. scient Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997	Trygve Hesthagen	Dr. philos Zoology	Population responses of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997	Jan Østnes	Dr. scient Zoology	Cold sensation in adult and neonate birds
1998	Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins
1998	Thor Harald Ringsby	Dr. scient Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998	Erling Johan Solberg	Dr. scient Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998	Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity
1998	Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro
1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservation biological approach
1998	Bente Gunnveig Berg	Dr. scient Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach
1999	Hans Kristen Stenøien	Dr. scient Botany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999	Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway

1999	Ingvar Stenberg	Dr. scient Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*
1999	Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis
1999	Trina Falck Galloway	Dr. scient Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)
1999	Marianne Giæver	Dr. scient Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gadus morhua*) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*
1999	Ingrid Bysveen Mjølnerød	Dr. scient Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient Zoology	Social evolution in monogamous families:
1999	Gunnbjørn Bremset	Dr. scient Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient Zoology	Host specificity as a parameter in estimates of arthropod species richness
1999	Sonja Andersen	Dr. scient Zoology	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial control of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000	Odd A. Gulseth	Dr. philos Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species

2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forest systems
2001	Ingebrigt Uglem	Dr. scient Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001	Bård Gunnar Stokke	Dr. scient Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient Zoology	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002	Mariann Sandsund	Dr. scient Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient Zoology	The function of scent marking in beaver (*Castor fiber*)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr. philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and the Ral GTPase from *Drosophila melanogaster*
2002	Henrik Jensen	Dr. scient Biology	Causes and consequences of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003	Marit Stranden	Dr. scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003	Kristian Hassel	Dr. scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*
2003	David Alexander Rae	Dr. scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003	Åsa A Borg	Dr. scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr. scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo salar* L.) parr and smolt
2004	Torkild Bakken	Dr. scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)

2004	Ingar Pareliussen	Dr. scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004	Tore Brembu	Dr. scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004	Liv S. Nilsen	Dr. scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004	Hanne T. Skiri	Dr. scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*)
2004	Lene Østby	Dr. scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr. scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr. scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004	Børge Moe	Dr. scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr. scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr. scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr. scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelien	PhD Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr. scient Biology	Studies on antifreeze proteins
2005	Eugen G. Sørmo	Dr. scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyroid hormone and vitamin A concentrations
2005	Christian Westad	Dr. scient Biology	Motor control of the upper trapezius
2005	Lasse Mork Olsen	PhD Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	PhD Biology	Implications of mate choice for the management of small populations
2005	Ariaya Hymete Sahle Dingle	PhD Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia
2005	Anders Gravbrøt Finstad	PhD Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	PhD Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr. scient Biology	The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation

2006	Kari Mette Murvoll	PhD Biology	Levels and effects of persistent organic pollutans (POPs) in seabirds, Retinoids and α-tocopherol – potential biomakers of POPs in birds?
2006	Ivar Herfindal	Dr. scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006	Nils Egil Tokle	PhD Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*
2006	Jan Ove Gjershaug	Dr. philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr. scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	PhD Biology	*Acesta oophaga* and *Acesta excavata* – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	PhD Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	PhD Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	PhD Biology	Wildlife conservation and local land use conflicts in Western Serengeti Corridor, Tanzania
2006	Anna Maria Billing	PhD Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction
2006	Henrik Pärn	PhD Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	PhD Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	PhD Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	PhD Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine
2007	Kasper Hancke	PhD Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007	Tomas Holmern	PhD Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007	Kari Jørgensen	PhD Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens*
2007	Stig Ulland	PhD Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, (*Mamestra brassicae* L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007	Snorre Henriksen	PhD Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007	Roelof Frans May	PhD Biology	Spatial Ecology of Wolverines in Scandinavia
2007	Vedasto Gabriel Ndibalema	PhD Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania
2007	Julius William Nyahongo	PhD Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania

2007	Shombe Ntaraluka Hassan	PhD Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007	Per-Arvid Wold	PhD Biology	Functional development and response to dietary treatment in larval Atlantic cod *(Gadus morhua* L.) Focus on formulated diets and early weaning
2007	Anne Skjetne Mortensen	PhD Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008	Brage Bremset Hansen	PhD Biology	The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008	Jiska van Dijk	PhD Biology	Wolverine foraging strategies in a multiple-use landscape
2008	Flora John Magige	PhD Biology	The ecology and behaviour of the Masai Ostrich (*Struthio camelus massaicus*) in the Serengeti Ecosystem, Tanzania
2008	Bernt Rønning	PhD Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, *Taeniopygia guttata*
2008	Sølvi Wehn	PhD Biology	Biodiversity dynamics in semi-natural mountain landscapes - A study of consequences of changed agricultural practices in Eastern Jotunheimen
2008	Trond Moxness Kortner	PhD Biology	The Role of Androgens on previtellogenic oocyte growth in Atlantic cod (*Gadus morhua*): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations
2008	Katarina Mariann Jørgensen	Dr. scient Biology	The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation
2008	Tommy Jørstad	PhD Biology	Statistical Modelling of Gene Expression Data
2008	Anna Kusnierczyk	PhD Biology	*Arabidopsis thaliana* Responses to Aphid Infestation
2008	Jussi Evertsen	PhD Biology	Herbivore sacoglossans with photosynthetic chloroplasts
2008	John Eilif Hermansen	PhD Biology	Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania
2008	Ragnhild Lyngved	PhD Biology	Somatic embryogenesis in *Cyclamen persicum.* Biological investigations and educational aspects of cloning
2008	Line Elisabeth Sundt-Hansen	PhD Biology	Cost of rapid growth in salmonid fishes
2008	Line Johansen	PhD Biology	Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution
2009	Astrid Jullumstrø Feuerherm	PhD Biology	Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease
2009	Pål Kvello	PhD Biology	Neurons forming the network involved in gustatory coding and learning in the moth *Heliothis virescens:* Physiological and morphological characterisation, and integration into a standard brain atlas
2009	Trygve Devold Kjellsen	PhD Biology	Extreme Frost Tolerance in Boreal Conifers
2009	Johan Reinert Vikan	PhD Biology	Coevolutionary interactions between common cuckoos *Cuculus canorus* and *Fringilla* finches

2009	Zsolt Volent	PhD Biology	Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter
2009	Lester Rocha	PhD Biology	Functional responses of perennial grasses to simulated grazing and resource availability
2009	Dennis Ikanda	PhD Biology	Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions (*Panthera leo*) in Tanzania
2010	Huy Quang Nguyen	PhD Biology	Egg characteristics and development of larval digestive function of cobia (*Rachycentron canadum*) in response to dietary treatments - Focus on formulated diets
2010	Eli Kvingedal	PhD Biology	Intraspecific competition in stream salmonids: the impact of environment and phenotype
2010	Sverre Lundemo	PhD Biology	Molecular studies of genetic structuring and demography in *Arabidopsis* from Northern Europe
2010	Iddi Mihijai Mfunda	PhD Biology	Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. The Case of Serengeti Ecosystem, Tanzania
2010	Anton Tinchov Antonov	PhD Biology	Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis
2010	Anders Lyngstad	PhD Biology	Population Ecology of *Eriophorum latifolium*, a Clonal Species in Rich Fen Vegetation
2010	Hilde Færevik	PhD Biology	Impact of protective clothing on thermal and cognitive responses
2010	Ingerid Brænne Arbo	PhD Medical technology	Nutritional lifestyle changes – effects of dietary carbohydrate restriction in healthy obese and overweight humans
2010	Yngvild Vindenes	PhD Biology	Stochastic modeling of finite populations with individual heterogeneity in vital parameters
2010	Hans-Richard Brattbakk	PhD Medical technology	The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits
2011	Geir Hysing Bolstad	PhD Biology	Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy
2011	Karen de Jong	PhD Biology	Operational sex ratio and reproductive behaviour in the two-spotted goby (*Gobiusculus flavescens*)
2011	Ann-Iren Kittang	PhD Biology	*Arabidopsis thaliana* L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS: The science of space experiment integration and adaptation to simulated microgravity
2011	Aline Magdalena Lee	PhD Biology	Stochastic modeling of mating systems and their effect on population dynamics and genetics
2011	Christopher Gravningen Sørmo	PhD Biology	Rho GTPases in Plants: Structural analysis of ROP GTPases; genetic and functional studies of MIRO GTPases in Arabidopsis thaliana
2011	Grethe Robertsen	PhD Biology	Relative performance of salmonid phenotypes across environments and competitive intensities
2011	Line-Kristin Larsen	PhD Biology	Life-history trait dynamics in experimental populations of guppy (*Poecilia reticulata*): the role of breeding regime and captive environment
2011	Maxim A. K. Teichert	PhD Biology	Regulation in Atlantic salmon (*Salmo salar*): The interaction between habitat and density

2011	Torunn Beate Hancke	PhD Biology	Use of Pulse Amplitude Modulated (PAM) Fluorescence and Bio-optics for Assessing Microalgal Photosynthesis and Physiology
2011	Sajeda Begum	PhD Biology	Brood Parasitism in Asian Cuckoos: Different Aspects of Interactions between Cuckoos and their Hosts in Bangladesh
2011	Kari J. K. Attramadal	PhD Biology	Water treatment as an approach to increase microbial control in the culture of cold water marine larvae
2011	Camilla Kalvatn Egset	PhD Biology	The Evolvability of Static Allometry: A Case Study
2011	AHM Raihan Sarker	PhD Biology	Conflict over the conservation of the Asian elephant (*Elephas maximus*) in Bangladesh
2011	Gro Dehli Villanger	PhD Biology	Effects of complex organohalogen contaminant mixtures on thyroid hormone homeostasis in selected arctic marine mammals
2011	Kari Bjørneraas	PhD Biology	Spatiotemporal variation in resource utilisation by a large herbivore, the moose
2011	John Odden	PhD Biology	The ecology of a conflict: Eurasian lynx depredation on domestic sheep
2011	Simen Pedersen	PhD Biology	Effects of native and introduced cervids on small mammals and birds
2011	Mohsen Falahati-Anbaran	PhD Biology	Evolutionary consequences of seed banks and seed dispersal in *Arabidopsis*
2012	Jakob Hønborg Hansen	PhD Biology	Shift work in the offshore vessel fleet: circadian rhythms and cognitive performance
2012	Elin Noreen	PhD Biology	Consequences of diet quality and age on life-history traits in a small passerine bird
2012	Irja Ida Ratikainen	PhD Biology	Foraging in a variable world: adaptations to stochasticity
2012	Aleksander Handå	PhD Biology	Cultivation of mussels (*Mytilus edulis):* Feed requirements, storage and integration with salmon (*Salmo salar*) farming
2012	Morten Kraabøl	PhD Biology	Reproductive and migratory challenges inflicted on migrant brown trout (*Salmo trutta* L.) in a heavily modified river
2012	Jisca Huisman	PhD Biology	Gene flow and natural selection in Atlantic salmon
2012	Maria Bergvik	PhD Biology	Lipid and astaxanthin contents and biochemical post-harvest stability in *Calanus finmarchicus*
2012	Bjarte Bye Løfaldli	PhD Biology	Functional and morphological characterization of central olfactory neurons in the model insect *Heliothis virescens*.
2012	Karen Marie Hammer	PhD Biology	Acid-base regulation and metabolite responses in shallow- and deep-living marine invertebrates during environmental hypercapnia
2012	Øystein Nordrum Wiggen	PhD Biology	Optimal performance in the cold
2012	Robert Dominikus Fyumagwa	Dr. Philos Biology	Anthropogenic and natural influence on disease prevalence at the human –livestock-wildlife interface in the Serengeti ecosystem, Tanzania
2012	Jenny Bytingsvik	PhD Biology	Organohalogenated contaminants (OHCs) in polar bear mother-cub pairs from Svalbard, Norway. Maternal transfer, exposure assessment and thyroid hormone disruptive effects in polar bear cubs
2012	Christer Moe Rolandsen	PhD Biology	The ecological significance of space use and movement patterns of moose in a variable environment

2012	Erlend Kjeldsberg Hovland	PhD Biology	Bio-optics and Ecology in *Emiliania huxleyi* Blooms: Field and Remote Sensing Studies in Norwegian Waters
2012	Lise Cats Myhre	PhD Biology	Effects of the social and physical environment on mating behaviour in a marine fish
2012	Tonje Aronsen	PhD Biology	Demographic, environmental and evolutionary aspects of sexual selection
2012	Bin Liu	PhD Biology	Molecular genetic investigation of cell separation and cell death regulation in *Arabidopsis thaliana*
2013	Jørgen Rosvold	PhD Biology	Ungulates in a dynamic and increasingly human dominated landscape – A millennia-scale perspective
2013	Pankaj Barah	PhD Biology	Integrated Systems Approaches to Study Plant Stress Responses
2013	Marit Linnerud	PhD Biology	Patterns in spatial and temporal variation in population abundances of vertebrates
2013	Xinxin Wang	PhD Biology	Integrated multi-trophic aquaculture driven by nutrient wastes released from Atlantic salmon (*Salmo salar*) farming
2013	Ingrid Ertshus Mathisen	PhD Biology	Structure, dynamics, and regeneration capacity at the sub-arctic forest-tundra ecotone of northern Norway and Kola Peninsula, NW Russia
2013	Anders Foldvik	PhD Biology	Spatial distributions and productivity in salmonid populations
2013	Anna Marie Holand	PhD Biology	Statistical methods for estimating intra- and inter-population variation in genetic diversity
2013	Anna Solvang Båtnes	PhD Biology	Light in the dark – the role of irradiance in the high Arctic marine ecosystem during polar night
2013	Sebastian Wacker	PhD Biology	The dynamics of sexual selection: effects of OSR, density and resource competition in a fish
2013	Cecilie Miljeteig	PhD Biology	Phototaxis in *Calanus finmarchicus* – light sensitivity and the influence of energy reserves and oil exposure
2013	Ane Kjersti Vie	PhD Biology	Molecular and functional characterisation of the IDA family of signalling peptides in *Arabidopsis thaliana*
2013	Marianne Nymark	PhD Biology	Light responses in the marine diatom *Phaeodactylum tricornutum*
2014	Jannik Schultner	PhD Biology	Resource Allocation under Stress - Mechanisms and Strategies in a Long-Lived Bird
2014	Craig Ryan Jackson	PhD Biology	Factors influencing African wild dog *(Lycaon pictus*) habitat selection and ranging behaviour: conservation and management implications
2014	Aravind Venkatesan	PhD Biology	Application of Semantic Web Technology to establish knowledge management and discovery in the Life Sciences
2014	Kristin Collier Valle	PhD Biology	Photoacclimation mechanisms and light responses in marine micro- and macroalgae
2014	Michael Puffer	PhD Biology	Effects of rapidly fluctuating water levels on juvenile Atlantic salmon (*Salmo salar* L.)
2014	Gundula S. Bartzke	PhD Biology	Effects of power lines on moose *(Alces alces)* habitat selection, movements and feeding activity
2014	Eirin Marie Bjørkvoll	PhD Biology	Life-history variation and stochastic population dynamics in vertebrates
2014	Håkon Holand	PhD Biology	The parasite *Syngamus trachea* in a metapopulation of house sparrows
2014	Randi Magnus Sommerfelt	PhD Biology	Molecular mechanisms of inflammation – a central role for cytosolic phospholiphase A2

2014	Espen Lie Dahl	PhD Biology	Population demographics in white-tailed eagle at an on-shore wind farm area in coastal Norway
2014	Anders Øverby	PhD Biology	Functional analysis of the action of plant isothiocyanates: cellular mechanisms and in vivo role in plants, and anticancer activity
2014	Kamal Prasad Acharya	PhD Biology	Invasive species: Genetics, characteristics and trait variation along a latitudinal gradient.
2014	Ida Beathe Øverjordet	PhD Biology	Element accumulation and oxidative stress variables in Arctic pelagic food chains: *Calanus*, little auks (*Alle alle*) and black-legged kittiwakes (*Rissa tridactyla*)
2014	Kristin Møller Gabrielsen	PhD Biology	Target tissue toxicity of the thyroid hormone system in two species of arctic mammals carrying high loads of organohalogen contaminants
2015	Gine Roll Skjervø	Dr. philos Biology	Testing behavioral ecology models with historical individual-based human demographic data from Norway
2015	Nils Erik Gustaf Forsberg	PhD Biology	Spatial and Temporal Genetic Structure in Landrace Cereals
2015	Leila Alipanah	PhD Biology	Integrated analyses of nitrogen and phosphorus deprivation in the diatoms *Phaeodactylum tricornutum* and *Seminavis robusta*
2015	Javad Najafi	PhD Biology	Molecular investigation of signaling components in sugar sensing and defense in *Arabidopsis thaliana*
2015	Bjørnar Sporsheim	PhD Biology	Quantitative confocal laser scanning microscopy: optimization of in vivo and in vitro analysis of intracellular transport
2015	Magni Olsen Kyrkjeeide	PhD Biology	Genetic variation and structure in peatmosses (*Sphagnum*)
2015	Keshuai Li	PhD Biology	Phospholipids in Atlantic cod (*Gadus morhua* L.) larvae rearing: Incorporation of DHA in live feed and larval phospholipids and the metabolic capabilities of larvae for the de novo synthesis
2015	Ingvild Fladvad Størdal	PhD Biology	The role of the copepod *Calanus finmarchicus* in affecting the fate of marine oil spills
2016	Thomas Kvalnes	PhD Biology	Evolution by natural selection in age-structured populations in fluctuating environments
2016	Øystein Leiknes	PhD Biology	The effect of nutrition on important life-history traits in the marine copepod *Calanus finmarchicus*
2016	Johan Henrik Hårdensson Berntsen	PhD Biology	Individual variation in survival: The effect of incubation temperature on the rate of physiological ageing in a small passerine bird
2016	Marianne Opsahl Olufsen	PhD Biology	Multiple environmental stressors: Biological interactions between parameters of climate change and perfluorinated alkyl substances in fish
2016	Rebekka Varne	PhD Biology	Tracing the fate of escaped cod (*Gadus morhua* L.) in a Norwegian fjord system
2016	Anette Antonsen Fenstad	PhD Biology	Pollutant Levels, Antioxidants and Potential Genotoxic Effects in Incubating Female Common Eiders (*Somateria mollissima*)
2016	Wilfred Njama Marealle	PhD Biology	Ecology, Behaviour and Conservation Status of Masai Giraffe (*Giraffa camelopardalis tippelskirchi*) in Tanzania
2016	Ingunn Nilssen	PhD Biology	Integrated Enviromental Mapping and Monitoring: A Methodological approach for end users.
2017	Konika Chawla	PhD Biology	Discovering, analysing and taking care of knowledge.

2017	Øystein Hjorthol Opedal	PhD Biology	The Evolution of Herkogamy: Pollinator Reliability, Natural Selection, and Trait Evolvability.
2017	Ane Marlene Myhre	PhD Biology	Effective size of density dependent populations in fluctuating environments
2017	Emmanuel Hosiana Masenga	PhD Biology	Behavioural Ecology of Free-ranging and Reintroduced African Wild Dog (*Lycaon pictus*) Packs in the Serengeti Ecosystem, Tanzania
2017	Xiaolong Lin	PhD Biology	Systematics and evolutionary history of *Tanytarsus* van der Wulp, 1874 (Diptera: Chironomidae)
2017	Emmanuel Clamsen Mmassy	PhD Biology	Ecology and Conservation Challenges of the Kori bustard in the Serengeti National Park
2017	Richard Daniel Lyamuya	PhD Biology	Depredation of Livestock by Wild Carnivores in the Eastern Serengeti Ecosystem, Tanzania
2017	Katrin Hoydal	PhD Biology	Levels and endocrine disruptive effects of legacy POPs and their metabolites in long-finned pilot whales of the Faroe Islands
2017	Berit Glomstad	PhD Biology	Adsorption of phenanthrene to carbon nanotubes and its influence on phenanthrene bioavailability/toxicity in aquatic organism
2017	Øystein Nordeide Kielland	PhD Biology	Sources of variation in metabolism of an aquatic ectotherm
2017	Narjes Yousefi	PhD Biology	Genetic divergence and speciation in northern peatmosses (*Sphagnum*)
2018	Signe Christensen-Dalgaard	PhD Biology	Drivers of seabird spatial ecology - implications for development of offshore wind-power in Norway
2018	Janos Urbancsok	PhD Biology	Endogenous biological effects induced by externally supplemented glucosinolate hydrolysis products (GHPs) on *Arabidopsis thaliana*
2018	Alice Mühlroth	PhD Biology	The influence of phosphate depletion on lipid metabolism of microalgae
2018	Franco Peniel Mbise	PhD Biology	Human-Carnivore Coexistence and Conflict in the Eastern Serengeti, Tanzania
2018	Stine Svalheim Markussen	PhD Biology	Causes and consequences of intersexual life history variation in a harvested herbivore population
2018	Mia Vedel Sørensen	PhD Biology	Carbon budget consequences of deciduous shrub expansion in alpine tundra ecosystems
2018	Hanna Maria Kauko	PhD Biology	Light response and acclimation of microalgae in a changing Arctic
2018	Erlend I. F. Fossen	PhD Biology	Trait evolvability: effects of thermal plasticity and genetic correlations among traits
2019	Peter Sjolte Ranke	PhD Biology	Demographic and genetic and consequences of dispersal in house sparrows
2019	Mathilde Le Moullec	PhD Biology	Spatiotemporal variation in abundance of key tundra species: from local heterogeneity to large-scale synchrony
2019	Endre Grüner Ofstad	PhD Biology	Causes and consequences of variation in resource use and social structure in ungulates
2019	Yang Jin	PhD Biology	Development of lipid metabolism in early life stage of Atlantic salmon (*Salmo salar*)
2019	Elena Albertsen	PhD Biology	Evolution of floral traits: from ecological contex to functional integration
2019	Mominul Islam Nahid	PhD Biology	Interaction between two Asian cuckoos and their hosts in Bangladesh

2019	Knut Jørgen Egelie	Phd Biology	Management of intellectual property in university-industry collaborations – public access to and control of knowledge
2019	Thomas Ray Haaland	Phd Biology	Adaptive responses to enviromental stochasticity on different evolutionary time-scales
2019	Kwaslema Malle Hariohay	Phd Biology	Human wildlife interactions in the Ruaha-Rungwa Ecosystem, Central Tanzania
2019	Mari Engvig Løseth	Phd Biology	Exposure and effects of emerging and legacy organic pollutants in white-tailed eagle (*Haliaeetis albicilla*) nestlings
2019	Joseph Mbyati Mukeka	Phd Biology	Human-Wildlife Conflicts and Compensation for Losses in Kenya: Dynamics, Characteristics and Correlates
2019	Helene Løvstrand Svarva	Phd Biology	Dendroclimatology in southern Norway: tree rings, demography and climate
2019	Nathalie Briels	Phd Biology	Exposure and effects of legacy and emerging organic pollutants in developing birds – Laboratory and field studies
2019	Anders L.Kolstad	Phd Biology	Moose browsing effects on boreal production forests – implications for ecosystems and human society
2019	Bart Peeters	Phd Biology	Population dynamics under climate change ad harvesting: Results from the high Arctic Svalbard reindeer