A probabilistic view of forbidden links: their prevalence and their consequences for the robustness of mutualistic networks

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The data will be available on Zenodo upon manuscript acceptance.

R codes used for analyses are available here: https://github.com/f-duchenne/EPHI_paper

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The authors declare no competing interests.

Author contributions:

FD designed the study, with inputs from ElB and CHG, and performed all analyses. IGV, TS and MM were responsible for country level scientific and logistic coordination/data collection with major assistance from TM-S, TBZ, AN, FR, and EBr. HB, RB, DB, EBr, NB, APC, NE, ARG, JACJ, MK, TM-S, MM-R, CGM, ASMF, AN, RO, FR, BGR, LLR, WLS, DSV, and

KZ collected the data. EBa, FD, CB, EBr, MK, TS, TM-S, RW, BW, and IGV curated the data. FD wrote the first draft and all authors contributed to final writing and editing.

Abstract

Understanding how species extinctions affect communities of interacting species is an important challenge of ecology. The presence of unfeasible interactions, termed forbidden links, due to physiological or morphological barriers, is likely to decrease the plasticity of interaction networks, affecting their robustness to species extinctions. However, the existence of these forbidden links has been long debated, stressing the need to learn more about their prevalence and putative consequences for community robustness to extinctions. To tackle this gap, we used a dataset of plant-hummingbird interactions collected in Brazil, Costa Rica and Ecuador along elevation gradients. We used a Bayesian hierarchical model, to assess the probabilistic importance of exploitation barriers in determining species interactions. We found evidence for exploitation barriers between flowers and hummingbirds with a shorter bill than the corolla. We also showed that the proportion of forbidden links can change drastically among communities, because of changes in trait distributions. Finally we showed that networks with a high proportion of forbidden links had low robustness, because of constraints on interaction rewiring. Our results suggest that exploitation barriers are not rare and strongly limit interaction rewiring, and thus the rescue of species experiencing partner extinction may be limited.

Introduction

Understanding the organization of the *entangled bank* of species and what factors influence species interactions is a major goal of ecology. The organization of species interactions shapes the stability of natural communities (Bascompte 2009; Kéfi *et al.* 2016; Thébault & Fontaine 2010). Ecologists have investigated the mechanisms that determine species interactions, henceforth linkage rules, highlighting that interactions are often structured by species abundances and morphological traits rather than species identity (Bartomeus *et al.* 2016; Gravel *et al.* 2013; Machado-de-Souza *et al.* 2019; Vázquez *et al.* 2009b, a). Given that rules are associated with traits and abundance, species can interact with different sets of species through space and time (CaraDonna *et al.* 2017; Tylianakis & Morris 2017), which makes communities less vulnerable to the loss of specific species (Kaiser-Bunbury *et al.* 2010; Ramos-Jiliberto *et al.* 2012; Vizentin-Bugoni *et al.* 2020). To date, much progress has been made on identifying rules that influence the presence of species interactions but not what causes the absence of interactions. While the latter is simply the other side of the same coin, a focus on what influences the absence of interactions might highlight constraints on the distribution and flexibility of interspecific interactions that are otherwise overlooked.

Understanding the absence of interactions is crucial because ecological networks are often very sparse, meaning that the number of observed interactions is often much lower than the number of possible interactions (Busiello *et al.* 2017; Jordano 2016). A few explanations have been proposed to explain the sparsity of ecological networks: insufficient sampling where some interactions are missed (Doré *et al.* 2021; Jordano 2016), low species abundances (Vázquez *et al.* 2009a, b) or trait matching constraints (Santamaría & Rodríguez-Gironés 2007). Trait matching often considers trait complementarity and barrier (Santamaría & Rodríguez-Gironés 2007). Trait complementarity is a continuous measure such as similarity between corolla length and proboscis or bill length (Gonzalez & Loiselle 2016; Junker *et al.* 2013; Sonne *et al.* 2020; Vázquez *et al.* 2009a), while trait barrier refers to compatible *versus* incompatible traits, which lead to an on/off mechanism, called an exploitation barrier (Stang *et al.* 2009). Among the many missing interactions in a network only the ones due to exploitation barriers are forbidden links (*i.e.* links invariantly absent). The proportion of these forbidden links is important for understanding spatio-temporal dynamics of communities, because they are links that would be absent regardless of the context, such as species abundances, or sampling frequency.

Evidencing a forbidden link requires demonstrating that the absence of interaction is not due to insufficient sampling or stochasticity, but to an exploitation barrier. So far, forbidden links mainly have been identified using indirect evidence by looking at network properties, such as the distribution of interaction frequencies (Eklöf *et al.* 2013; Jordano *et al.* 2003) and topological characteristics of interaction networks (Santamaría & Rodríguez-Gironés 2007). These indirect evidences do not explicitly link the forbidden links with their causal mechanisms, but see Olesen *et al.* (2010). To obtain direct evidence of forbidden links, we need to investigate the mechanisms driving the absence of interactions between pairs of species. However, statistical models simultaneously testing different trait matching linkage rules in empirical mutualistic networks are scarce (but see Stang *et al.* 2009). Studies often either consider trait complementarity (Klumpers *et al.* 2019; Sonne *et al.* 2020; Zhao *et al.* 2022) or exploitation barrier (Vizentin-Bugoni *et al.* 2014) or both rules but in separate models (Sazatornil *et al.* 2016). In addition, the concept of forbidden links has been criticized

because studies often neglect the intraspecific trait variability that might reduce their prevalence (González-Varo & Traveset 2016). Overcoming these limitations requires repeated sampling and a probabilistic view of species interactions (Song *et al.* 2020) to measure forbidden links.

In addition, understanding the relative importance of trait complementarity and exploitation barrier for species interactions provides insights into the robustness of the interaction networks to perturbation. Robustness is often assessed by simulating species extinctions and evaluating how fast a given network collapses. A robust network is a network that needs a high number of primary extinctions to collapse. Species' ability to change interaction partners, referred to as rewiring, is a key mechanism influencing network robustness (Kaiser-Bunbury *et al.* 2010; Ramos-Jiliberto *et al.* 2012; Vizentin-Bugoni *et al.* 2020). The more species are able to rewire when their interactions are lost due to primary extinctions, the higher the robustness. Forbidden links would limit the possibility of interaction rewiring, and thus are critical for understanding and assessing community robustness.

To assess how linkage rules and trait distributions determine the sparsity of ecological networks and their robustness, we used plant-hummingbird interaction data collected over three different elevation gradients from different biogeographic regions (Dalsgaard *et al.* 2021; McGuire *et al.* 2014). These regions include the mountains in the Atlantic Forest, in Brazil, the Tropical Andes, in Ecuador, and the Talamanca Mountains, in Costa Rica. We developed a mechanistic and hierarchical Bayesian model considering two linkage rules: possible or forbidden links due to exploitation barrier and a gradient of interaction frequencies due to trait complementarity. Then, merging estimated linkage rules and the observed variation in trait distribution over elevation, we used simulations to estimate how network robustness to plant extinction depended on the linkage rules (Fig. 1). We show that linkage rules and trait distribution together drive the robustness of plant-hummingbird communities to species extinctions.

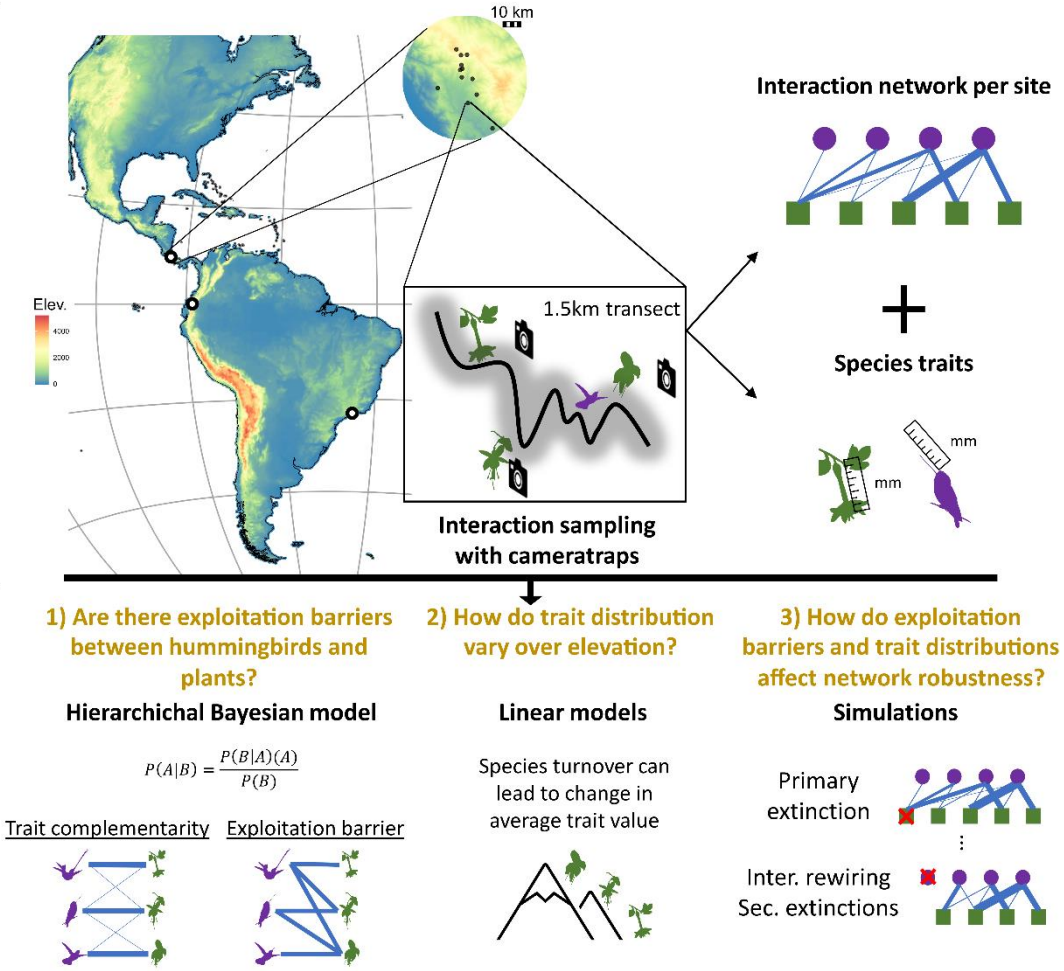

Figure 1: Schematic representation of the methodological steps to investigate drivers of sparsity and their effects on network robustness. *On the map, the white points show the location of the three regions, while the zoomed map shows an example of one region, 12 study sites in Costa Rica and a hypothetical transect in one study site. The right part of the figure describes data collection that was done in the transect in a schematic way. Research questions are highlighted below in yellow, while bold black titles represent the methodological steps followed to answer the questions. Elev. = elevation (in meters above sea level); Inter. rewiring = interaction rewiring; Sec. extinctions = secondary extinctions.*

Methods

Interaction dataset

We collected data in 32 sites located in Brazil, Costa Rica and Ecuador, between 10 and 3500 meters above sea level. Each site was sampled during about two years, spread between February 2017 and December 2022 (*cf.* Table S1, Fig. 1). Each site consisted of one 1.5 km transect along which we tracked plant-hummingbird interactions by installing 12 time-lapse cameras at ~1 meter distance from open flowers, up to 2 m above the ground, during ~3 days. The cameras took an image every second from dawn to dusk (~ 12 h), generating ~ 43,200 images per camera per day. Images were analyzed with DeepMeerkat software (Weinstein 2018) which returned candidate frames with hummingbirds. These candidate frames were reviewed manually to identify birds to the species level and determine pairwise plant-hummingbird interactions. In parallel, every month, a flower census was done on each transect to estimate the abundance of available flowers (*cf.* Supplementary Methods).

The overall dataset includes 80,988 interactions detected between 79 hummingbird species and 640 plant species. Since we are interested in linkage rules of mutualistic interactions, we excluded 5,678 interactions in which hummingbirds were observed robbing nectar instead of entering the flower by the corolla opening. These interactions are likely not mutualistic because when piercing, hummingbirds do not contact the reproductive organs of the flower, and thus do not contribute to pollination. Furthermore, since we are interested in trait complementarity and exploitation barrier, we used only the subset of 441 plant species and 73 hummingbird species for which we have trait measures, corresponding to 69,201 interactions. Countries exhibited strong differences in species richness. The studied sites in Ecuador were three times more diverse than those in Brazil (Fig. S1), thus we decided to fit one model per country.

For each camera and each hummingbird species, we summed interactions recorded with the focal plant. When no interaction was detected with a hummingbird species that was known to occur at that site (at least one recorded interaction along the transect over the entire sampling period), the observed interaction count was set to zero. We then modelled this observed interaction count to disentangle the mechanisms producing these zeros (*cf.* below).

Morphological traits of plants and hummingbirds

To calculate trait matching between a hummingbird and a plant, we used the corolla length for plant flowers and the bill length of hummingbirds measured in the field and compiled from the literature (cf. Supplementary Methods).

The signal of trait matching between corolla and bill length in determining interaction frequencies could likely be blurred by: (i) the fact that hummingbird protrude their tongues beyond the tips of their bill to reach nectar allowing them to interact with flowers with a corolla longer than their bill (Paton & Collins 1989), and (ii) trait matching is not necessarily the rule in mutualism, coevolution between plant and pollinators can turn in an arms race maintaining trait mismatch between interacting species (Paudel et al. 2016; Week & Nuismer 2021). To deal with these potential issues, we used the bill length to inform two latent variables for each hummingbird species, one modelling the preferred corolla length and the other modelling the barrier threshold, the maximum corolla length a flower can have for a given bird to interact with (cf. below).

Inferring linkage rules

To assess linkage rules, we developed a hierarchical Bayesian model including all species and sites together, correcting for spatial and temporal autocorrelation. In an interaction dataset, non-observed interactions (zeros) can be due to three statistical reasons: (i) non-detection due to insufficient sampling pressure; (ii) overdispersion in the distribution of interaction frequencies that can lead to over-representation of zero; (iii) additional zero-inflation in the distribution of interactions.

To distinguish these three statistical sources of zeros, we modelled interaction frequency using a zero-inflated negative-binomial distribution accounting for the sampling duration. We chose this distribution because it deals well with overdispersed data, typical of sparse interaction networks. Our model encompassed two nested submodels, equations (1) and (2), modelling zero-inflation and interaction counts, respectively. The submodel of zero-inflation, called the exploitation barrier submodel, was divided in two parts: an intercept (β_0) capturing zero-inflation due to unknown processes and an effect of the exploitation barrier (β_1) capturing the zero-inflation due to forbidden links. The submodel of interaction counts, called

the trait complementarity submodel, modelled the number of observed interactions as a function of trait complementarity (β_3), hummingbird phenology (β_4) and sampling duration ($\log(D_c)$). We also included random effects accounting for plant effect (θ_j), site effect (θ_s), temporal variations (θ_{sv}) and hummingbird abundances (θ_{si}).

For each country, the model is described by the following equations.

Exploitation barrier submodel

$$O_{jic} \sim \text{Bernoulli}(\psi_{ji})\,;\, logit(\psi_{ji}) = \beta_0 + \beta_1 \times barrier_{ij} \quad (1)$$

Trait complementarity submodel

$$F_{jismvc} | O_{jic} \sim \text{NB}(r, p_{jismv})\,;\, p_{jismvc} = \frac{r}{r + \lambda_{jismvc} O_{jic}}\,;$$

$$log(\lambda_{jismvc}) = \beta_2 + \beta_3 \times compl._{ij} + \beta_4 \times pheno_{ism} + \log(D_c) + \theta_j + \theta_s + \theta_{sv} + \theta_{si} \quad (2)$$

Latent variables

$$barrier_{ij} = \begin{cases} 1 \; if \; corolla_j > L1_i \\ 0 \end{cases}; L1_i \sim \mathcal{N}(bill_i, 0.2 \times bill_i) T(max\,(bill_i, L2_i), 2 \times bill_i) \quad (3)$$

$$compl._{ij} = -1 \times |corolla_j - L2_i|; L2_i \sim \mathcal{N}(\text{bill}_i, 0.2 \times \text{bill}_i) T(0.5 \times bill_i, 1.5 \times bill_i) \quad (4)$$

First, in equation (1), we modelled the binary ability of plant species *j* and hummingbird *i* to interact in front of camera *c* (O_{jic}), as a function of exploitation barrier. We used a generalized linear model (GLM) with a binomial error structure and a logit link function (equation (1)), which models the effect of exploitation barrier (β_1) on the probability of interaction (ψ_{ji}) between plant species *j* and hummingbird *i*. Since our measure of exploitation barrier is done at the camera level, it includes a stochastic variability that can be caused by intra-specific trait variability in plants (González-Varo & Traveset 2016). Thus, our estimated probability of interaction indirectly included intraspecific variability in trait values.

Second, in equation (2), we modelled the number of interactions between each plant species *j* and hummingbird *i* on site *s*, month *m*, date *v* and camera *c* (F_{jistmc}), conditionally to the ability of both species to interact. We used a GLM with a negative binomial error structure (with r the target for number of successful trials and p_{jistm} the probability of success in each trial) and a log link function. The average interaction frequencies (λ_{jismv}) are modelled as a function of a general intercept (β_2), the effect of trait complementarity between the plant and the hummingbird ($\beta_3 \times compl._{ij}$), the hummingbird phenology ($\beta_4 \times pheno_{im}$, cf. Supplementary methods). Finally, the sampling duration, in hours of daylight ($\log(duration_c)$), was set as an offset in that model, resulting in the fact that we modelled a number of interactions per hour of sampling.

This submodel also included random effects: a plant species random effect ($\theta_j \sim \mathcal{N}\left(0, \sigma^2_{\theta_j}\right)$) to account for heterogeneity in plant species attractiveness for hummingbirds and a site random effect to account for heterogeneity among sites. To account for spatial autocorrelation among sites we structured the variance-covariance of this random effect using the Euclidean distance among sites: $\theta_s \sim \mathcal{N}\left(0, \sigma^2_{\theta_s}\Sigma\right)$ where Σ is the spatial variance-covariance matrix among sites, filled with $e^{-\rho d_{ss}}$ where ρ is the scale parameter governing

the distance-dependent decay of the spatial correlation and d_{ss} is the pairwise distance between sites, scaled to be one at the maximum distance. We also included a date (month-year) random effect, modelled as a temporal random walk of order one for each site ($\theta_{sv} \sim \mathcal{N}\left(\theta_{sv-1}, \sigma^2_{\theta_v}\right)$; $\theta_{s,v=1} \sim \mathcal{N}\left(0, \sigma^2_{\theta_v}\right)$) was used to account for temporal autocorrelation. Finally, a hummingbird random effect for each site, was used to account for the fact that the abundance of hummingbirds varies over space ($\theta_{si} \sim \mathcal{N}\left(0, \sigma^2_{\theta_{si}}\right)$).

Latent thresholds ($L1_i$) were estimated for the exploitation barrier for each hummingbird species. This threshold represents the corolla length above which the hummingbird species is not able to interact. To inform the model and accelerate convergence, we used an informative prior, drawing this latent threshold from a Gaussian distribution centred on bill length with standard deviation of 20% of the bill length. We truncated this prior distribution from left and right sides: from half the bill size because we assume that optimal corolla length should not be too far from bill length, and at twice the bill length value, because empirical measures show that tongues are unlikely to extend by more than twice the bill length (Paton & Collins 1989).

The second latent variable ($L2_i$), also estimated for each hummingbird species, corresponds to the optimal corolla length (*i.e.* maximizing its interaction frequencies) for the focal bird. Similarly, we used an informative prior, drawing this latent variable from a Gaussian distribution centred on the bill length with standard deviation of 20% the bill length, but truncated to keep values only between the half of bill length and a half times the bill length, to avoid unrealistic values. The estimated values of $L1_i$ and $L2_i$ are displayed in Figure S2.

All parameters were estimated simultaneously using Markov Chain Monte Carlo simulations, as implemented in *R2jags* R package (Su & Yajima 2012), with 3 chains, 750,000 iterations with a burnin of 650,000 and a thin rate of 5, which was enough to reach convergence for each of the three countries (≥99% of parameters with Rhat<1.1). Priors are detailed in Supplementary methods.

Percentage of zeros generated by each linkage rule

To understand how the linkage rules contributed to the sparsity of the networks, we evaluated the percentage of non-interactions (relative to the number of possible interactions) by predicting the percentage of zeros generated by each linkage rule (trait complementarity, exploitation barrier and unknown linkage rule) using the Bayesian model described above (cf. Supplementary Methods). Since the percentage of zeros generated by trait complementarity depended on the sampling duration, we estimated the percentage of zeros generated by each linkage rule as a function of sampling duration.

Trait distribution over elevation gradient

To study how species traits vary across elevation, we used a linear mixed-effect model regressing the mean trait value (corolla or bill length) for species detected in a site *s* as a function of the elevation of site *s*. We modelled one elevation trend per guild per country by including a triple interaction between elevation, the guild of the species (plant or bird) and the country. We also included the site as a random effect on the intercept.

To study the effect of variation in trait values across elevation on the structure of the networks, we assessed the proportion of forbidden links as the average of $\psi_{ji} - \frac{e^{\beta_0}}{e^{1+\beta_0}}$ across all pairs of plants and hummingbirds present at a given site. We studied the proportion of forbidden links across elevation using a GLM with a quasi-binomial error structure instead, including elevation in interaction with the country as the response variables.

Network robustness

To assess network robustness, we used a measure based on coextinction rates, which is the area below the attack tolerance curve (Albert *et al.* 2000). This curve represents the fraction of persisting species of one trophic level, hummingbirds here, as a function of the eliminated species from the other trophic level, plants (Memmott *et al.* 2004; Vizentin-Bugoni *et al.* 2020).

For each site, we started from the initial interaction networks predicted by our statistical model (*cf.* Supplementary Methods). Then, we simulated sequential plant extinctions, and between each primary extinction we calculated the probability of secondary extinction for each hummingbird species (*cf.* Supplementary Methods). The probability of extinction depended on the proportion of interactions lost after rewiring. A hummingbird could rewire the interactions lost because of primary plant extinctions if the remaining plant species had compatible traits. To test the effects of forbidden links on robustness we performed simulations with two different cases of rewiring: constrained by trait complementarity only or constrained by trait complementarity and exploitation barriers (*cf.* Supplementary Methods). To see how our results depend on the sequence of extinctions and strength of rewiring, we also performed simulations for two different scenarios of plant extinctions, removing plant species from the more generalists to the more specialists or the opposite, and for three different values of rewiring rate, $\alpha \in [0,1,2]$, where $\alpha = 0$ corresponds to a complete rewiring if no zero-inflation, and $\alpha = 2$ corresponds to a rewiring strongly constrained by trait matching (*cf.* Supplementary Methods).

We performed 100 simulations for each case (with or without forbidden links, plant extinction scenario, value of rewiring rate and site), and for each we measured the area under the attack tolerance curve. This area is bounded between 0, lowest robustness possible, and 1, highest robustness possible. For each site, we estimated the robustness over the 100 simulations.

The effect of forbidden links on network robustness was assessed with a Wilcoxon test for paired samples, comparing the robustness with and without forbidden links for each site and each simulation scenario (plant extinction scenario and value of rewiring rate).

Path analysis

This effect of forbidden links on network robustness could arise either directly, through a limit to rewiring, or indirectly, through modification of the network structure, which has been shown to influence robustness significantly: nestedness, modularity and connectance (Memmott *et al.* 2004; Pastor *et al.* 2012). To assess these two possibilities through a substantial variation of network structures, we pooled all countries together and performed a single path analysis. In our path analysis we included the direct influence of forbidden links on network robustness as well as indirect links considering network structure. To do so, we

calculated weighted connectance, nestedness, modularity and species richness of each initial network (*cf.* Supplementary Methods), and we implemented all relationships presented in Fig. 5 in the path analysis using linear models.

Results

Our model gave strong evidence for the existence of both kinds of trait matching, namely trait complementarity and exploitation barriers, with similar patterns across countries (Fig. 2a-b). Interaction frequencies strongly depended on the morphological match between flower corolla length and hummingbird bill length (Fig. 2a & Fig. S2), suggesting that trait complementarity strongly determines plant-hummingbird interactions. On the top of trait complementarity, we found a significant exploitation barrier effect in plant-hummingbird interactions (Fig. 2b). This exploitation barrier is evidenced by the strong decrease in the probability of interaction between plants and hummingbirds if the corolla is too long relative to the hummingbird's bill. This result provides evidence for forbidden links: when there was an exploitation barrier, the probability of observing an interaction dropped, while the probability of observing an invariant zero increased.

In addition to these linkage rules, we found significant zero-inflation (Fig. 2b), highlighted by the fact that even when there was no exploitation barrier between two species, their probability of interacting together was much lower than one. This zero-inflation was captured by an overall intercept, which did not inform about the mechanism, suggesting that we do not know why an important number of pairwise interactions among plants and hummingbirds do not occur. The reason could be imperfect detections, exploitation barriers due to unconsidered traits (e.g. flower orientation and curvature) or any stochastic process (e.g. environmental conditions). Regardless of the mechanism behind this zero-inflation, this showed that interaction networks are highly sparse.

Our model allowed us to distinguish invariant zeros, generated by exploitation barrier and unknown processes, from the "flexible" zeros, generated by trait complementarity and sampling pressure (Fig. S3). On average, 14.5% of possible interactions were forbidden because of exploitation barrier, but with strong variation among sites and countries, from 3.5% in high elevation sites in Costa Rica to 29% in the lowlands of Brazil (Fig. 2c).

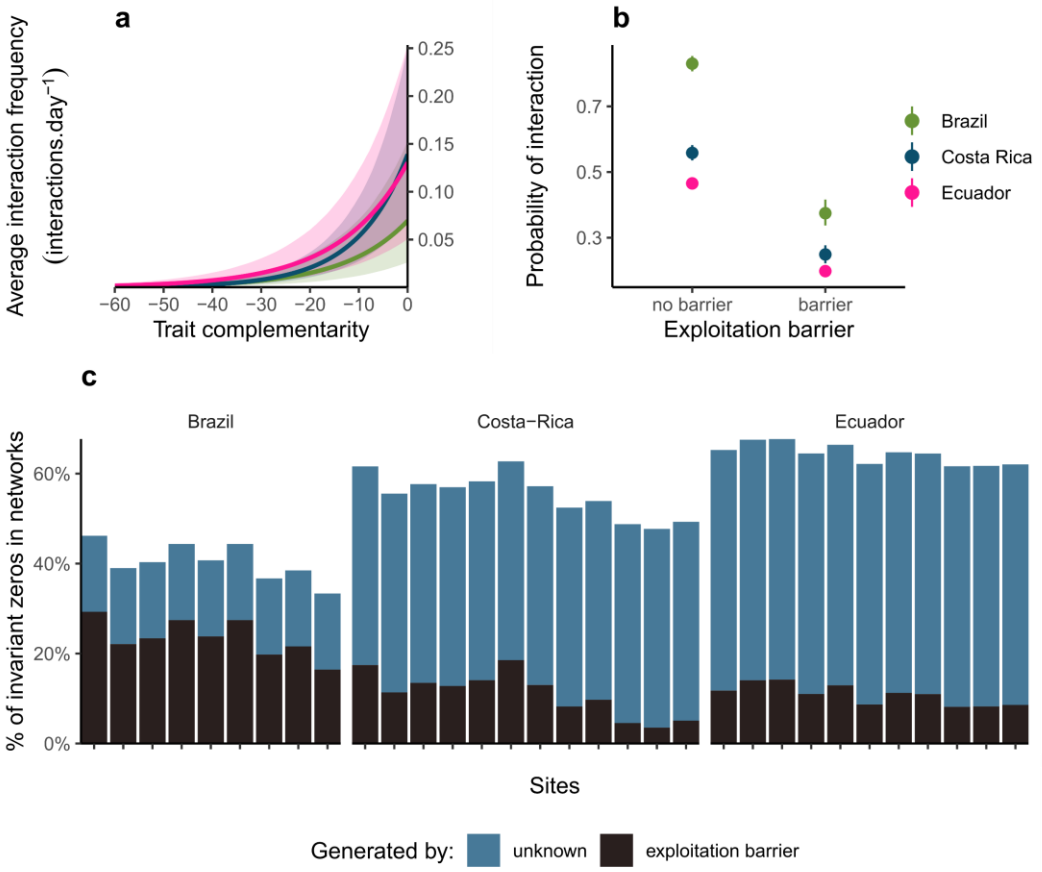

Figure 2: Trait complementarity and exploitation barrier determine plant-hummingbird interactions, and the sparsity of the interaction networks. *(a) Predicted average interaction frequencies as a function of trait complementarity between plants and hummingbirds. (b) Probability of interaction between plants and hummingbirds as a function of the presence of exploitation barrier or not. (c) Percentage of invariant zeros as a function of the linkage rule generating them: exploitation barrier or unknown process (additional zero-inflation). Within each country, sites are ranked by increasing elevation, from left to right.*

Variation in the proportion of forbidden links across sites was explained by the distribution of species traits across sites. We found that flower corolla length tended to decrease with elevation in all countries, although the trend was significantly negative in Costa Rica and Ecuador only (Fig. 3a & S4), while the distribution of hummingbird bill length remained constant over elevation (Fig. 3a & S4; Table S2). This pattern of trait distribution can be translated into an elevation gradient in the proportion of forbidden links: higher elevation communities exhibited fewer forbidden links than lower elevation communities (Fig. 3b & *Table S2).*

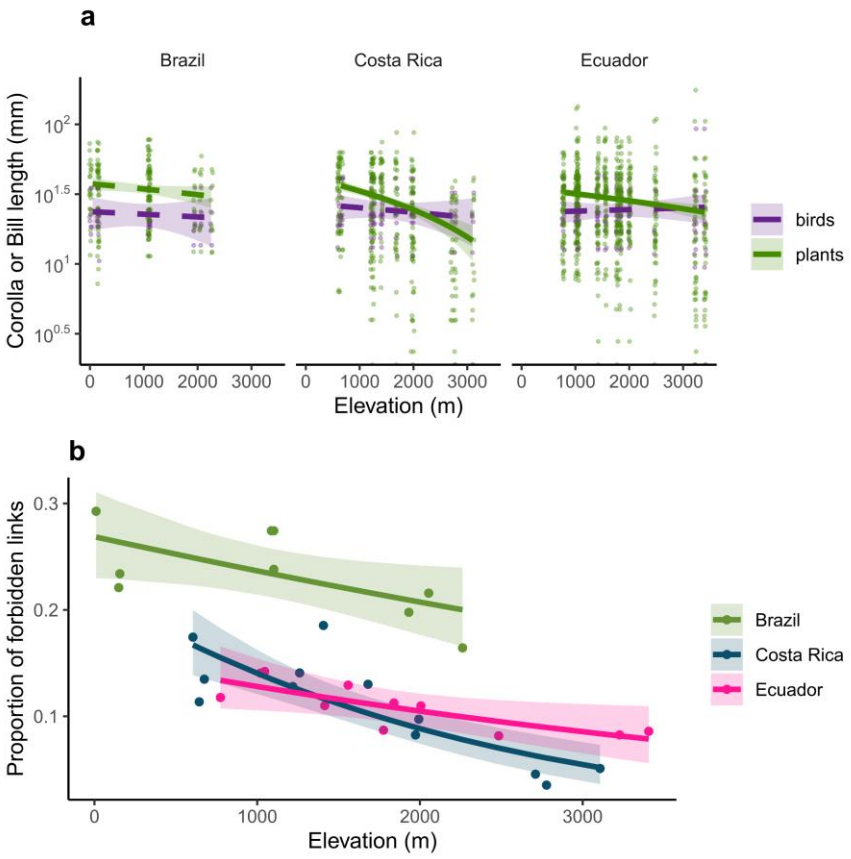

Figure 3: Flower corolla length and proportion of forbidden links decrease over elevation. *(a) Corolla or bill length as a function of elevation for every species present at each site, for each country. Note that the y-axis is log-transformed to improve readability. (b) Proportion of forbidden links for each site as a function of elevation and country. In all panels, lines show model predictions and ribbons the associated 95% confidence intervals. Solid lines show trends significantly different from zero while dashed lines show trends non-significantly different zero.*

In all countries, most of the simulations showed a significant decrease of network robustness when accounting for forbidden links (Fig. 4a & S5), although this effect oscillated between marginally significant and significant (p-value<0.05) in Costa Rica (Fig. S5). Including forbidden links in simulations decreased robustness overall (Fig. 4b). The higher the proportion of forbidden links in a given site, the more negative the effect on robustness (Fig. 4c). In some cases, when forbidden links were rare, they increased the network robustness (Fig. 4b-c), likely because by preventing some interactions, forbidden links limit the effect of species extinctions to compatible partners.

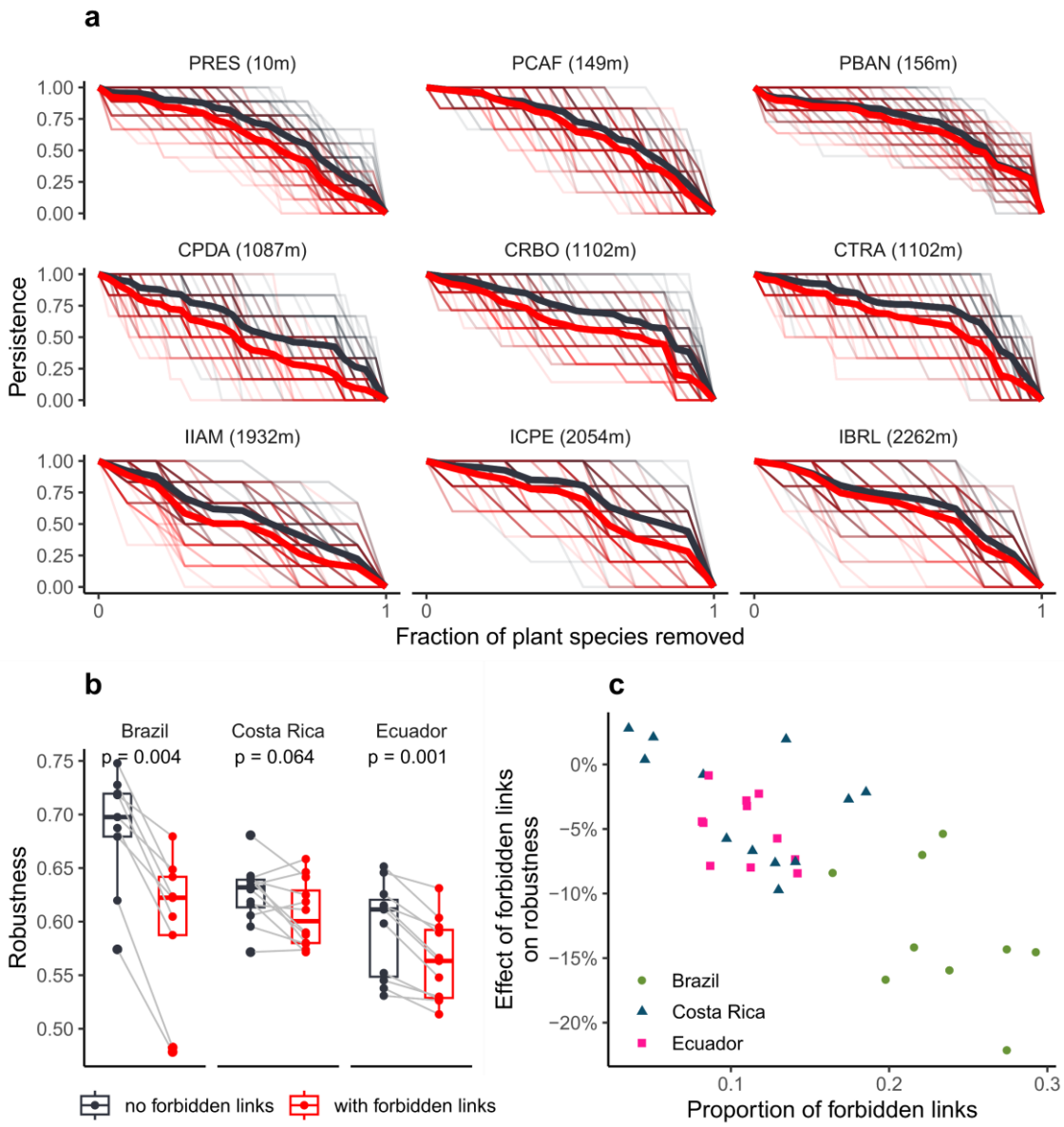

Figure 4: Robustness to plant extinctions is strongly limited by forbidden links, especially at low elevation. *(a) Attack tolerance curve for each simulation and each site in Brazil (site acronyms with their elevation, in meters above sea level) when accounting for forbidden links (red) or when neglecting them (black). Thick lines show the average value over the 100 simulations, for each site, while thin lines show individual simulations. (b) Robustness (area under the attack tolerance curve) for each site when accounting for forbidden links (red) or when neglecting them (black). P-values of the paired Wilcoxon test are indicated. (c) Effect of forbidden links on robustness (relative to the case without forbidden links) as a function of the proportion of the forbidden links, for each site. Robustness simulations and values are presented for the scenario "generalists first" and α = 1 (cf. Fig. S5).*

This effect of forbidden links on network robustness could arise either directly, through a limit of rewiring, or indirectly, through modification of the network structure. The path analysis shows that the proportion of forbidden links had a strong direct effect on robustness, which was stronger than the indirect effects mediated by network structure (Fig. 5). This suggests, as expected, that forbidden links negatively affect robustness through interaction rewiring mainly and not through structural modifications of the network. In addition,

forbidden links decreased connectance, which turned into an indirect positive effect on network robustness (i.e., indirects are calculated by multiplying the direct effects). Consistent with previous findings we also found that network robustness was positively linked to nestedness and modularity. The effect of the different measures of network structure on robustness depended on but the proportion of forbidden links was robust to changes in the strength of the rewiring (Fig. S6).

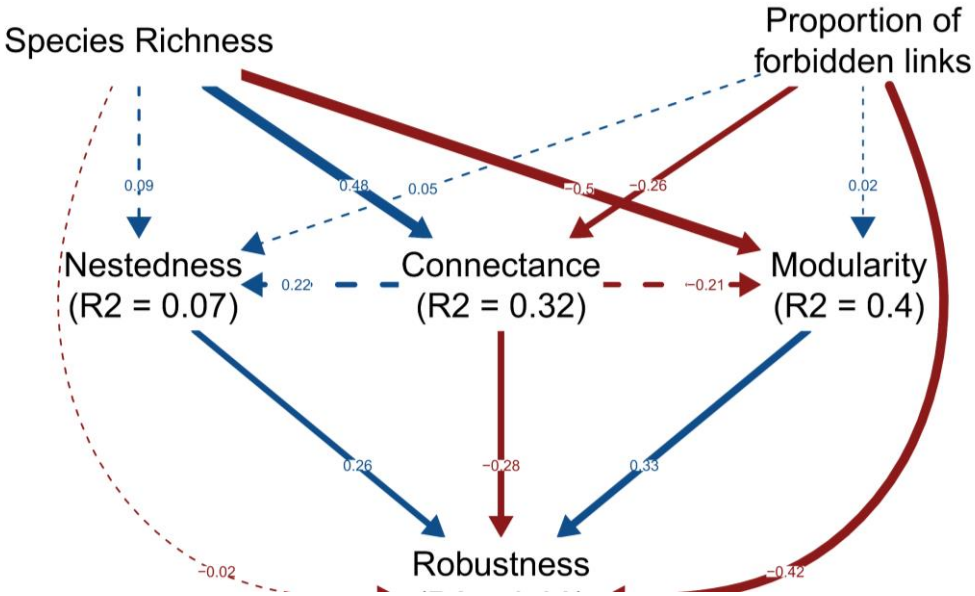

Fig. 5: Path analysis highlights forbidden links as the main determining factor of robustness. *Path analysis showing standardized effects between variables. Solid lines correspond to either positive (blue) or negative (red) significant effects, while dashed lines represent non-significant effects. Numbers under the variable names are* r*-squared values of the linear model explaining the associated variable (R2). Path analysis performed for robustness values when using the scenario "generalists first" and α = 1. Species richness is the total number of species in the network (plants + hummingbirds).*

Discussion

Our results substantiate the idea that forbidden links are not a myth, but instead are common in nature. We extended the existing set of evidence (Eklöf *et al.* 2013; Jordano *et al.* 2003; Olesen *et al.* 2010; Santamaría & Rodríguez-Gironés 2007) by establishing a statistical and direct link between interactions that have an invariantly low probability of occurring and exploitation barriers. We also show that the prevalence of forbidden links is given by the pool of traits available in the community, leading to strong heterogeneity in their prevalence over environmental gradients (*i.e.* elevation). Finally, by using simulations, we found that the higher the proportion of forbidden links, the lower the rewiring in case of local extinction and therefore the lower the robustness. Since our analyses suggest that exploitation barriers are common in nature, the rescue of species experiencing partner extinction because of interaction rewiring could be much more limited than previously suggested (Ramos-Jiliberto *et al.* 2012; Sheykhali *et al.* 2020; Vizentin-Bugoni *et al.* 2020).

We evaluated two aspects of trait matching that are often studied separately, trait complementarity and exploitation barrier, and show that they are both important in determining species interactions. This result is consistent with the hummingbird-plant

interaction literature, which have shown that trait complementarity (Dalsgaard *et al.* 2021; Maglianesi *et al.* 2014; Sonne *et al.* 2020) and trait barrier (Vizentin-Bugoni *et al.* 2014) are important factor influencing interaction frequencies, but have studied them independently. By simultaneously evaluating these two linkage rules, we were able to separate their relative importance, and thus to bring direct statistical evidence for the existence of forbidden links, resulting from exploitation barriers.

The existence of exploitation barrier, producing forbidden links, has been extensively debated (González-Varo & Traveset 2016; Olesen *et al.* 2010). Several studies have shown that they are needed to explain the departure from the scale-free topologies observed in mutualistic networks (Vázquez 2005). However, critiques have been raised about the lack of consideration of spatio-temporal variation as well as intraspecific trait variability that make forbidden links more labile than initially thought, so not really forbidden (González-Varo & Traveset 2016). Here, we partially overcome these limitations by using a probabilistic definition of forbidden links. In our statistical approach, the presence of forbidden links is defined as an invariant decrease in the interaction probability due to exploitation barrier, regardless the context (site, time, etc.). This is important because it means that what we call forbidden links could eventually happen, but if they do, it would be with a much lower probability than an equivalent non-forbidden link. We were able to use such a probabilistic approach because our interaction sampling was repeated over different plant individuals, in different contexts. Even if species traits were used at the species level, interaction data used to estimate exploitation barrier involved intraspecific variation. Our probabilistic approach gave evidence for exploitation barrier and thus forbidden links, while accounting for other possible sources of missing interactions. Thus, our results bridge two points of view: forbidden links are real and potentially important for community structure (Santamaría & Rodríguez-Gironés 2007), but to understand their strength it is important to see them through a probabilistic framework (González-Varo & Traveset 2016).

Furthermore, we show that the prevalence of exploitation barriers is not constant but varies over space, depending on how species trait distribution changes. We found that, on average, plant corollas are much longer than hummingbird bills at lower elevation, leading to many forbidden links. In the Atlantic forest networks, the higher occurrence of forbidden is due to the occurrence of long-tubed flowers of Bromeliaceae in lowlands South America. In contrast, at high elevation most of the plant species have relatively short corolla flowers, leading to a decrease in the proportion of forbidden links across elevation. This gradient of flower size over elevation could be due to the fact that large flowers have a strong physiological cost at higher elevation, such as water loss (Galen *et al.* 1999). Thus, the cost-benefit balance of producing large flowers could change over elevation (Galen 1999), which can be partially driven by pollinators (Basnett *et al.* 2019; Dalsgaard *et al.* 2009).

Last but not least, we found that these forbidden links strongly decreased the robustness of the community to local extinction. Several previous studies have highlighted that robustness to local extinction is determined by the ability of species to rewiring the interaction lost because of the extinction (Kaiser-Bunbury *et al.* 2010; Ramos-Jiliberto *et al.* 2012; Sheykhali *et al.* 2020; Vizentin-Bugoni *et al.* 2020). Consistent with these results, we also found that network robustness strongly increases as interaction rewiring increases (Fig. S5). However, in the presence of forbidden links rewiring is partially constrained, resulting in a decrease in robustness regardless of the rewiring rate. Thus, relying on interaction rewiring to buffer the effect of local extinctions due to global change might be a dangerous bet, since rewiring could be more limited than previously expected because of these forbidden links.

It is important to note that we studied forbidden links in terms of mutualistic interactions because we excluded cheating interactions in which hummingbirds pierce the corolla or use

an existing hole to rob the nectar. These interactions can allow species to have access to unavailable partners (Duchenne *et al.* 2023; Rojas-Nossa *et al.* 2016), and thus blur the limit between forbidden and possible interactions. However, these interactions are likely to be antagonistic rather than mutualistic because plants pay the cost of nectar production but do not get pollinated, suggesting that these interactions remain forbidden for mutualism.

Moreover, what we call forbidden links mainly makes sense when focusing on ecological dynamics only. When including evolutionary dynamics, forbidden links would be temporarily forbidden only because species traits can evolve through time. One of the next important steps would be to assess the evolutionary lability of forbidden links and to understand how they shape eco-evolutionary dynamics of natural communities. However, regardless of their evolutionary lability, our study shows that on ecological time scales forbidden links appear to be common and decrease community robustness to species extinctions, thus increasing their fragility to the increasing rates of local extinctions and colonizations (Dornelas *et al.* 2019).

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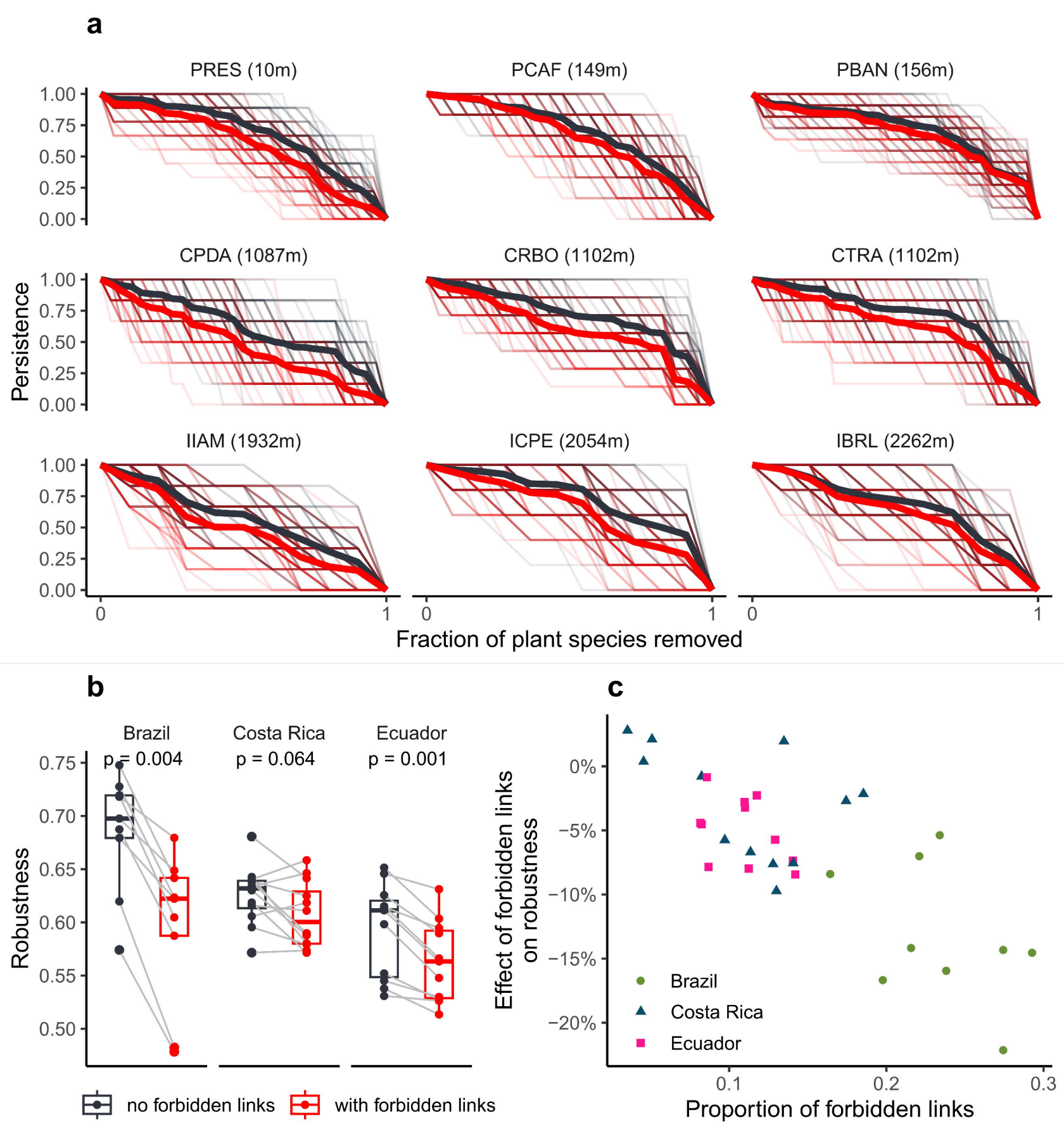
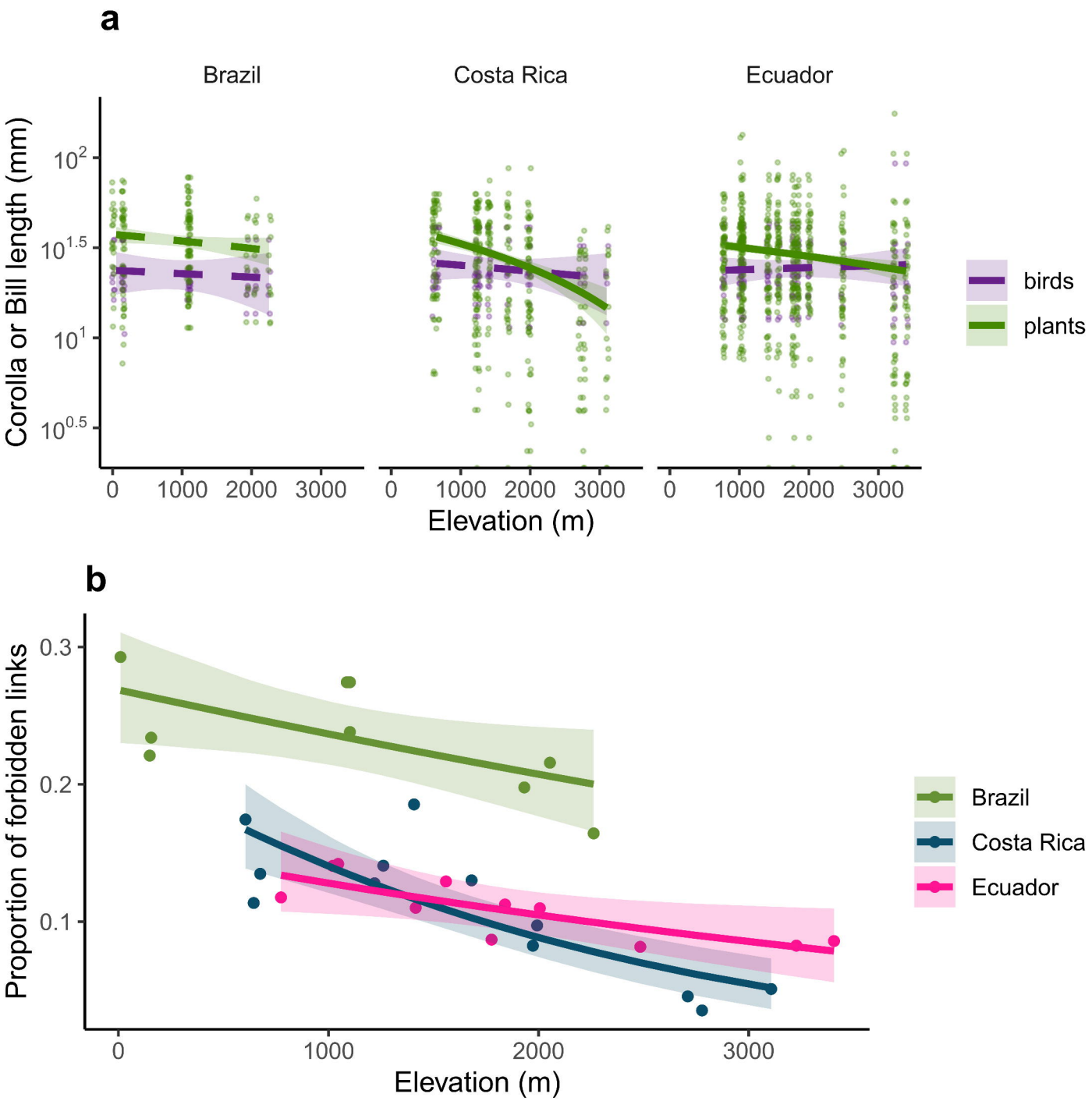
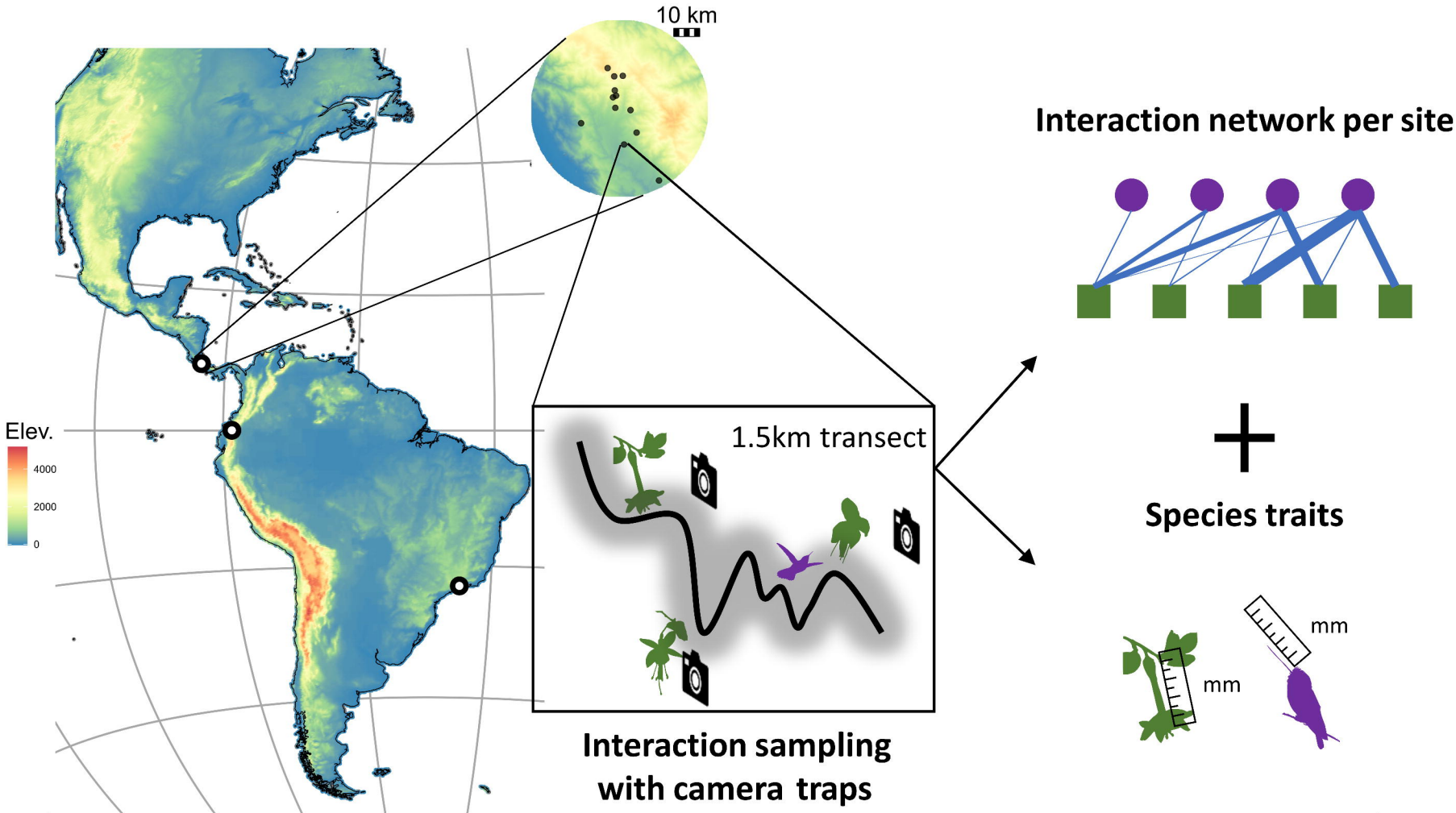

a
PRES (10m)
PCAF (149m)
PBAN (156m)
CPDA (1087m)
CRBO (1102m)
CTRA (1102m)
IIAM (1932m)
ICPE (2054m)
IBRL (2262m)
Persistence
1.00
0.75
0.50
0.25
0.00
0
1
Fraction of plant species removed
b
Brazil
p = 0.004
Costa Rica
p = 0.064
Ecuador
p = 0.001
Robustness
0.75
0.70
0.65
0.60
0.55
0.50
no forbidden links
with forbidden links
c
Effect of forbidden links on robustness
0%
−5%
−10%
−15%
−20%
Brazil
Costa Rica
Ecuador
0.1
0.2
0.3
Proportion of forbidden links


a
Brazil
Costa Rica
Ecuador
Corolla or Bill length (mm)
10^2
$10^{1.5}$
10^1
$10^{0.5}$
0
1000
2000
3000
Elevation (m)
birds
plants
b
Proportion of forbidden links
0.3
0.2
0.1
0
1000
2000
3000
Elevation (m)
Brazil
Costa Rica
Ecuador



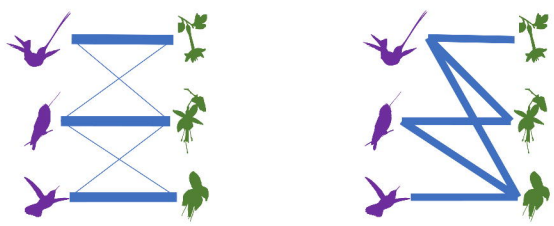
1) Are there exploitation barriers between hummingbirds and plants?

Hierarchichal Bayesian model

$$P(A|B) = \frac{P(B|A)(A)}{P(B)}$$

Linkage rules:

Trait complementarity | Exploitation barrier



2) How do trait distribution vary over elevation?

Linear models

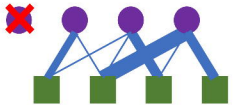
Species turnover can lead to change in average trait value

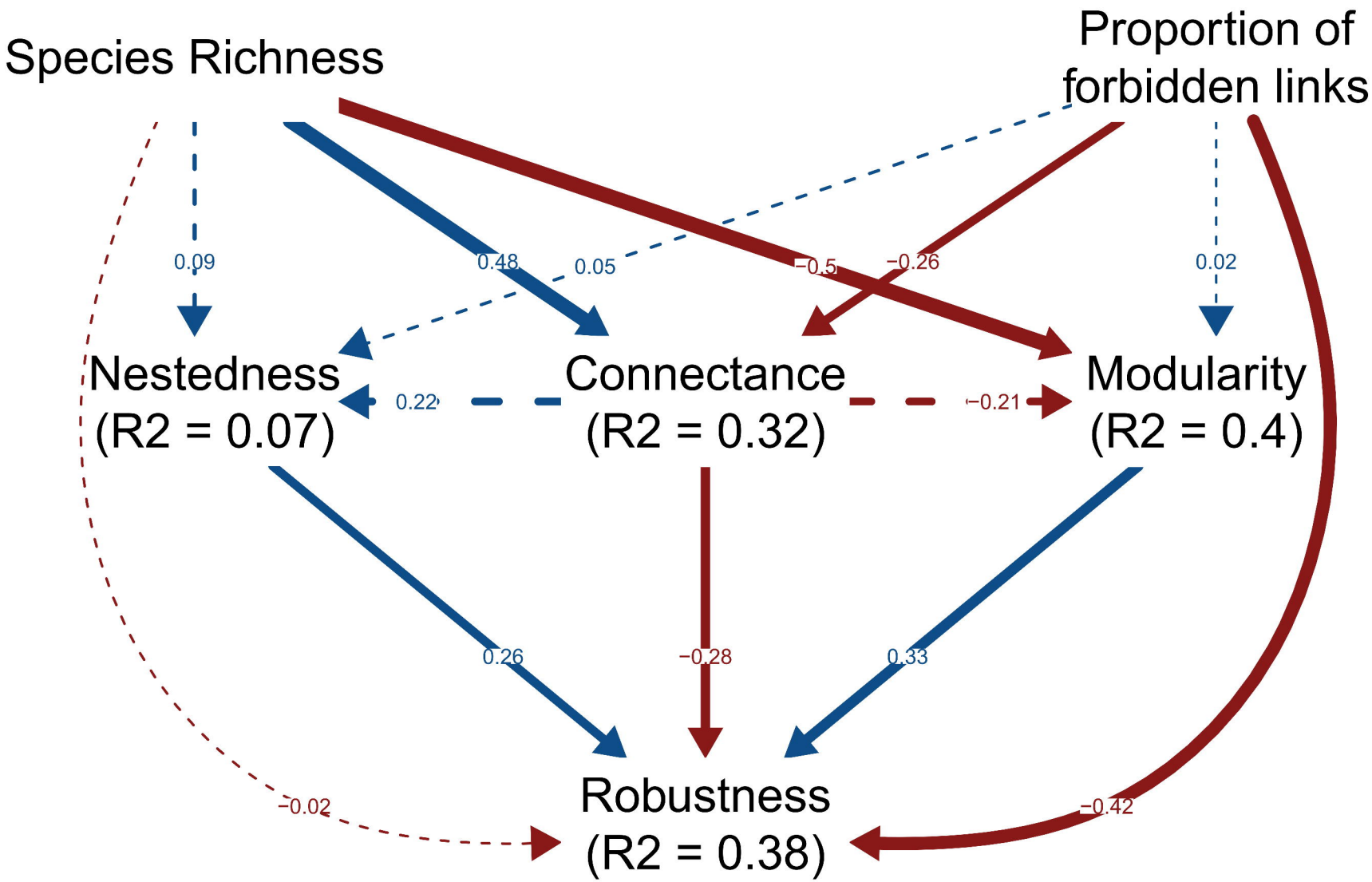
3) How do exploitation barriers and trait distributions affect network robustness?

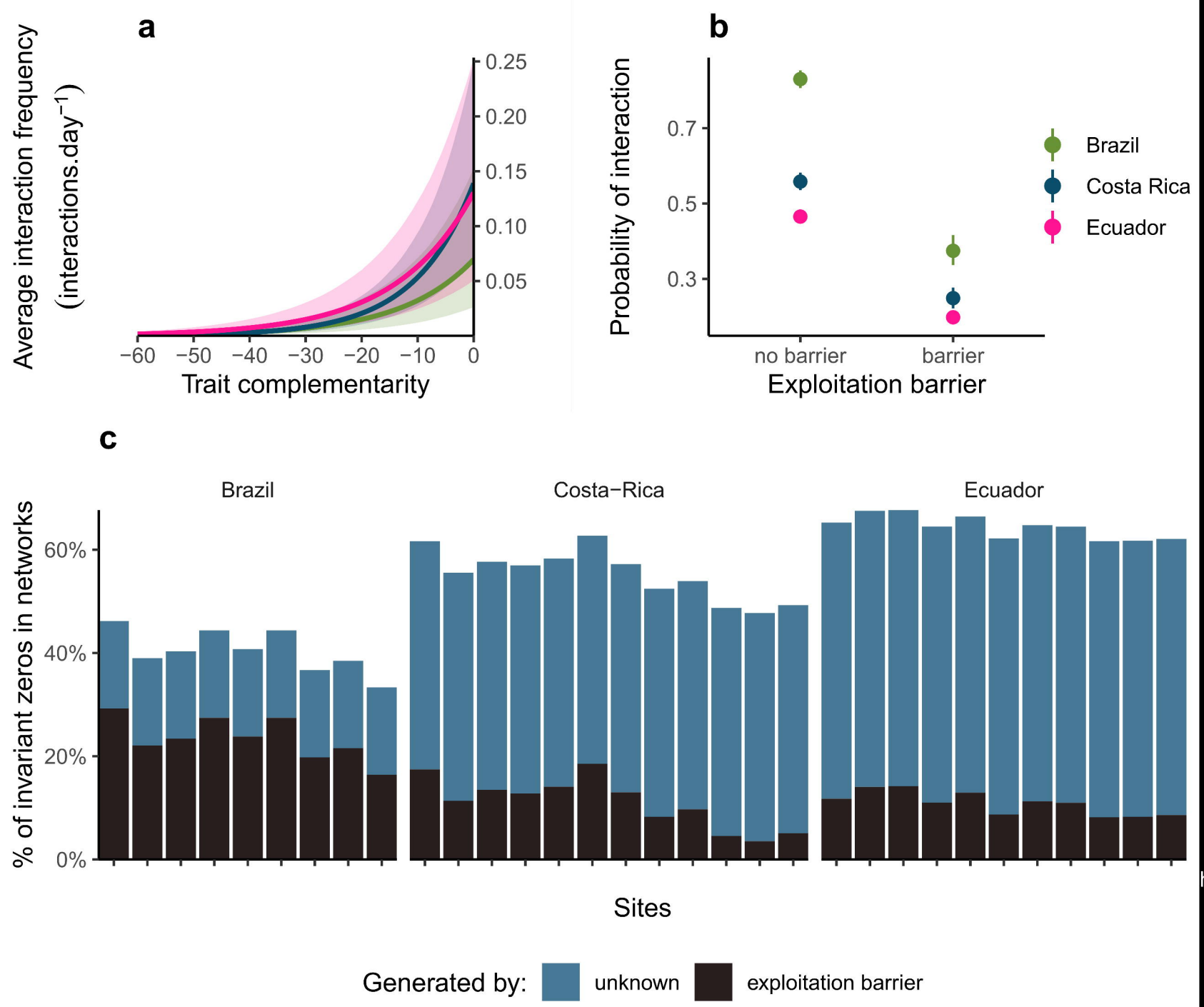
Simulations

Primary extinction

Inter. rewiring
Sec. extinctions




Species Richness
Proportion of forbidden links
0.09
0.48
0.05
−0.5
−0.26
0.02
Nestedness (R2 = 0.07)
0.22
Connectance (R2 = 0.32)
−0.21
Modularity (R2 = 0.4)
0.26
−0.28
0.33
−0.02
−0.42
Robustness (R2 = 0.38)


a
Average interaction frequency
(interactions.day^{-1})
0.25
0.20
0.15
0.10
0.05
−60
−50
−40
−30
−20
−10
0
Trait complementarity
b
Probability of interaction
0.7
0.5
0.3
no barrier
barrier
Exploitation barrier
Brazil
Costa Rica
Ecuador
c
Brazil
Costa−Rica
Ecuador
% of invariant zeros in networks
60%
40%
20%
0%
Sites
Generated by:
unknown
exploitation barrier