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RESEARCH ARTICLE

Deforestation alters species interactions

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Abstract

Interspecific interactions are a major determinant of stability in ecological communities and are known to vary with biotic and abiotic conditions. Deforestation is the primary driver of the ongoing sixth mass extinction, yet its effect on species interactions remains largely unexplored. We investigate how deforestation affects species interactions using a complex systems model and a co-occurrence dataset of 363 bird species, observed across 134 sites, from 5 regions across the Brazilian Atlantic Forest totalling 27,226 interactions. Both theoretical and empirical results show that interspecific interactions vary non-monotonically with forest cover and are more positive than average in areas with higher forest cover, and to a lesser extent in highly deforested areas. Observed differences in interactions reflect both species turnover and changes in pairwise interactions. Our results point to changes in stability across the gradient of deforestation that may lead to varying community resilience to environmental perturbations.

Key Interdisciplinary Aspects

- Species interactions are expected to vary due to the biological, chemical and physical changes caused by deforestation on their local environment.
- We use a mathematical complex systems approach, as well as ecological data, to show that species interactions are more positive in highly forested areas.
- We propose that the alteration of species interactions caused by deforestation will affect the stability of communities and their resilience to future perturbations (e.g. climate change).

KEYWORDS
complex systems, deforestation, ecological communities, habitat loss, species interactions

INTRODUCTION

Species and ecological communities are experiencing high levels of environmental change and subsequent population decline as a result of anthropogenic activities.[1–4] Although many studies have observed a decline in biodiversity associated with anthropogenic disturbances, such as habitat loss and fragmentation, its effects on species interactions and, specifically, intra-trophic interactions remain poorly understood (although see Ref. [5]). Interspecific interactions are a key component determining the assembly and richness of ecological communities, ultimately ensuring their stability.[6,7] Changes to the magnitude and sign (i.e. positive or negative) of interactions among organisms have been shown to destabilise communities, potentially leading to shifts in species abundance and composition.[8,9] As such, identifying if and how interspecific interactions respond to environmental change is vital when considering the long-term stability of ecological communities and their associated populations in this rapidly changing world.

Ecologists have long studied how interactions vary across gradients, specifically abiotic gradients, such as altitude, temperature and soil composition.[10–12] Most of this literature has focused on sessile organisms,[13,14] finding that interactions become more positive (facilitation and mutualism) as environments become more stressful.[10,13,15,16] This phenomenon known as the stress gradient hypothesis[17,18] is well studied and generally accepted in sessile organisms, however, whether it also applies to mobile organisms is less clear. [14,17] Interactions between species have also been found to vary temporally, spatially and with the presence, absence and density of other species, though the sign and magnitude of this variation are unclear.[12,19–23]

The interactions exerted upon an individual, population or species can change in two ways: through the addition or removal of interactions or via shifts in existing interactions.[12,24] The addition or removal of interactions is a relatively simple concept and most commonly occurs due to species turnover when species join or disappear from a community.[24] Shifts in existing interactions between pairs of species can be more complex and difficult to study, but there are examples describing these changes in the literature.[10,12,23] For instance, some shifts in inter- and intraspecific interactions result from changes in population density, and generally, interactions become more negative (competition) as population density increases.[25,26]

Habitat loss is one of the most significant drivers of biodiversity loss.[3,27] Despite this, research into its effects on interactions between species has been surprisingly scarce, with the majority of research focused on the effect of deforestation on food webs (Refs. [28–30]; though see Ref. [31]). A number of factors already known to shift species interactions are associated with deforestation, including abiotic changes, such as reduced humidity and increased soil erosion,[32,33] changes in the quantity and type of resources[34] and species turnover.[24] However, these factors can influence species interactions in different directions, and thus, the overall effect of deforestation on species interactions remains unclear. For forest-dwelling species, deforestation reduces the resources available[35] and causes a "crowding effect",[36] both of which likely increase competition resulting in more negative interactions between species.[26,34,35] Contrastingly, abiotic changes associated with deforestation such as increased humidity and increased frequency of extreme weather events[32,37] can create a stressful environment for forest-dwelling species, and as described above, stressful conditions have been linked to more positive interactions.[14,17] Deforestation can also lead to changes in species composition due to removal of shelter, nesting sites and foraging substrate[38–40] that will affect interactions via the addition and removal of species as well as changing the interaction types and strengths among species.[22]

Here we look to assess the effect of deforestation on intra-trophic interactions between species using an empirical dataset and a Complex Systems modelling approach. We expect interactions to vary both as a result of the loss and gain of interactions via community turnover, and interaction changes between existing pairs of species. We expect the latter to be driven by behavioural shifts caused by alterations in resource availability which we expect to cause more negative interactions in heavily deforested areas. We chose to use a joint empirical and modelling approach to increase the reliability of results as the accuracy of methods used to infer interactions from empirical datasets is relatively unknown. Additionally, corroborations of models of empirical results suggest that findings are generalisable and not specific to the dataset used.

METHODS

Tangled Nature model

The modified Tangled Nature Model (hereafter known as "TaNa model") used in this study is similar to that described by Brinck,[41] in that it is a short-term spatially explicit version of the original TaNa developed by Christensen et al. (2002). The TaNa model integrates an approach of complex systems on ecological communities, whereby the properties of the community at the macroscopic scale emerge from the interactions and movement of individuals at the microscopic scale. The dynamics of the TaNa model used in this study are in many ways similar to that of a neutral model, in that they are individual-based and stochastic. Though, unlike a neutral model, the survival of individuals and, therefore, populations is highly influenced by interactions with cohabitants and the environment. Previous studies have shown that the TaNa models accurately recreate realistic ecological results, including species–area relationships, trophic networks and species abundance distributions.[42–44] An overview of the TaNa model and detailed descriptions of the modifications implemented in our version are given below.

Overview of TaNa model

Landscape

A landscape of 75 equally sized grid cells (15 × 5) was used, in which individuals were able to move up to a maximum dispersal distance of 2 cells at each time step. This size of landscape was used to ensure there were enough cells to create heterogeneous landscapes, whilst being computationally viable. Cells are able to exist in two states: forested or deforested. To start, all cells were created as forested (100% forest cover landscape), but at time t_0, we simulated deforestation by replacing a predetermined number of forested cells with deforested cells (0%–90% forest cover landscape).

Habitat type (forested or deforested) influenced the probability of reproduction differently depending on an individual's specialism value (see Equation 4).

Species traits

TaNa model set-up includes a species pool of 50 species, with each species differing in 2 distinct traits: specialism and interactions with other species in the pool. In our study, we generated pools of 50 species for each run, as this was comparable to the number of species found per site in the empirical studies. Specialism is defined a priori by a parameter randomly drawn from a uniform distribution with values between 0 and 1, where 0 represents a habitat generalist species, and 1 represents a complete habitat specialist species (in our case, a forest specialist). The specifics of how a species' specialism value affects its chance of reproduction can be seen in Equation (4), but essentially, a species with a high specialism value will have higher fitness in a forested area than one with a low specialism value (all else being equal). Conversely, the fitness of the same high specialism species will be more heavily reduced in a deforested area than a comparable low specialism species.

Interactions between species are defined a priori and stored in a matrix J of dimensions $M \times M$ where M is the total number of species S in the species pool. Every species interacts with every other species, via the interaction link $J(S^\alpha, S^\beta)$ with reciprocal interactions between species equal $J\ (S^\alpha, S^\beta) = \ J(S^\beta, S^\alpha)$ to most closely resemble interactions on a single trophic level. Interactions between species are randomly drawn from a normal distribution constrained between -1 and $+1$ with a mean of 0 to match the findings of Wootton and Stouffer[45] that weak interactions are common, and strong interactions are rare. For instance, an interaction value of 0.3 would represent a relatively weak positive interaction. Full details of how interactions affect the probability of an individual reproducing can be found in Equations (1)–(3), but for simplicity, positive interactions increase, whereas negative interactions decrease the fitness of an individual.

The strength of interactions acting upon an individual at time t is given by

$$J_f\ (S^\alpha, t) = \sum_{S \in S} \frac{J\,(S^\alpha, S^x)\, n_f\,(S^x, t)}{N_f\,(t)} \tag{1}$$

where $J(S^\alpha, S)$ is the interaction link between S^α and species S^x, which represents any species, $n_f(S^x, t)$ is the number of individuals of species S^x in grid cell f at time t and $N_f(t)$ is the total number of individuals in cell f at time t.

Model dynamics

TaNa model simulated four dynamic processes: death, migration, immigration and reproduction. At each time step, these dynamics are run sequentially cell by cell, starting from cell 1, completing 50 iterations of each dynamic per cell.

Description of each dynamic in each cell and iteration

I. Death: An individual is randomly chosen and removed from the cell with a constant probability of 0.15; a value used in previous TaNa studies and shown to have minimal impact on the model outcome.[46,47]

II. Migration: An individual is randomly chosen from the cell and moved to another cell up to its maximum dispersal distance (maximum dispersal distance of two). The probability that an individual will migrate is defined by a density-dependent function, whereby the probability of migration increases as the population density of a cell increases; for full details see Brinck.[41]

III. Immigration: An individual selected randomly from the initial pool of 50 species is introduced to the cell with a probability of 0.05 before deforestation and 0.001 after deforestation. The high level of immigration before deforestation ensured a good initial distribution of species through the landscape (every species had on average 25 attempts to immigrate into each cell during this period), whereas the lower level of immigration after deforestation was chosen to represent less frequent immigration in more deforested areas (species had on average 2 immigration attempts into each cell during this period).[48]

IV. Reproduction: an individual is randomly chosen and reproduces with probability $P_{\text{off}}P_{\text{off}}$, which is defined as follows:

$$P_{\text{off}}\ (S^\alpha, t, f) = \frac{\exp\left(\Xi\,(S^\alpha, t, f)\right)}{1 + \exp\left(\Xi\,(S^\alpha, t, f)\right)} \in (0, 1) \tag{2}$$

where the reproductive capability Ξ is given by

$$\Xi\ (S^\alpha, t, f) = \omega_J\, J_f\,(S^\alpha, t) + \mu - \frac{N_f\,(t)}{R_f} \tag{3}$$

where R_f is the carrying capacity of cell f(set to 10), ω_J is the weighting of interactions (set to 10) and the habitat effect μ is given by

$$\mu\ (S^\alpha, t, f) = \pm\omega_s\, C\,(S^\alpha) \tag{4}$$

where μ is positive when species S^α is in a forested cell f and negative when S^α is in a deforested cell f, $C$is the specialism value of S^α and ω_s is the weighting of specialism (set to 4). Cells deforest at the predetermined time $t0$, so the sign of μ is dependent on t.

To bring the above equations into an ecological context, interactions act between an individual and all other individuals in the same cell, with positive interactions increasing the probability of reproduction, whereas negative interactions decrease this. Multiple interactions between individuals of the same species have an equal effect on an individual's probability of reproduction, though the probability of reproduction does decrease as the population of cells increases, which ensures populations cannot grow indefinitely and mimics a shared limiting resource (e.g. space). Specialism acts independently of interactions and always increases the probability of reproduction in forested cells, whereas decreasing it in matrix cells. A species' specialism value defines to what extent its probability of reproduction is affected by its presence in the forest or matrix. For example, a species with a specialism value of 0.9 would have a large increase to the probability of reproduction in a forested cell, but a large decrease in a matrix cell, whereas a species with a specialism value of 0.001 would have a near identical probability of reproduction in a forested or deforested cell.

Model Set-up and output

We defined 80 different species pools, each formed by 50 species varying in their specialism and interactions. At model set-up, every cell was populated by 100 individuals of randomly assorted species; the initial population size was chosen for computational efficiency and has no bearing on the final community. For each species pool, 11 model scenarios were run to represent varying degrees of deforestation (occurring at time $t0$) and ranging from 0% to 100% at 10% increments. In total, we ran 880 models. For comparison with an empirical dataset, the 80 species pools could be considered broad study regions with the 11 landscape scenarios representing discrete sampling units (Figure 1).

All models were run for 2500 time steps, with deforestation after 500 steps ($t0 = 500$). We evaluated the following model output: The occurrence of each species in each cell at $t = 2500$ and for all species with at least 10 individuals present in the landscape, we extracted interactions from the matrix J.

Empirical data

Data collection

We used bird occurrence data from five independent studies conducted in different regions of the Brazilian Atlantic Forest (Table S1, Figure 1). The Brazilian Atlantic Forest is characterised by heterogeneous abiotic conditions, and elevation, encompassing tropical and subtropical climatic conditions, annual rainfall ranging from 1000 mm to 4000 m and elevation changes from 0 to 2900 m. The vegetation structure is also varied, including areas of tropical rainforest, as well as deciduous, *Araucaria* pine and Lauraceae-dominated forests.[49] All five studies were conducted in ombrophilous forest at elevations varying from 100 to 900 m. Each study provided point counts of bird species in multiple forest patches which differed in size, each of which we refer to as a site (range 14–36 sites per study). Sites varied in the amount of surrounding forest cover, as well as the land use of the matrix in which they were embedded in: pasture, agriculture and silviculture. Each study differed in sampling effort and observers, but these variables were controlled for within the studies. In total, occurrence data on 363 bird species were gathered across 134 sites (Table S1).

The percentage forest cover of each site calculated at a 600m radius was taken from Ref. 50, each of these 600 m radius areas around sites can be thought of as equivalent to the full 75 cell landscape of the TaNa. Forest cover was calculated from the highest definition map available for each site, and a mixture of QuickBird, WorldView, SOS Mata Atlântica and Instituto Florestal was used. In each of these maps, forest cover included primary, secondary and semi-natural forest types. A buffer size of 600 m was used as it captures the relatively restricted movement of most species in the studies,[51] better reflects the sampling design of the original studies and is similar to that used in other studies.[52,53]

Defining empirical interactions

Six methods for inferring interactions from co-occurrence data were used to estimate pairwise interactions from the point count data from the five empirical datasets from the Brazilian Atlantic Forest: correlation, partial correlation, GLMs, graphical lasso on log-transformed counts, Gaussian copula graphical models and Gaussian copula graphical models with forest cover as an environmental variable. All methods were run in R 4.0.3 (R[54] following the methodology used in Harris[55] for correlation, partial correlation, and GLMs; the methodology used in Popovic et al. (2019) for graphical lasso on log-transformed counts and Gaussian copula graphical models).

Specifically, correlations were estimated using the cor function in base R, which finds the sample correlation between species presence–absence matrices, which summarises their marginal association. Using the corpcor package,[56] partial correlation is closely related to linear regression and summarises species conditional relationships. The GLM method includes the use of regularised logistic regression models which were run in base R, where the presence of a species is predicted using the presence or absence of the other species. This method produces two near-identical interaction estimates which were averaged to produce a single-interaction term between species pairs. Graphical lasso on log-transformed counts used the glasso package[57] which estimates a sparse inverse covariance matrix using a lasso penalty; for full details, see Ref. [58]. Lastly, the ecoCopula approach was carried out using the ecoCopula package[59] and uses Gaussian copula graphic models, which look at direct and indirect associations in data (in our case species); see Popovic et al.[59] for full details.

These methods were chosen because they either performed well in previous studies[55,59] or in our own performance tests where we compared known interactions in the TaNa to inferred interactions using the aforementioned methods (Table S2). Other methods such as Markov networks[55] and Markov random fields[60] could not be tested due to data limitations; our data contained too many species for Markov networks to be computationally viable and many rare or extremely common (but not ubiquitous) species which caused errors when running Markov random fields.

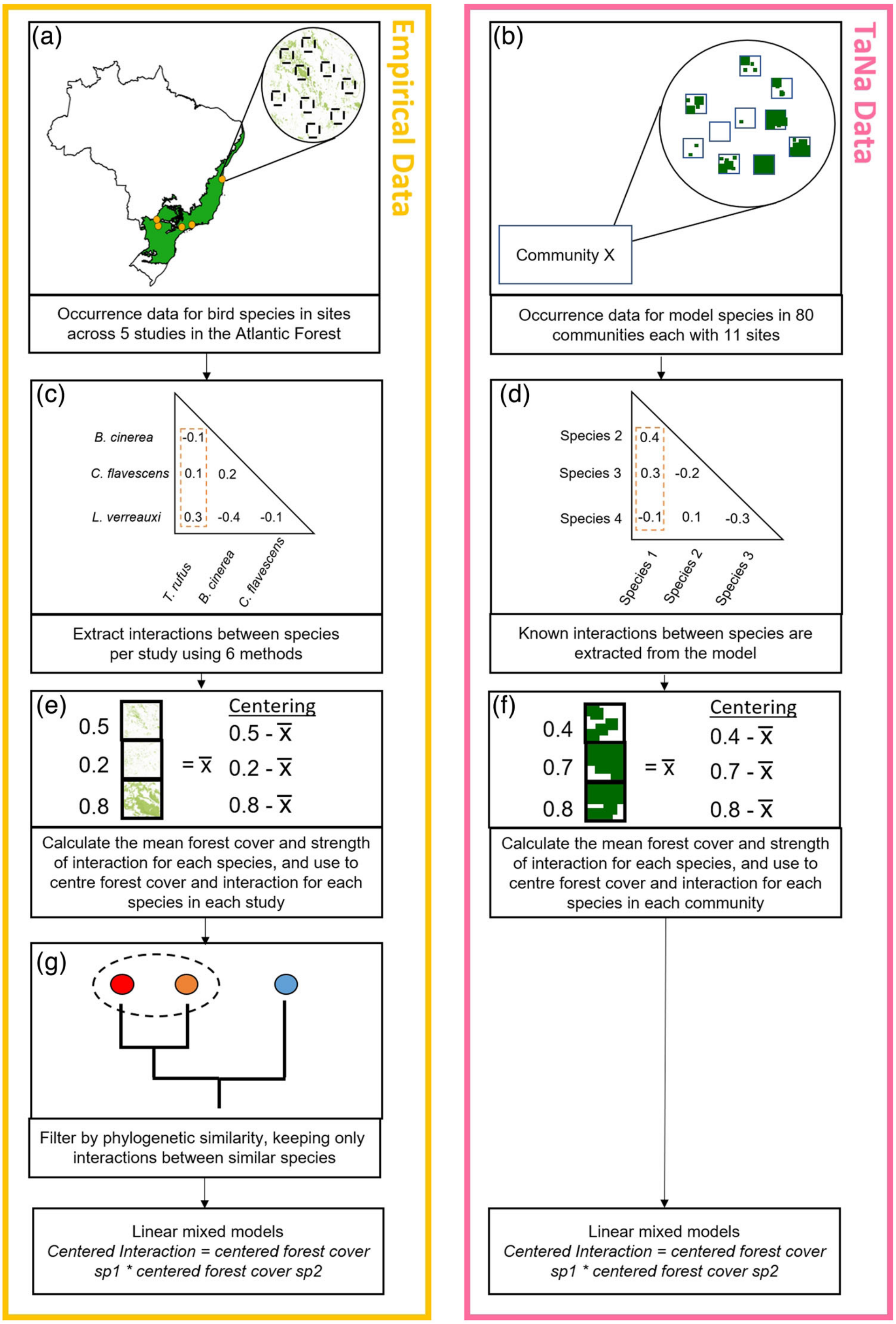

FIGURE 1 Methodological framework used: (a) Locations of the five studies from the Atlantic Forest; (b) visualisation of the 11 landscape scenarios run in TaNa models for each community; (c and d) triangular matrix of example interactions from the empirical and TaNa model data; (e and f) calculate the mean interaction and forest cover for a species in the empirical and TaNa model data, then use this value to centre the forest cover and interaction for each species and species pair by subtracting the mean (figure shows forest cover as an example); (g) filtering of interactions to keep phylogenetically similar interactions (red and orange circles), and removing phylogenetically dissimilar interactions (blue circle).

All methods estimate reciprocal pairwise interactions meaning they cannot accurately represent interactions between trophic levels (e.g. predation ±), but outputs were on different scales, and most were found to differ significantly when analysed using a GLM and post hoc comparison in emmeans[61] (Figure S1). However, all showed significant positive correlations (mean $R^2 = 0.69$, SD $R^2 = 0.18$) indicating that methods generally identified the same interactions as more or less positive. Thus, for comparison, all estimates were re-scaled between −1/+1 using the largest absolute value for each method across all studies as the upper and lower limits. Then, we calculated the mean interaction across methods for each pair of species in each study.

Data preparation

Empirical and TaNa model data

Empirical data and TaNa model outputs both describe pairwise interactions in different sampling units (studies/landscapes), for which the forest cover of sites and landscapes is known or defined, and both were prepared for analyses following the steps below.

Centring forest cover and interactions

We are interested in assessing relative interaction changes as a result of the forest cover a species is found in. However, species naturally occur in different levels of forest cover, meaning that a study with 70% forest cover could be a "deforested" area for a species found primarily in fully covered areas, but a forested area for a species found primarily in areas with 20% forest cover. As such, in order to compare shifts in interactions with forest cover across species with varying forest cover requirements, we centred forest cover for each species, which gave us a relative measure of whether the species was in a higher or lower forest cover area compared to its average (hereafter references to "higher" or "lower" forest cover or interactions are relative to the species average).

In the empirical dataset, centred forest cover was calculated by first finding the arithmetic mean forest cover of a species found across all sites of all studies. Then for each study, the mean forest cover a species was found in was calculated, and the previously calculated overall forest cover means for that species was subtracted from the study mean. In the TaNa model data, species are not comparable across communities, so all centring was done within communities. As such, centred forest cover was calculated by taking the mean forest cover across all landscapes a species occurred in, and then subtracting that from the forest cover of each individual landscape a species occurred in (Figure S2). Similarly, interactions were also centred for both the empirical and TaNa model data using the same methods but calculating the mean interaction a species was involved in across all studies or landscapes, and then subtracting that from each individual interaction a species was involved in (Figure S2). In the empirical dataset, interactions between the same pairs of species were also centred by calculating the mean interaction that the specific pair of species were involved in and subtracting that value from each individual interaction between that pair of species. After doing this, for each pair of species interacting, we had a centred forest cover for species 1 and 2 (where species 1 was the focal species in the analyses), centred interaction and centred pair interaction.

Phylogenetic filtering for the empirical data

The empirical dataset produced 121,996 pairs of interactions based on co-occurrence, but we focused our analyses on intra-trophic interactions due to the limitations of reciprocal inferred interactions by the co-occurrence methods, and to those species more likely to represent significant ecological interactions. We defined these as interactions between species with more shared evolutionary history, which has been found to closely correlate with shared traits and ecological requirements.[62] To define shared history, we created a phylogenetic tree representing the 363 unique bird species in the dataset by trimming the open tree of life[63,64] with the R package ape[65] and adding distance using the "compute.brlen" function and GRAFEN method. The distances between nodes of species were examined, and a consistent cut-off distance was chosen based on the visual inspection of distances between known similar species. For example, only interactions between the predatory species *Accipiter striatus* and relatively similar predatory species *Harpagus diodon* and *Ictinia plumbea* were retained. However, interactions between the dove species *Leptotila rufaxilla* and all other dove and pigeon species (e.g. *Columbina talpacoti*, *Claravis pretiosa* and *Leptotila verreauxi*) remained. This identified 8842 closely related pairs of species, composed of 313 unique species from which our dataset described 27,226 pairs of interactions.

We also carried out our analysis without phylogenetic filtering and found qualitatively identical results (Table S5).

Statistical analysis

We first carried out analyses to test the accuracy of the co-occurrence methods at inferring interactions. To do this, we ran the TaNa 159 times and inferred interactions from the results using co-occurrence and abundance versions of the previously discussed co-occurrence methods. We then compared these inferred interactions to the known interactions from the TaNa using simple linear models, extracting the R^2 value as a measure of predictive accuracy. Full details of this preliminary analysis can be found in Supporting Information section.

We used linear mixed effect models for the analysis of the empirical and TaNa model data. A first model analysed all data with centred interaction as the response variable and centred forest cover species 1, centred forest cover species 2 and their interaction as explanatory variables. A second model analysed only data from pairs of species recorded in multiple studies predicting the response variable centred pair interaction by the predictors centred forest cover species 1, centred forest cover species 2 and their interaction. The random effect structure was chosen for each linear mixed model using the methods outlined in Zuur[66] with all models, including random slopes and interaction terms for centred forest cover for species 1 and 2 (equations for full models can be seen in Supporting Information section). All statistical analysis was carried out in R 4.0.3 (R[54] using the lme4 package).[67]

RESULTS

Analysis of empirical and TaNa model data

Both TaNa model and empirical data showed interactions that were more positive than average in landscapes and sites with higher forest

TABLE 1 Coefficient estimates (and standard errors) obtained from linear mixed effect models predicting changes in species interactions as a function of relative forest cover.

Data	Response variable	Centred forest cover species 1	Centred forest cover species 2	Interaction term
Empirical	Centred interaction	0.118* (0.017)	0.109* (0.017)	0.935* (0.075)
TaNa model	Centred interaction	0.088* (0.030)	−0.075* (0.029)	0.829* (0.046)
Empirical	Centred pair interaction	0.057* (0.018)	0.089* (0.017)	0.305* (0.061)

Note: Results marked with an * are significant to $p < 0.05$.

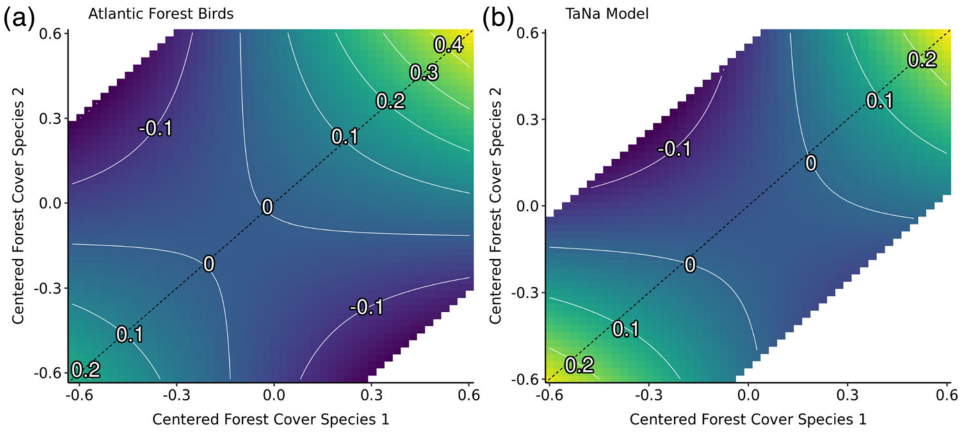

FIGURE 2 Predicted changes in species interaction values (colour gradients reflect predicted centred interaction) as a function of relative local forest cover for interacting species (centred forest cover species 1 and 2) in the empirical (a) and complex system TaNa model (b) datasets. The lowest interaction values occur when forest cover is above average for one species but below average for the other species. Average forest cover varies considerably among species (minimum = 0.06, maximum = 0.99). Regression estimates in Table 1.

cover, with a significant interaction term showing synergetic benefits when both species were in areas with higher than average forest cover (Table 1, Figure 2). Similarly, in both the TaNa model and empirical data, interactions were also more positive than average in areas with lower forest cover, a pattern consistent with the stress gradient hypothesis. This was particularly evident for TaNa model data where the predicted change to interactions was almost equal at comparably higher and lower forest cover.

Changes in TaNa data were solely caused by species turnover because, in this model, pairwise interaction values were defined a priori and could not change over space or time. However, pairwise interaction values in the empirical dataset can also shift within a given species pair, such that two species would have a positive interaction in one region and a negative in another. To evaluate the potential role of interaction shifts within pairs of species across the gradient of deforestation, we analysed only empirical data from pairs of species that appeared in at least two studies together (180 species, 8179 interactions) and found consistent results with more significant positive interactions when both species occurred in higher forest cover areas (Table 1, Figure 3). However, we did not find evidence for higher than average positive interactions between pairs of species at lower levels of forest cover.

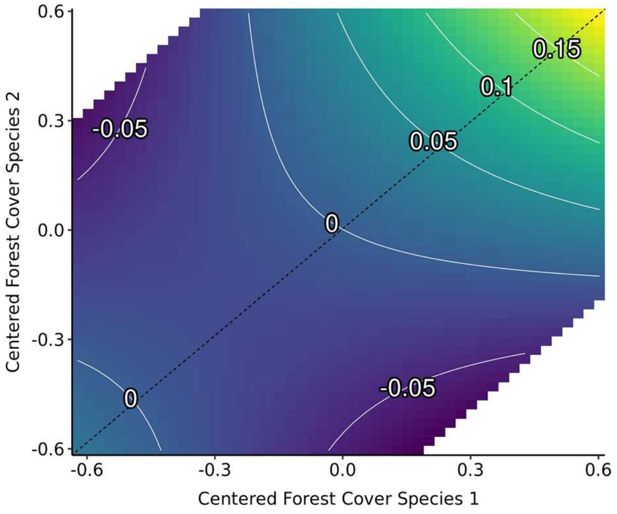

FIGURE 3 Predicted changes in pairwise interaction values (colour gradient reflects values of predicted centred pair interaction) as a function of relative local forest cover for interacting species (centred forest cover species 1 and 2); regression estimates in Table 1.

DISCUSSION

Our results show that species interactions vary non-monotonically between ecological communities distributed along a gradient of forest cover. Both the empirical and TaNa model results showed interactions that were more positive than average in sites where all species are present in areas of higher forest cover. Interactions were also found to some extent to become more positive than average when species were at lower levels of forest cover. We found that shifts towards more positive interactions in higher forested cover areas occurred both due to species turnover and shifts in interactions within pairs of species, which likely arise from changes in competition and behaviour. However, shifts towards more positive interactions in low forest cover areas were primarily due to species turnover. We suggest that ecological communities occurring in areas of higher forest cover are more stable, as they are predicted to have a larger proportion of facilitative interactions, as well as weaker antagonistic interactions. This increased stability will likely mean elevated resilience to ecological perturbations, such as invasive species, removal of species or changes to the abiotic environment.[68,69]

Deforestation was found to alter species interactions via both changes in community composition as well as shifts in interaction strength within pairs of species, as shown in the analysis of the subset of empirical data. Shifts towards more positive interactions in highly forested areas may have occurred due to reduced competition for resources, especially amongst forest specialists, both due to increased resource density and reduced population density.[26] Interaction shifts could also have occurred via benefits from facilitative behaviours such as mixed species flocks, which are expected to occur more frequently in highly forested areas,[70] in which individuals from different species gain fitness by increased foraging efficiency (e.g. disturbing prey species) and decreased mortality from predators (e.g. alarm calling).[71,72]

Competition and flock forming will also be influenced by changes to species composition from turnover. Disturbance-adapted species may appear in deforested areas and outcompete forest specialists, and the prevalence of behaviours such as mixed species flocks will depend on the presence of forest specialists, which are found in higher proportions and abundances, conferring functional redundancy, in areas of higher forest cover.[73–77] Indeed, certain forest specialist species in the dataset analysed such as *Habia rubica* and *Thamnomanes caesius* are known to be vital to the formation and maintenance of mixed-species flocks,[78,79] and their absence from lower forested areas has previously led to the disintegration of such behaviours.[31,80]

Species interactions became more positive at higher forest cover levels across all models. Recent studies on the stability of ecological communities have highlighted the importance of facilitative interactions, finding that network stability increases with higher proportions of facilitative interactions.[7,81] Similarly, a decrease in the strength of negative interactions has been found to stabilise communities under most conditions.[82] For example, Lurgi et al.[81] found that food webs with a high proportion of mutualistic interactions between plants and animals were more stable than their antagonistic heavy counterparts, whereas Qian and Akçay[7] showed that communities with more mutualistic interactions are more resistant to invasion. As such, it is expected that communities composed of species in areas of higher forest, which we found to have more positive interactions, will be more stable.

On the other hand, we found that more negative interactions occur when one species in the interacting pair is in higher levels of forest cover, and the other species in lower levels of forest cover. This may occur when the interacting pair is composed of species with contrasting forest cover requirements. This type of community is expected to exist in intermediately deforested areas, where disturbance-adapted species have colonised, but many forest specialist species still persist due to previous populations.[83] Based on studies by Loreau and de Mazancourt[82] and Lurgi et al.,[81] we would expect this shift towards more negative interactions in these communities to decrease their stability and resilience to further environmental change. However, note that some studies have found stabilising effects of antagonistic interactions, though these are usually focused on food webs as opposed to intra-trophic interactions.[84–86]

The results of the TaNa model dataset, and to a lesser extent, the full empirical dataset suggest an increase in positive interactions at lower forest cover; however, this was very weak in the model analysing interaction changes between pairs of species that occurred together in multiple studies. This suggests that this effect is primarily caused by the loss or addition of interactions via species turnover, and no changes to the existing species interactions per se. A decrease in forest cover is often associated with an influx of disturbance-adapted species and a loss of forest specialist species.[73,75–77] Disturbance-adapted species are often associated with weak interactions and low levels of competition.[45] Our findings suggest that these communities have more positive interactions and are likely to be stable and relatively resilient to environmental changes.[7,69,81]

If we assume species interactions have implications for community stability,[7,69,81] then based on our results, it appears that communities vary in their stability along the gradient of deforestation, and the most stable communities occur in both highly forested and highly deforested areas. We hypothesise that communities in highly forested and highly deforested areas may be in contrasting stable states, whereas communities in intermediary forest cover may exist in long last transitory states[87] (Figure 4). We propose that this occurs as the majority of species in these communities occur at either higher or lower forest cover than their average and are, therefore, predicted to have more positive interactions which provide stability.[81] On the other hand, our findings suggest more negative interactions in intermediately forested areas with mixed species composition (many species found in higher and lower forest covers) due to the influx of disturbance-adapted species and the loss of forest specialist species, which are expected to be less stable.[88]

Stable communities in "degraded habitats" such as highly deforested areas may be seen as detrimental to conservation, as they are likely dominated by disturbance-adapted species.[53,89,90] If these communities are stable, they could be resistant to external perturbation, including restoration efforts, as found in previous studies[91–93]

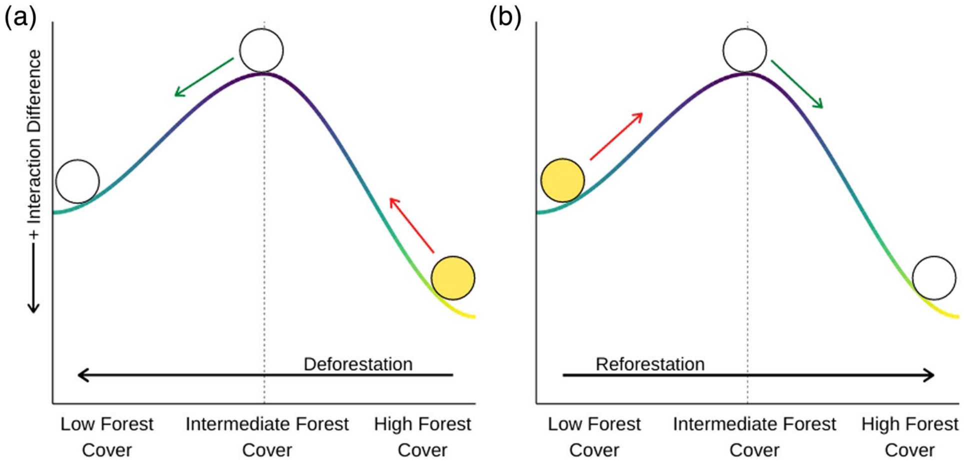

FIGURE 4 Cup and ball diagrams of hypothesized stable states under deforestation (a) and reforestation (b) based on the observed changes in proportions of positive and negative interactions in communities at different relative forest covers shown in Figure 2a. In very highly forested areas, nearly all species will be at, or above, their average forest cover, where we expect an overall shift towards more positive interactions, with a similar, albeit weaker, result for highly deforested areas, where nearly all species will be at or below their average forest cover. On the other hand, we expect the highest proportion of species with contrasting forest cover requirements to occur in intermediately forested areas resulting in a shift towards more negative interactions. Arrow colours represent the hypothesized size of perturbation required to move the community to a new stable state (red = large, green = small). We expect that communities in highly forested and deforested areas to be relatively resilient to environmental changes (deforestation and restoration respectively), whereas those in intermediate forest areas to be comparatively sensitive to them.

(Figure 4). This reinforces the idea that restoration efforts may be better placed in areas of intermediary deforestation, not only because these communities may be less stable, but also due to a lack of source populations in highly deforested areas causing low recolonisation rates and the need for the translocation of species.[53,94,95] Our study further suggests that restoration efforts coupled with species translocation to highly deforested areas may still not be enough, and that translocated species would be unlikely to persist due to the stability and resistance of the established community. Lastly, the observed shift in species interactions as a result of forest cover seen in our study may foreshadow and predict larger community changes in the future, as previous studies have found that interaction loss occurs at a faster rate than species loss.[96]

Recently, methods used to estimate interactions from co-occurrence data have come under severe criticism[97]; however, our own evaluation of these methods against known interactions in the TaNa model provided surprisingly accurate results; five of the six tested methods had R^2 above 0.4 (Table S2). Additionally, previous studies have found that abundance data provide more accurate approximations of interactions[59]; however, we did not find this in our evaluation (Table S3). Although the co-occurrence methods are unlikely to fully capture true interactions, the similarity between our results from these methods and the TaNa provides confidence that we are capturing a true pattern of interaction change. Similarly, although our empirical results are limited to bird species, we consider the results transferable across taxa, as the mechanisms expected to cause the observed interaction changes are universal. Despite this, the study could be built upon in the future by including functional traits for every species, as this may uncover varying trends in how interactions change with forest cover dependent on species niche.[98]

In conclusion, we provide the first theoretical and empirical evidence that interspecific interactions are altered in a predictable manner with varying forest cover. Interactions were consistently found to be more positive when species were in higher forest cover across all datasets and TaNa models, which we believe could confer greater stability and resilience to external perturbations. Species in lower forest cover were similarly found to have more positive interactions, albeit to a lesser extent, and with less consistency across datasets. Future studies predicting community shifts as a result of environmental changes should account for this variation, as should conservation and restoration efforts, which should consider focusing more heavily on restoring areas of intermediate forest cover.

AUTHOR CONTRIBUTIONS

Conceptualisation; formal analysis; investigation; methodology; visualisation; writing – original draft; writing – review and editing: Benjamin Howes. *Methodology; supervision; writing – review and editing*: Manuela González-Suárez and Henrik Jeldtoft Jensen. *Data curation; writing – review and editing*: Luiz dos Anjos, José Carlos Morante-Filho and Alexandre Uezu. *Data curation; methodology; supervision; writing – review and editing*: Cristina Banks-Leite.

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ETHICS STATEMENT

The authors confirm that they have adhered to the ethical policies of the journal.

CONFLICT OF INTEREST STATEMENT

Co-author Cristina Banks-Leite has previously been an editor of Natural Sciences but was not involved in the handling of the peer-review process of this submission.

DATA AVAILABILITY STATEMENT

The data and novel code that support the findings of this study are available on Figshare at https://doi.org/10.6084/m9.figshare.16903246.v1 and https://doi.org/10.6084/m9.figshare.19732966.v1.

PEER REVIEW

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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