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RESEARCH ARTICLE

Including rewiring in the estimation of the robustness of mutualistic networks

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Abstract

1. Species are entangled within communities by their interactions in such a manner that their local extinction may unchain coextinction cascades and impact community dynamics and stability. Despite increasing attention, simulation models to estimate the robustness of interaction networks largely neglect the important role of interaction rewiring, that is, the ability of species to switch partners.
2. Here we propose a new method to incorporate the potential of species to replace lost partners into a widely used coextinction model to estimate network robustness. In this model, species are allowed to rewire their interactions after initial loss of partners according to probabilities derived from well-known mechanisms that determine mutualistic interactions, for example, trait matching, phenological overlap and abundances. To illustrate the use of this method, we analyzed a well-sampled dataset of mutualistic plant–hummingbird interactions.
3. We found that (a) in general, rewiring increases the estimated robustness, (b) networks are similarly robust to the loss of pollinators or plants, (c) morphological matching and phenological overlap leads to higher robustness, (d) when multiple rewiring mechanisms are combined, however, robustness increases little, and (e) rewiring tends to increase robustness more in scenarios when the loss of generalist species occurs first.
4. Our results suggest that the same mechanisms known to drive plant–hummingbird network structure are relevant in buffering the effects of species loss via rewiring. The method proposed here can be applied to a wide range of interaction networks and is flexible to the inclusion of other variables important in determining interactions for specific systems. It also allows changes on the assumptions regarding the importance of distinct mechanisms, for instance including a hierarchical relationship, which facilitates insights into the relative importance of multiple variables influencing network disassembling. The analytical framework we offer here represents a step towards a more realistic estimation on how species loss may affect the integrity of interaction networks.

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KEYWORDS

abundances, bipartite networks, cascading effects, coextinctions, forbidden links, morphological matching, network stability, phenological overlap

1 | INTRODUCTION

What escapes the eye, however, is a much more insidious kind of extinction: the extinction of ecological interactions. (Janzen, 1974)

No species occur isolated in nature, but entangled in multiple interactions with other species that they depend on to different extents. Because species form complex networks of interactions, the loss of one species may have far reaching direct and indirect influences on other species within the community (Eklöf & Ebenman, 2006; Memmott, Waser, & Price, 2004; Paine, 1966). Hence, the extinction of one species affects other species, which may in turn also suffer extinction (Eklöf & Ebenman, 2006; Janzen, 1974; Memmott et al., 2004). In fact, species loss may unchain coextinction cascades and impact community structure and functioning, affecting important ecosystem functions (Colwell, Dunn, & Harris, 2012; Paine, 1966; Symstad, Tilman, Willson, & Knops, 1998; Valiente-Banuet et al., 2015).

Due to increasing habitat loss, species invasions and climate change, high rates of species extinctions tend to become a pervasive phenomenon in most ecosystems (Colwell et al., 2012), affecting critical mutualistic interactions such as pollination (Memmott et al., 2004; Potts et al., 2010). The ability to anticipate effects of species loss on ecological networks and a deeper understanding of coextinction dynamics is crucial to mitigate its effects on biodiversity (Colwell et al., 2012; Kaiser-Bunbury, Muff, Memmott, Müller, & Caffisch, 2010). Models of network robustness, that is, estimating the tolerance of ecological networks to coextinctions, have been widely employed on many different types of interactions (e.g. Bane, Pocock, & James, 2018; Burgos et al., 2007; Eklöf & Ebenman, 2006; Memmott et al., 2004). Several distinct approaches have been developed but the so-called 'knockout extinction models', where the tolerance of networks are estimated using simulated primary extinctions, have become widely used tools (see Bane et al., 2018 and references therein).

Early simulations of coextinctions in interaction networks have mostly assumed that a species must go extinct following the extinction of all partners it is connected to (Burgos et al., 2007; Memmott et al., 2004). Results from these models have led to a notion that mutualistic networks are considerably robust to loss of specialists (i.e. species interacting with few partners), while highly susceptible to loss of generalists (Memmott, Waser, & Price, 2004). However, despite the importance and frequent use of these methods, they rarely consider explicitly the ability of species to 'rewire', that is, switch partners, which is a remarkable feature of ecological networks (Bastazini, Debastiani, Azambuja, Guimarães, & Pillar, 2019; Costa et al., 2018; Kaiser-Bunbury et al., 2010; Poisot, Canard, Mouillot, Mouquet, &

Gravel, 2012; Ponisio, Gaiarsa, & Kremen, 2017; Timóteo, Ramos, Vaughan, & Memmott, 2016; Vizentin-Bugoni et al., 2019), therefore limiting the realism of the simulations. A major obstacle is the integration of rewiring based on the multiple mechanisms that determine species interactions (Bartomeus et al., 2016; Olesen, Bascompte, Elberling, & Jordano, 2008; Vázquez, Blütghen, Cagnolo, & Chacoff, 2009; Vizentin-Bugoni, Maruyama, & Sazima, 2014; Vizentin-Bugoni et al., 2018). The incorporation of relatively simple rules of 'partner switching' into modelling of network robustness indicates that the possibility of reallocating interactions increases the estimated robustness of mutualistic networks to climate change (Schleuning et al., 2016) and to partner loss in small time-scales (Kaiser-Bunbury et al., 2010). However, such modelling approaches do not explicitly incorporate mechanisms known to determine how interactions are organized and that are likely to determine rewiring, such as (a) probability of encounter based on species abundances, (b) trait matching and (c) spatiotemporal overlaps in species distributions (Vázquez, Bluthgen, et al., 2009; Vizentin-Bugoni et al., 2018).

Here we build upon a framework to estimate coextinction rates in interaction networks (Burgos et al., 2007; Memmott et al., 2004) and incorporate species-specific information on traits, temporal occurrence and abundances to derive rewiring probabilities. Specifically, we model network robustness taking into account the possibility of rewiring based on distinct determinants of interaction in the system studied, for example, chance of encounter based on abundances, morphological matching and phenological overlap. We then illustrate its use by estimating the robustness of a well-sampled Neotropical plant-hummingbird pollination network and by comparing the effect sizes of models including distinct rewiring rules to the baseline model which assumes no rewiring. Although we demonstrate this framework using a particular system and specific determinants of rewiring, by allowing multiple user-defined inputs, this framework is broadly applicable to a wide range of mutualistic networks and can be extended to other interaction types.

2 | MATERIALS AND METHODS**2.1 | Study system and the dataset for study case**

In order to illustrate the application of this method, we analyzed a plant-hummingbird network from the Neotropical Atlantic Rainforest. Data were collected along 12,000 m of transects including field trails, dirt roads and forest borders in southeastern Brazil (latitude: -23.2830; longitude: -45.0500). Detailed descriptions of sampling methods and data are available in the study by Vizentin-Bugoni et al. (2016). In summary, the dataset encompasses information on frequencies of plant-hummingbird interactions and, for each species, data on

abundances, phenologies and morphologies. Interactions were sampled monthly over 2 years by observing each species of all flowering plants for around 50 hr, to record and identify hummingbirds visiting flowers legitimately (touching plants' reproductive organs), constituting a potential pollination network. The number of visits recorded was used as a measure of interaction intensity in quantitative networks. Estimation of sampling sufficiency indicates that approximately 82% of the links in the community were detected (Vizentin-Bugoni et al., 2016), which makes this network considerably well sampled in comparison to other networks (Jordano, 2016). Concomitantly, abundances and phenologies of each species in the community were quantified systematically once a month along transects. Plant abundances were defined as the number of open flowers per hummingbird-pollinated species over the study. For Asteraceae inflorescences, each capitulum was counted as a flower. For hummingbirds, abundance was estimated as the frequency of occurrence (proportion of days a species was recorded over the study period regardless of whether they were interacting with plants) which approximates the number of individuals heard or seen along transects, with the advantage of providing abundances' estimate for all species in the community (Vizentin-Bugoni et al., 2014). Phenology was measured as the presence of open flowers or pollinator species every month over the study period. Morphological data (i.e. effective corolla length and bill length) were measured from fresh flowers collected in the field and, for hummingbirds, from specimens in local museums.

2.2 | Measuring robustness while considering rewiring

We here present a metric (named R_w) which represents the simulated rate of coextinctions while allowing species that lost partners the chance to rewire their interactions to surviving partners. This metric builds upon the metric R (Burgos et al., 2007) implemented as the *robustness* function in the R-package *bipartite* (Dormann, Fründ, Blütgen, & Gruber, 2009). R estimates the proportion of species in a trophic level that remains in a bipartite network after sequential extirpations of species in the other trophic level. It assumes that a species goes extinct when all partners to whom it is connected are lost. It is calculated as the area below the Attack Tolerance Curve, which represents the curve of the fraction of surviving species of one trophic level as a function of the eliminated species from the other trophic level. R ranges from 0 to 1, with values closer to 1 indicating higher robustness of the system, meaning that coextinction rates are slower (Burgos et al., 2007). R_w follows the same calculation, differing in that every time a species loses a partner, it is assigned a probability of rewiring its interactions to the persisting potential partners. This probability of rewiring is defined by a set of rules based on mechanisms known to drive interactions – and therefore rewiring – in the system under consideration. Plant–hummingbird interactions have been shown to be primarily influenced by morphological traits and phenologies (Maruyama, Vizentin-Bugoni, Oliveira, Oliveira, & Dalsgaard, 2014; Vizentin-Bugoni et al., 2016). We chose, therefore, to use these variables

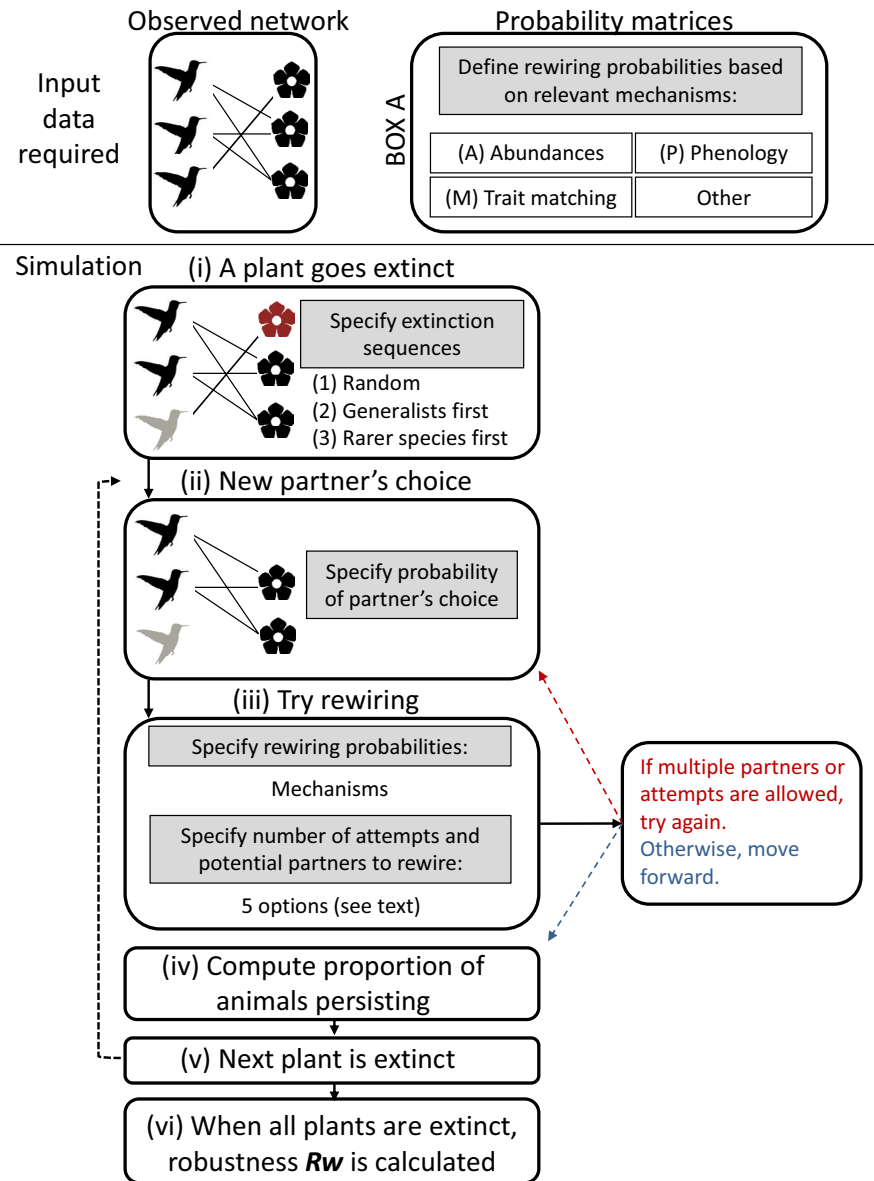
to derive 'probabilities of rewiring' in this study. However, we also included abundance which is an important driver of interactions in other pollination systems (e.g. Vázquez et al., 2009). Because the processes influencing interactions may vary across systems and interaction types, we stress that users should estimate probabilities of rewiring based on the knowledge on the most important processes in their specific study system. The incorporation of rewiring (Section 2.3) and the definition of rewiring rules and rewiring probabilities (Section 2.4) are exemplified as follows.

2.3 | Incorporating rewiring

For estimation of pollinator's robustness to plants loss, for example, the method follows this sequence (see Figure 1 for a schematic representation):

- (i) step i: the first plant goes extinct based on user-defined simulated order of extinctions. The sequential extinction options are (1) at random within the trophic level, (2) from most generalized to least generalized (i.e. based on species' degrees), and (3) from the species with the lowest number of realized individual interactions (i.e. visits) to the species with highest number of interactions ('number of interactions' here is computed as the marginal totals of the observed interaction matrix, which in our case is the sum of all visits performed by a pollinator species on plants, or the sum of all visits a plant received by all pollinators);
- (ii) step ii: each pollinator species linked to the now extinct plant species 'chooses' another plant species from among the surviving species to potentially rewire to. The partners' choice may be random or based on probabilities defined by mechanisms specified by the user (Section 2.4);
- (iii) step iii: once the potential partner is chosen, the probabilities of rewiring will be defined by mechanisms of interest specified by the user (Section 2.4). Subsequently, a binomial distribution defines whether or not rewiring will occur. At this step, the number of attempts to rewire may also be specified by the user: (1) *only one attempt with a single partner*, (2) *multiple attempts with a single partner*, (3) *multiple attempts with multiple independent partners* and the same partner can be chosen more than once, (4) *one attempt with each partner* until the species rewire to one partner or run out of attempts, or (5) *multiple attempts with each partner* until species rewire all interactions or run out of attempts. When multiple attempts are allowed (2, 3 and 5), the number of attempts equals the number of interactions observed between the species and its lost partner. For 3, 4 and 5, the choice of partners follows specification from step ii generating a loop between steps iii and ii for the choice of the next partner. The option for the user to designate the number of partners or attempts at rewiring accounts for the fact that probabilities of interaction and species behaviours may vary across systems which make multiple attempts more or less likely. For instance, nectar may not be of sufficient quantity in the first attempted

FIGURE 1 Illustration of the six steps of the methodological framework to estimate the robustness of mutualistic networks taking rewiring into account. Red = extinct species, grey = species that will attempt to rewire because the partner was lost. Grey boxes are user-defined settings based on the specifics of the study system. In Box A, for example, the mechanisms used to estimate probabilistic of rewiring are based on variables widely recognized to be important for plant-hummingbird interactions



- plant (e.g. large pollinator with high energy demand) so that a pollinator will keep searching for other plants, thereby making multiple attempts (with differing outcomes) a possibility;
- (iv) step iv: once all attempts of rewiring are completed, the proportion of surviving pollinator species is then calculated;
- (v) step v: the next plant is removed and steps (ii), (iii) and (iv) are repeated until all plants are extinct;
- (vi) step vi: once all plants are extinct, R_w is calculated (Section 2.2).

2.4 | Defining probabilities of rewiring based on species data

Probability of rewiring can be derived from any number of variables that influence interactions in a specific system. In this example, we include the determinants known to be important in our

study system: species abundances, phenologies and morphological traits.

Abundance (A): the probability of one species rewiring to another partner is proportional to the relative abundances of the surviving species in the other trophic level, so that a species has higher probability of rewiring its interactions to abundant rather than rarer partners. This assumes that chances of encounter (and subsequent interaction) are governed by species' relative abundances, which is often the case in pollination networks (Simmons et al., 2019; Vázquez, Bluthgen, et al., 2009; Vizentin-Bugoni et al., 2018).

Temporal overlap (P): the probability of rewiring is proportional to the amount of time species co-occur. Specifically in our case, we divided the number of months each pair of species overlap by the total extent of the study (24 months). Thus, a pollinator has a higher chance to rewire to plants with longer flowering periods, and cannot rewire to partners whom it does not overlap temporally. While

the model assumes that temporal overlap is a basic requirement of interaction realization (if species do not overlap, probability equals zero), it also assumes that the resources available over longer periods of time are more likely to be used, as reported for pollination networks (Vázquez, Chacoff, & Cagnolo, 2009; Vizentin-Bugoni et al., 2014).

Trait matching (M): the probability of rewiring is proportional to the extent of matching in traits that are known to influence interactions, such as bill length and corolla depth. We used a modified Gower similarity (Legendre & Legendre, 2012) where the probability of rewiring (P_{ij}) between a pollinator i and a plant j is calculated as the difference between bill length (x_i) and corolla depth (y_j) standardized by the range of values in x and y of all species in the network. Formally:

$$P_{ij} = 1 - \frac{|x_i - y_j|}{\max\{x, y\} - \min\{x, y\}}$$

Thus, partners with similar trait lengths have higher probabilities of rewiring. Trait matching drives interactions via differences in foraging efficiency which is an ultimate consequence of intraguild competition among hummingbirds for floral resources and among plants for pollinators (Bergamo, Wolowski, Maruyama, Vizentin-Bugoni, & Sazima, 2018; Brown & Bowers, 1985; Maglianesi, Blüthgen, Böhning-Gaese, & Schleuning, 2014; Vizentin-Bugoni et al., 2014; Weinstein & Graham, 2017). Thus, this model accounts for the fact that competition tends to drive hummingbirds to use flowers that are similar to their bill lengths (Maglianesi, Böhning-Gaese, & Schleuning, 2015) so that the more similar bills and corollas are, the higher the probability of interactions. In short, long-billed hummingbirds are more likely to interact with longer than shorter corollas, while short-billed hummingbirds are likely to interact with shorter corollas but unlikely to interact with long corollas.

Trait resemblance (T): Here the probability of rewiring depends on trait resemblance within the same trophic level where, for example, a pollinator will have a higher probability of rewiring to plants that interact with other pollinators with similar traits to itself. Because trait redundancy may play an important role in network stability, extinctions are expected to have a small effect on robustness if all species are functionally similar (high trait resemblance), but a large effect if species have different trait values (Fonseca & Ganade, 2001). To derive probabilities, we followed Bastazini et al. (2017), using fuzzy set theory to scale up the trait data from hummingbirds and plants to the network level. Based on within-guild trait similarity, every species in each trophic level defines a fuzzy set to which every species in the same trophic level belongs with a certain degree of belonging, ranging between 0 and 1. Fuzzy membership is defined using a symmetric similarity measure, in our case similarity based on Euclidean distances (Bastazini et al., 2017; Pillar & Orlóci, 1991). The degree of belonging of each species is the element comprised in the fuzzy set matrices, and a high degree of belonging (close to 1) means the species is similar

to other species within the trophic level. Each element of the main diagonal of fuzzy matrix can be interpreted as the self-belonging of a given species to its defined fuzzy set, while the off-diagonal elements of the fuzzy matrix can be read as the cross-belonging of each species in relation to all other species present in that same trophic level (Duarte, Debastiani, Freitas, & Pillar, 2016). The calculated fuzzy matrix is then multiplied by the quantitative interaction matrix in order to estimate the probability of interaction of a species in one trophic level with a species in the other trophic level, weighted by their trait similarities within the same trophic level (further details in Bastazini et al., 2017).

Combined variables: because multiple mechanisms may concomitantly contribute to constraining or facilitating interactions (Vázquez, Chacoff, et al., 2009), it may be relevant to define the probability of rewiring combining distinct variables. This combination may be done by multiplying the probability of rewiring from multiple variables using Hadamard (element wise) product (e.g. Vázquez, Chacoff, et al., 2009).

2.5 | Application of the method on a plant-hummingbird dataset

To illustrate the use of our method, we calculated Rw incorporating distinct drivers of rewiring. We considered each mechanism in isolation (A, P, M and T) or in distinct combinations (AP, AM, AT, MP, TP, AMP and ATP). We did not produce models combining M and T as both refer to distinct ways morphology may influence interactions. As a benchmark for comparison, we also calculated robustness using the classic model where no rewiring is allowed (R). For each of these models we repeated simulations 1,000 times and calculated robustness at the end of each simulation. In order to quantify the magnitude of the increment in robustness for each model, we calculated effect size as $D = \text{mean } Rw - \text{mean } R$ (Borenstein, Hedges, Higgins, & Rothstein, 2009), where Rw is the simulated robustness of each of 1,000 simulations of a specific model, and R is the robustness calculated assuming no rewiring for the same model. Thus, $D = 0$ indicates no increase in robustness and 1 indicates the maximum theoretical increase in robustness. Note that when no rewiring is allowed and the extinction sequence is based on *degree* or *abundance* (methods 2 and 3 in step i, above), only one extinction sequence is possible, except if species are tied in their ranks. In this case, D is calculated based on a single R , rather than the average R obtained from 1,000 iterations.

We illustrate possible variations of our method by manipulating assumptions of the model. Specifically, Rw was estimated for the extinction of animals and plants separately. We also recalculated Rw for multiple scenarios: following three distinct sequences of species extinctions (*step i*; Figure 1): (1) at random, (2) from the species with highest to lowest degrees, and (3) from the species with lower number of realized interaction (i.e. visits) to the one with most interactions. In addition, we specified two distinct criteria for partners' choice (*step ii*; Figure 1): (1) random and (2) based on partners abundances (therefore, in this case 'abundance' is not included as

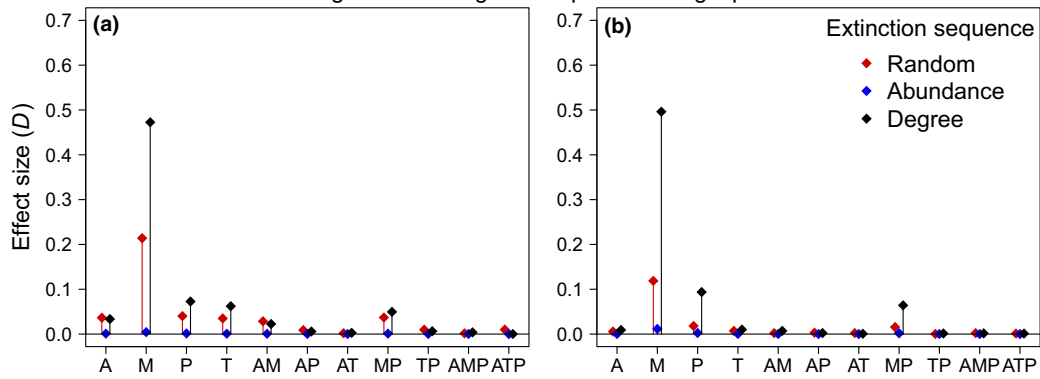


Extirpation of pollinators

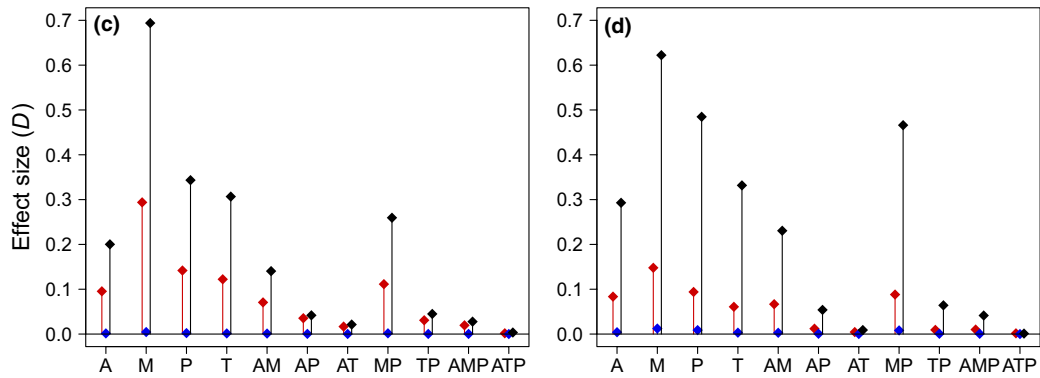
Extirpation of plants



Probability of partner's choice: Random
 Rewiring method: Single attempt with a single partner

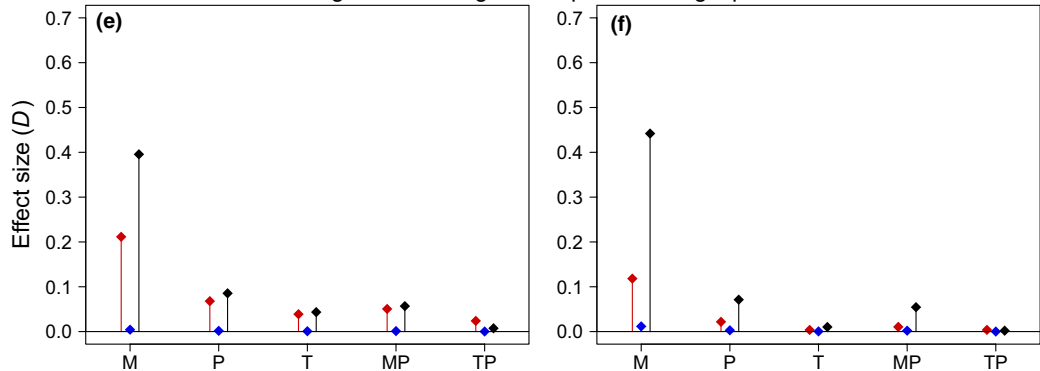


Rewiring method: One attempt with each partner



Probability of partner's choice: Abundances

Rewiring method: Single attempt with a single partner



Rewiring method: One attempt with each partner

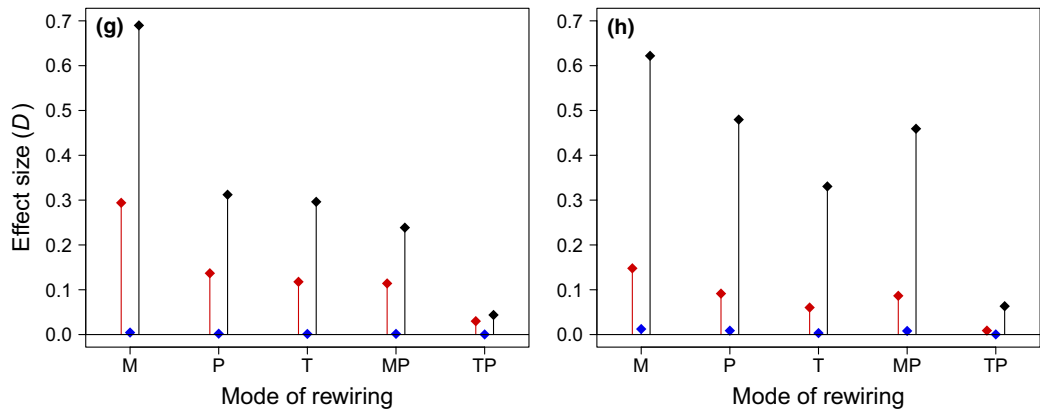


FIGURE 2 Effect sizes representing the increase in robustness, compared to simulations without possibility of rewiring, for each scenario of simulated extinction including rewiring for a Neotropical mutualistic plant-hummingbird network. We simulated separately the loss of pollinators (a, c, e, g) and plants (b, d, f, h). Multiple scenarios were simulated varying in the probability of partners' choice, rewiring method and sequence of partners' extirpation. *Partners' choice* was by random (a, b, c and d) and proportional to partners' abundances (e, f, g and h). *Rewiring method* was a single attempt with a single partner (a, b, e and f), and one attempt with each surviving partner (c, d, g and h). *Sequences of partners' extirpation* was by random (red), from the most to the least generalist (black) and from the least to the most interactive, that is, higher number of interactions (blue). D is calculated as the difference between the mean estimated robustness of the model without rewiring and each model's mean robustness where rewiring is allowed. The larger the bar, the larger the effect sizes (i.e. increase) in robustness

a variable defining rewiring in *step iii*); and, finally, specified two methods of rewiring: assuming only *one attempt* with a *single partner* (method 1 in *step iii*), and assuming *one attempt* with *each partner* until the species rewire to the first partner or run out of attempts (method 4 in *step iii*).

3 | RESULTS

For most scenarios, the estimation of network robustness increased when rewiring was incorporated (Figure 2; Figure S1). However, *distinct mechanisms* had distinct impacts on robustness as revealed by the wide variation in effect sizes among models (Figure 2). Models including M, T and P consistently increased robustness to both animal (Figure 2a,c,e,g) and plant loss (Figure 2b,d,f,h). Model A and models including more than one mechanism tended to produce smaller effect sizes, with the exception of MP. When considering single mechanisms, M always had the highest effect size, being as high as $D = 0.69$ (Figure 2c; Tables S1–S3).

There was considerable variation on the R_w estimated among the *distinct extinction sequences* (Figure S1). In general, networks are more robust to the loss of species with few interactions (blue), than the random loss of species (red) or the extirpation of the most generalist species occurring first (black; Figure S1). When generalists are lost first, the inclusion of rewiring increased robustness substantially (i.e. largest observed effect sizes; Figure 2); however, only a moderate increase occurred when simulated extinctions happen at random and had negligible effects when species with fewer interactions are lost first (Figure 2).

With regard to *partners' choice*, the effects sizes were similar when partners were chosen by random (Figure 2a–d) or based on their abundances (Figure 2e–h). Regarding *methods of rewiring*, the assumption that plants have one attempt to rewire with each surviving pollinator (Figure 2c,g) led to higher effect sizes than when assuming only one attempt with only one pollinator (Figure 2a,e). The same trend was observed for pollinators when plants were extinct (Figure 2d,h and Figure 2b,f respectively).

4 | DISCUSSION

Although commonly employed, network robustness models assume that species that lose all interacting partners will in turn go extinct.

The resulting estimation of robustness consequently neglects the role of rewiring (partner switching) which is an important property of mutualistic interactions (CaraDonna et al., 2017; Costa et al., 2018; Ponisio et al., 2017). Here we propose a new method for incorporating rewiring based on species-specific variables related to mechanisms known to influence interactions into the calculation of network robustness.

4.1 | Applications of the method

Our method is, to the best of our knowledge, the first explicit attempt to incorporate mechanisms driving species interaction into the estimation of network robustness. There are at least three ways it may be useful for ecologists. First, the more obvious use is to obtain a descriptor of network robustness to species loss while taking rewiring into account. This metric can then be used, for example, to compare network stability in space (across communities) or time (e.g. along seasons or successional gradients). Second, it can be used to identify the most influential mechanisms driving network robustness, providing insight on the relative importance of processes associated with network disassembly and resilience. While several studies investigate mechanisms that define linkage rules and network assembly in mutualistic systems (Bartomeus et al., 2016; Krishna, Guimarães, Jordano, & Bascompte, 2008; Vázquez, Chacoff, et al., 2009; Vizentin-Bugoni et al., 2018), there are comparatively few studies exploring whether and to what extent distinct mechanisms influence network disassembly and response to disturbances. This represents a critical gap in network ecology (Lau, Borrett, Baiser, Gotelli, & Ellison, 2017), and our method represents an initial step to fill that gap. Third, our method may be used to explore the *hierarchical importance* of distinct mechanisms associated with network robustness. This is in line with recent studies on the drivers of network structure that highlight the existence of a hierarchy of importance among the mechanisms that define the occurrence and intensity of interactions (Bartomeus et al., 2016; Junker et al., 2013). The evidence accumulated so far indicates that the most basic requirement for interaction is that species coexist in space and time, then the chance of encounter of two species is dependent on their abundances and, finally, species-specific phenotypic characteristics, for example, trait matching and the nutritional content of resources and energetic demands of consumers (e.g. González-Castro, Traveset, & Nogales, 2012; Vázquez, Bluthgen, et al., 2009; Vizentin-Bugoni et al., 2014). Since our method allows the user to manipulate the

order that distinct mechanisms influence the chances that species partner with each other, the impacts of such hierarchical importance on robustness can be explored.

4.2 | Plant-hummingbird network robustness: a study case

Our analyses revealed that (a) in general, rewiring increases the estimated robustness, (b) networks are similarly robust to the loss of pollinators or plants, (c) morphological matching and phenological overlap have the largest positive impact on estimated robustness when rewiring is considered, (d) when multiple mechanisms are combined, robustness tend to increase little with rewiring in comparison to single mechanisms, (e) networks are far more susceptible to loss of generalist animals and plants than to the random species loss or the loss of species with few interactions and, thus, rewiring tends to increase the estimated robustness more in the first scenario.

Our results demonstrate that vertebrate pollinator-plant tropical networks are more susceptible to the loss of generalist than specialist species, mirroring previous findings obtained for temperate plant-pollinator networks dominated by insects (Memmott et al., 2004) and other kinds of mutualistic interactions (e.g. seed dispersal networks, Bastazini et al., 2019). Besides affecting a larger number of partners connected exclusively to them, the loss of generalist species may affect network cohesiveness because they connect distinct network modules, that is, subsets of species interacting more among them than with other members of the community (Olesen, Bascompte, Dupont, & Jordano, 2007). Yet, the cohesiveness promoted by generalists increases network stability and its ability to cope with disturbances (Kaiser-Bunbury et al., 2010). In fact, the high variability of robustness to random loss of species means certain species contribute more to network robustness than other species, that is, specialists (Bastazini et al., 2019).

Our results further show that rewiring may buffer the effects of the loss of generalists by increasing network robustness. At the same time, the existence of constraints to interactions may prevent major decelerations of coextinction rates. We found that when rewiring is driven by few mechanisms (Figure 2, models M, P or T), higher robustness to the loss of generalists is obtained. This indicates that the existence of potential partners with matching traits and phenological overlap provides species the opportunity to withstand sequential partner loss, as empirical removal experiments have shown (Biella et al., 2019). On the other hand, when multiple mechanisms are considered concomitantly, the robustness is low or does not increase considerably in comparison to the model 'without rewiring'. This is likely a consequence of the combination of rarity and constraints imposed by partners' phenologies and morphologies, which lead to lower probabilities of rewiring and higher probabilities of 'forbidden links'.

Another implication of our results is that networks strongly defined by trait matching, such as plant-hummingbird interactions studied here (Vizentin-Bugoni et al., 2014), are particularly susceptible to the loss of morphologically specialized species that interact

with many partners. For instance, 51% of the plant species in the system (24 of 47 species) interact with a single hummingbird species which has a bill longer than 30 mm (*Phaethornis eurynome*). Once this pollinator species is lost, most of these plant species are unlikely to rewire to the remaining pollinators because of their morphological specialization (corolla length = 31.04 ± 9.8 mm, mean \pm SD). In combination, these results reinforce the importance of morphologies and phenologies as drivers of frequencies of interactions (Maruyama et al., 2014; Vizentin-Bugoni et al., 2014), while also revealing that these same mechanisms that drive network structure also define network robustness and, potentially, disassembly.

4.3 | Perspectives and caveats

We illustrate here how to derive probabilities of interaction based on species-level variables which encompass important drivers of interactions in the system. While we do not provide exhaustive examples on how to integrate other mechanisms into this framework, this method is flexible for the incorporation of other variables and/or combinations of other mechanisms relevant in other systems. Virtually any quantitative variable may be used to derive probabilities of partners' choice and rewiring and, therefore, could be incorporated in our method. In fact, previous studies have provided the basis for the incorporation of, for example, probabilities of interaction based on species phylogenetic relationships (Bastazini et al., 2017; Vitória, Vizentin-Bugoni, & Duarte, 2018). The method may also be extended to other types of interactions as, for example, host-parasite, plant-herbivore and predator-prey bipartite networks. In this case, we stress that the application of the method is contingent on the biology of the system. For instance, parasites are intrinsically dependent on their hosts so that the dynamic of coextinction may be similar to plants that lose their pollinators; conversely, there is no obvious reason to expect that hosts will go extinct following the extinction of their parasites. We also stress that sampling completeness is likely to impact the realism and accuracy of the estimated robustness. Thus, we recommend the application of our method in well-sampled datasets, whose sampling sufficiency may be estimated via classic richness estimators applied to the context of networks (see Jordano, 2016, Vizentin-Bugoni et al., 2016).

In mutualistic networks, potential caveats may emerge from the assumption of mutual dependences of partners. When considering pollination networks, it is important to note that not all plants visited by animals rely strictly on pollinators for reproduction, as some of them may self-pollinate and/or produce offspring without pollination. However, the fact that the vast majority of flowering plants show characteristics in accordance with biotic pollination indicates the strength of this dependency (Ollerton, Winfree, & Tarrant, 2011). Moreover, the disadvantages of selfing are largely recognized, including inbreeding depression and the reduced capacity to respond to environmental changes (Crnokrak & Barrett, 2002). Thus, pollinator loss should reduce plants fitness, at least to some extent, in most cases. Species may not necessarily go extinct after partner loss and unsuccessful rewiring but some fitness reduction or population declines are likely

outcomes. In this sense, the incorporation of more direct measures of the effect of one species on the fitness of another as well as population declines (i.e. abundance reduction) before extinction may be an important next step towards a more realistic estimation of the impact of species loss on networks. However, obtaining fitness measures for multispecies assemblages is challenging (King, Ballantyne, & Willmer, 2013). Also, further advances may derive from models accounting for competitor release which is a phenomenon likely to follow species loss. Experimental removal of generalist plants suggests that the reorganization of interactions in pollination networks is largely governed by traits which, thus, may be partially encompassed in trait-matching models (Biella et al., 2019). However, competitor release may also lead to increasing overall community's generalization (Brosi & Briggs, 2013), which may be particularly influential on rewiring in systems whose interactions are not strongly constrained by traits.

Similar to previous models, our method assumes that species will not colonize (or recolonize) the community (Schleuning et al., 2016). This assumption may not be true if a meta-population dynamic exists and local populations are maintained by immigration. In fact, dispersal dynamics is known to influence network structure (Morales & Vázquez, 2008) and may influence network robustness. Furthermore, because biological invasion is a pervasive threat to biodiversity (Hui & Richardson, 2019), the realism of such models may increase by including the possibility of species invasions in the networks. The integration of recolonization and/or invasions in the models would require not only the probabilities of a species to enter the community but also the probability of its interaction with species persisting in the community, since the establishment of interactions with the local community is key for successful colonization (Hui & Richardson, 2019; Vizentin-Bugoni et al., 2019).

5 | CONCLUSIONS

Taking advantage of existing analytical frameworks and increasing knowledge on the mechanisms structuring interaction networks, we developed a method that arguably produces more realistic estimations of the robustness of ecological networks. Our method also represents the first step towards understanding the relative importance of distinct mechanisms for network disassembly. We provide evidence that secondary extinction may be buffered by rewiring of interactions to surviving partners. These findings further reinforce the importance of rewiring in mutualistic systems (CaraDonna et al., 2017; Costa et al., 2018; Ponisio et al., 2017) and indicate that it is a crucial component for the resilience of complex networks and perhaps to the assembling of novel communities (Vizentin-Bugoni et al., 2019). We expect that further studies aiming to incorporate other mechanisms into this framework and its application to other types of interaction will foster a deeper understanding of the patterns of robustness and their underlying mechanisms across systems. Moreover, experimental studies simulating species extirpation in the field and evaluating its impacts on rewiring and robustness (e.g. Biella et al., 2019; Costa et al., 2018; Timóteo et al., 2016) are

recommended so that these models can be fitted to data in order to test distinct mechanisms and improve the accuracy of species coextinction models.

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AUTHORS' CONTRIBUTIONS

All authors conceived ideas and designed the methods; J.V.-B. and P.K.M. collected the data; V.J.D. analysed the data and implemented the code, and J.V.B and V.A.G.B reviewed and edited the code. All authors wrote the manuscript and approved the final version.

DATA AVAILABILITY

The code for these analyses with examples illustrating their application is available in GitHub and Zenodo: github.com/vanderleidebastiani/rewiring and zenodo.org/record/3405384#.XYPBGX9711t (Debastiani et al., 2019).

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