

# Interaction intimacy organizes networks of antagonistic interactions in different ways

Mathias M. Pires and Paulo R. Guimarães Jr\*

*Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, 11294, CEP: 05422-970, São Paulo, Brazil*

Interaction intimacy, the degree of biological integration between interacting individuals, shapes the ecology and evolution of species interactions. A major question in ecology is whether interaction intimacy also shapes the way interactions are organized within communities. We combined analyses of network structure and food web models to test the role of interaction intimacy in determining patterns of antagonistic interactions, such as host–parasite, predator–prey and plant–herbivore interactions. Networks describing interactions with low intimacy were more connected, more nested and less modular than high-intimacy networks. Moreover, the performance of the models differed across networks with different levels of intimacy. All models reproduced well low-intimacy networks, whereas the more elaborate models were also capable of reproducing networks depicting interactions with higher levels of intimacy. Our results indicate the key role of interaction intimacy in organizing antagonisms, suggesting that greater interaction intimacy might be associated with greater complexity in the assembly rules shaping ecological networks.

**Keywords:** antagonism; ecological networks; food web; plant–herbivore interactions; specialization

## 1. INTRODUCTION

The ways in which species interactions are organized within biological systems affect different aspects of ecological and evolutionary dynamics, from community stability [1,2] to ecosystem functioning [3] and coevolution [4]. Ecologists have made substantial efforts to describe the structure and understand the assembly of ecological communities. Through these efforts, studies focusing on the biological attributes shaping species interactions have distinguished the key role of a few species traits in shaping patterns of interaction within ecological networks. These traits include abundance [5,6], interaction type [7] and interaction intimacy, the degree of biological integration among interacting individuals of different species [8–10].

There is compelling evidence that the degree of interaction intimacy shapes the ecology and evolution of species interactions [11]. High-interaction intimacy is often associated with the propensity of an individual to interact with few individuals of other species during most of its lifetime [8,11]. For example, in interactions established by symbiotic organisms, e.g. parasites and gall-forming insects, each individual spends a substantial part of its life within or attached to a single host. These interactions often involve a high degree of physiological

integration associated with trophic and physical dependence. High intimacy at the individual level does not necessarily imply in high specialization at species level, as is well known for some generalist parasites [12]. Nevertheless, owing to the high level of biological integration between individual consumers and their hosts, extreme patterns of specialization, such as monophagy [13], are a common feature of some high-intimacy interactions. In contrast, interactions with lower levels of intimacy, such as those between predators and prey [14], often imply an absence of physiological integration or trophic and physical dependence on any single individual interaction partner. For mutualisms, the analysis of networks describing species interactions with different levels of interaction intimacy shows that these networks possess distinct structural properties that might be a result of distinct ecological and evolutionary dynamics [9,15]. Recent analyses also suggest that interaction intimacy is particularly important in shaping mutualisms, whereas the effects of interaction intimacy on the network structure of antagonisms are less clear [10].

A fundamental question is how the underlying processes moulding ecological networks differ between interactions varying in their degree of intimacy. Food web theory provides a useful approach to explore the potential differences between the assembly rules of antagonisms showing low- and high-intimacy interactions. The development of models capable of reproducing the structure of food webs [16] has yielded insights into the formative processes underlying ecological interactions [17–20]. Despite

\*Author for correspondence (prguima@usp.br).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsif.2012.0649> or via <http://rsif.royalsocietypublishing.org>.

the simplicity of such models, the fit of a particular model to data suggests that it captures at least the most essential mechanisms of network assembly. Such food web models were originally developed to reproduce food webs that describe interactions across different trophic levels. However, recent work adapted these models to explore the mechanisms shaping two-mode ecological networks, such as plant–animal interactions [21,22].

This paper investigates the differences in the assembly rules of ecological networks related to interaction intimacy. We divided our analysis into two parts. First, we investigated the role of interaction intimacy in shaping patterns of interaction in antagonisms, such as parasitism, predation and variable types of plant–herbivore interactions. We expected that highly intimate interactions would have higher modularity due to different factors associated with the phenotypic integration among partners, including strong phylogenetic constraints and coevolution favouring specialization [9,23]. In contrast, high nestedness and low modularity are expected for interactions with low intimacy, in which differences in abundance [6] and body size [14] are hypothesized to play a key role. Second, the approach based on food web models allowed us to investigate whether the assembly of two-mode antagonistic networks varies across distinct levels of interaction intimacy. We tested the hypothesis that models with more complex rules would be required to reproduce networks with high levels of interaction intimacy.

## 2. METHODS

### 2.1. *The dataset and the characterization of interaction intimacy*

To test if antagonistic networks with varying levels of interaction intimacy show different structural patterns related to different assembly rules, we used 26 two-mode antagonistic networks available online from the Interaction Web Database and compiled from the literature (see the electronic supplementary material, appendix A). This dataset encompasses a broad range of antagonisms, including parasitism, predation, grazing and different types of plant–herbivore interactions, with networks ranging from small networks with no more than 16 species and 15 interactions to large networks with more than 300 species and 700 interactions (see the electronic supplementary material, appendix A). As in any dataset of ecological networks, certain types of interactions are under-represented (e.g. few aquatic antagonisms). However, we attempted to minimize the over-representation of particular types of interactions, such as parasite–host interactions, opting for a smaller dataset encompassing representatives of a variety of antagonisms. We did not use entire food webs because they often include different types of interactions varying in their degree of intimacy [16]. Conversely in two-mode networks all links represent the same kind of ecological interaction and thus are presumably subjected to similar ecological and evolutionary processes [23]. Moreover, we did not analyse networks in which a considerable proportion of nodes (‘species’) are actually sets of species that are assumed to be

ecologically similar because two species sharing similar resources or consumers may differ strongly in their degree of intimacy. Although the preponderance of plant–herbivore networks in our dataset can be viewed as a potential bias, it is important to note that insects represent much of the animal diversity worldwide as well as most of the lifestyles found in nature [24].

Interaction intimacy can be viewed as a function of the degrees of physiological integration, trophic and physical dependence of interacting individuals of different species [8]. We opted to use a conservative approach [10], classifying each interaction according to three levels (low, intermediate and high) of interaction intimacy. Interactions with low intimacy ( $n = \text{eight networks}$ ) are characterized by an absence of physiological integration and physical dependence and by highly mobile consumers that are able to feed upon many different individual prey throughout their lifetimes. Examples include predation, grazing by mammalian herbivores and interactions between plants and leaf-chewing insects, such as grasshoppers. Interactions with intermediate intimacy ( $n = \text{eight networks}$ ) are characterized by an absence of physiological integration and a certain degree of physical and trophic dependence. Examples include the interactions between plants and insect herbivores whose individuals feed mainly in one or a few individual hosts for long periods of time, such as the larvae of lepidopterans, coleopterans and dactyniine fruit flies. Finally, interactions with high intimacy ( $n = 10 \text{ networks}$ ) are characterized by extreme physiological integration and the physical and trophic dependence of consumers on single hosts for at least part of the consumer’s life cycle, such as fish parasites, gall-forming insects, leaf-mining insects and endophagous flower parasites.

### 2.2. *Structural analysis of antagonistic networks*

We used six metrics to characterize the structure of antagonistic networks: (i) connectance, the proportion of all possible interactions that are actually recorded; (ii) variance in the number of interactions among consumers,  $\sigma_c^2$  (iii) and among prey (hosts),  $\sigma_r^2$ ; (iv) nestedness; (v) modularity; and (vi) the number of modules. We used the metric *NODF* (nestedness metric based on overlap and decreasing fill) to characterize nestedness [25] and *M* to characterize modularity and compute the number of modules in the network [26]. We used general linear models (GLMs) to investigate if interaction intimacy (coded as an ordinal explanatory variable) explains differences in each of the structural metrics. Because species richness varies widely across networks potentially affecting network structure, we used the total species richness,  $S$ , as a covariate. Network metrics are often correlated, for that reason, we performed two complementary analyses. First, we used a principal component analysis (PCA) to test whether the combined information on the metrics provides a clear partition among interactions with different levels of intimacy (electronic supplementary material, appendix B). Second, we used null model analysis to determine if the differences in nestedness and modularity are consistent after controlling for other network properties (see the electronic supplementary material, appendix B).

### 2.3. Food web models and assembly rules of antagonistic networks

To test whether networks with different degrees of intimacy are better reproduced by different assembly rules, we compared the ability of three probabilistic food web models, namely the cascade model [17], and the one-dimensional and two-dimensional probabilistic niche models (PNMs), respectively [27], to predict interactions within networks. Each model represents distinct candidate assembly rules with increasing degree of complexity that may reproduce antagonistic networks.

The first model is a probabilistic version of the cascade model [17]. In the original cascade model, each species is given a position ( $n$ ) along an axis that represents a feeding hierarchy, and a given species  $i$  can only use species  $j$  as a resource if species  $j$  occupies a lower rank in the feeding hierarchy, i.e. if  $n_i > n_j$ . Because likelihood-based methods require that any interaction must have a non-zero probability of occurrence, we adapted the cascade model as a logit regression

$$\log \left[ \frac{P(a_{ij} = 1)}{P(a_{ij} = 0)} \right] = \alpha + \beta \phi_{i,j}, \quad (2.1)$$

in which  $a_{ij}$  is a cell in the matrix  $\mathbf{A}$  that depicts species interactions,  $\alpha$  and  $\beta$  are parameters to be estimated, and  $\phi_{i,j}$  equals 1 if  $n_i > n_j$  and 0 otherwise. Thus, the probability of an interaction between consumer  $i$  and resource  $j$  given a particular parameter set  $\theta = \{n_1, n_2, \dots, n_S, \alpha, \beta\}$  is

$$P(i, j | \theta) = \frac{e^{\alpha + \beta \phi_{i,j}}}{1 + e^{\alpha + \beta \phi_{i,j}}}. \quad (2.2)$$

To maintain consistency with the original rules of the cascade model, we constrain  $\alpha$  to be  $< 1$  and  $\beta > 1$  such that the probability of interaction is larger if  $n_i > n_j$ .

In the probabilistic niche model (PNM) [27,28], the consumer may use a set of resources within a determined diet range. The probability of an interaction between consumer  $i$  and resource  $j$  is a continuous function:

$$P(i, j | \theta) = v \prod_{d=1}^D \exp \left\{ - \left( \frac{n_{d,j} - c_{d,i}}{r_{d,i}/2} \right)^\gamma \right\}, \quad (2.3)$$

where  $n_{d,j}$  represents the position in the niche dimension  $d$  for resource  $j$ ,  $c_{d,i}$  represents the diet optimum of consumer  $i$  for dimension  $d$ ,  $r_{d,i}$  is the diet range for consumer  $i$  within dimension  $d$ ,  $\gamma$  controls the cutoff rate of the probability function and  $v$  is the maximum probability that  $i$  consumes any given prey, here set to 1 following Williams & Purves [27]. Because species in two-mode networks will only be consumers or resources, species positions ( $n$ ) are defined only for the  $R$  species that are used as resources, whereas diet positions and ranges ( $c$  and  $r$ ) are defined only for the  $C$  consumer species. Thus, the parameter set can be defined as  $\theta = \{n_{d,1}, n_{d,2}, \dots, n_{d,R}, c_{d,1}, c_{d,2}, \dots, c_{d,C}, r_{d,1}, r_{d,2}, \dots, r_{d,C}, \gamma\}$ . We restrict our analyses to the one-dimensional ( $D=1$ ) and two-dimensional ( $D=2$ ) niche models.

For each two-mode network represented by a matrix  $\mathbf{A}$ , we computed the probability of reproducing each link

under each model (cascade, one- and two-dimensional PNMs) for a given set of parameters. Therefore, we define the log-likelihood for a given parameter set as

$$L(\theta | \mathbf{A}) = \sum_i \sum_j \ln \left\{ \begin{array}{ll} P(i, j | \theta) & \text{if } a_{ij} = 1 \\ 1 - P(i, j | \theta) & \text{if } a_{ij} = 0 \end{array} \right\}. \quad (2.4)$$

The maximum-likelihood parameter set is that which maximizes the likelihood. All models have a large number of parameters. Therefore, to obtain maximum-likelihood estimates (MLEs) is an optimization problem. We used simulated annealing [29], an optimization procedure that is less prone to become trapped in suboptimal values, and the Latin hypercube, a sampling technique that allows to explore large parameter space [30]. We repeated the procedure 30 times for each combination of networks and models, starting from different points in parameter space to improve the reliability of the estimates.

To compare model performance, we used the corrected Akaike information criterion for finite sample sizes, AICc [31]. The model with the lowest relative value of AICc is that showing the best fit to the data. We also computed the expected fraction of correct links for each network under each model, an additional measure of model performance [32]. The expected number of correctly predicted links can be computed as  $N_c(\mathbf{A} | \theta) = \sum_i \sum_j a_{ij} P(i, j | \theta)$ . Therefore, the expected fraction of links predicted correctly,  $f_c$ , is obtained by dividing  $N_c$  by the number of interactions in the actual network. This approach is possible because MLEs for parameters imply that all models would tend to generate networks with connectances similar to the connectances of the real networks. We then tested whether the  $f_c$  differed between networks with high, intermediate and low intimacy. To control for the possible effect of network size on  $f_c$ , we used a GLM in which total species richness and level of interaction intimacy were factors. We performed the test separately for each food web model.

### 3. RESULTS

After controlling for species richness, all aspects of antagonistic network structure but the variance in the number of interactions per consumers ( $F_{2,23} = 1.36$ ,  $p = 0.28$ ) varied across the gradient of intimacy in predictable ways: low-interaction intimacy was associated with higher connectance ( $F_{2,23} = 5.74$ ,  $p = 0.01$ ), higher nestedness ( $F_{2,23} = 9.89$ ,  $p = 0.0009$ ), a higher variance in the number of interactions per resource ( $F_{2,23} = 17.36$ ,  $p < 0.0001$ ), lower modularity ( $F_{2,23} = 5.79$ ,  $p = 0.01$ ) and a smaller number of modules ( $F_{2,23} = 3.56$ ,  $p = 0.04$ ; figure 1). In all cases, only networks with low intimacy differed significantly from networks with intermediate and high intimacy (figure 1). PCA analysis corroborates these results; by showing low-intimacy interactions structurally differ from networks formed by interactions with average and high levels of intimacy. Along of the same lines, null model analysis used to evaluate nestedness and modularity significance led to similar results, in which low intimacy is associated with significant nestedness and high and intermediate intimacy

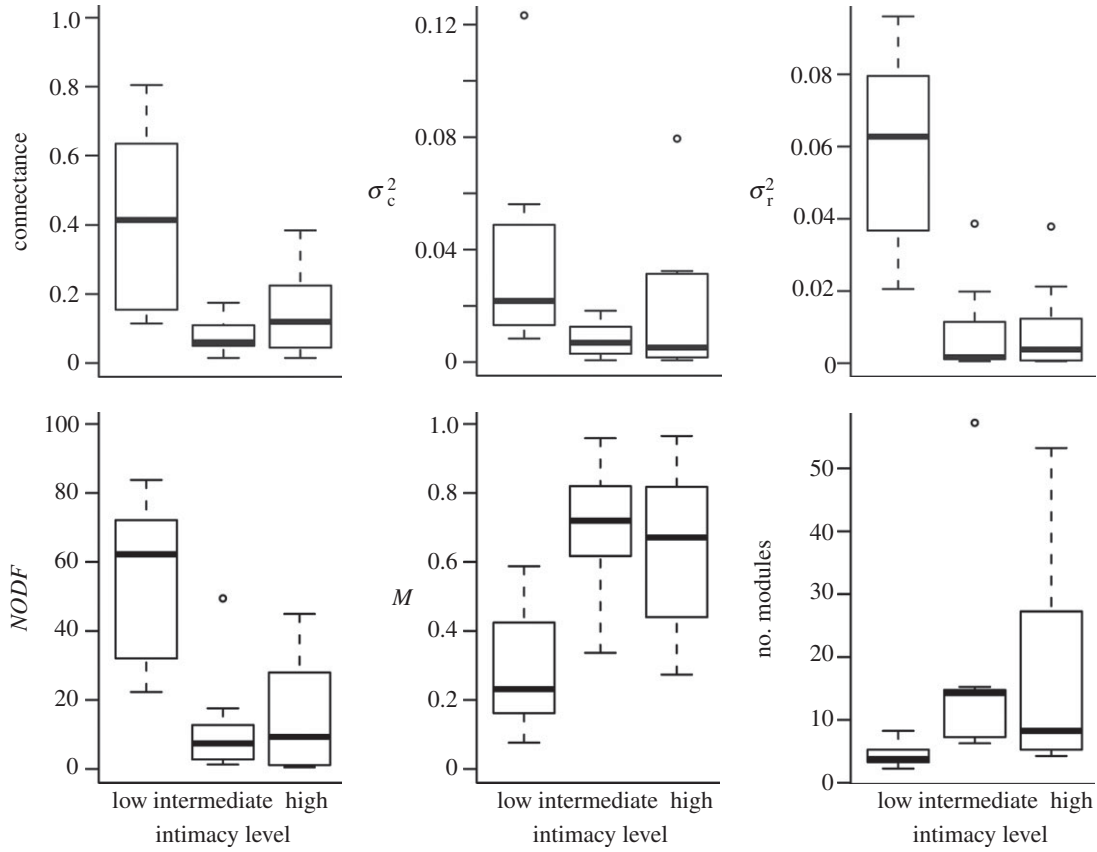


Figure 1. Boxplots for each structural metric of networks with different levels of interaction intimacy. The metrics are connectance; variance in the number of interactions among consumers,  $\sigma_c^2$ ; variance in the number of interactions among resources,  $\sigma_r^2$ ; nestedness, *NODF*; modularity, *M*; and the number of modules per network. The upper and lower limits of the box are the quartiles, the black band within a box represents the median and the error bars equal  $\pm 1.5$  times the interquartile range.

with significant modularity. For additional details on the analyses using the GLM, PCA and null model analysis, see the electronic supplementary material, appendix B.

The disparate structural patterns between antagonisms with low intimacy and higher degrees of intimacy produced differences in the model fit for networks depicting interactions with different levels of intimacy. The fraction of links correctly predicted by the cascade model (figure 2) was significantly higher for the low-intimacy networks (on average  $76 \pm 21\%$ ) than for the intermediate- ( $36 \pm 20\%$ ) and high-intimacy networks ( $41 \pm 26\%$ ,  $F_{3,22} = 6.27$ ,  $p < 0.01$ ). There were no significant differences in the performance of the one-dimensional PNM (low:  $78 \pm 20\%$ ; intermediate:  $70 \pm 23\%$ ; high:  $78 \pm 19\%$ ;  $F_{3,22} = 0.39$ ,  $p = 0.67$ ) and the two-dimensional PNM (low:  $81 \pm 20\%$ ; intermediate:  $86 \pm 10\%$ ; high:  $88 \pm 11\%$ ;  $F_{3,22} = 0.41$ ,  $p = 0.31$ ) models across networks depicting interactions with different levels of intimacy. The model selection procedure favoured different models for networks with different degrees of intimacy. The goodness of fit of the cascade model was the largest for six of the eight low-intimacy networks (figure 2). For intermediate and high levels of intimacy, the performance of the one-dimensional PNM was superior, showing the highest fit to the data for six of the eight intermediate-intimacy networks and six out of 10 of the high-intimacy networks (figure 2). The goodness of fit of the two-dimensional PNM was only larger for the largest intermediate-intimacy network and for one of the

largest high-intimacy networks (figure 2). However, for large networks the differences in the AICc between the two-dimensional PNM and the other two models were generally smaller and the disparity in the fraction of links correctly predicted was generally larger (figure 2).

#### 4. DISCUSSION

Our results showed clear differences between the structural properties of networks depicting low-intimacy antagonistic interactions and those of networks that depict antagonistic interactions with intermediate and high levels of intimacy. A long-lasting notion is that high modularity and low nestedness characterize antagonistic ecological networks [7,23]. Here, we show antagonisms can give rise to nested networks when interactions have a low degree of intimacy. At the community level, the presence of generalist lifestyles in interactions with low intimacy produced not only lower specialization (higher connectance), but also higher nestedness. In contrast, the higher-intimacy interactions are associated with high specialization (lower connectance) and also to higher modularity in antagonisms. Similar patterns were reported for mutualisms, in which intimate mutualisms are highly modular, whereas low-intimacy mutualisms are often highly nested [9]. Taken together, these results suggest the ecological and/or coevolutionary processes that



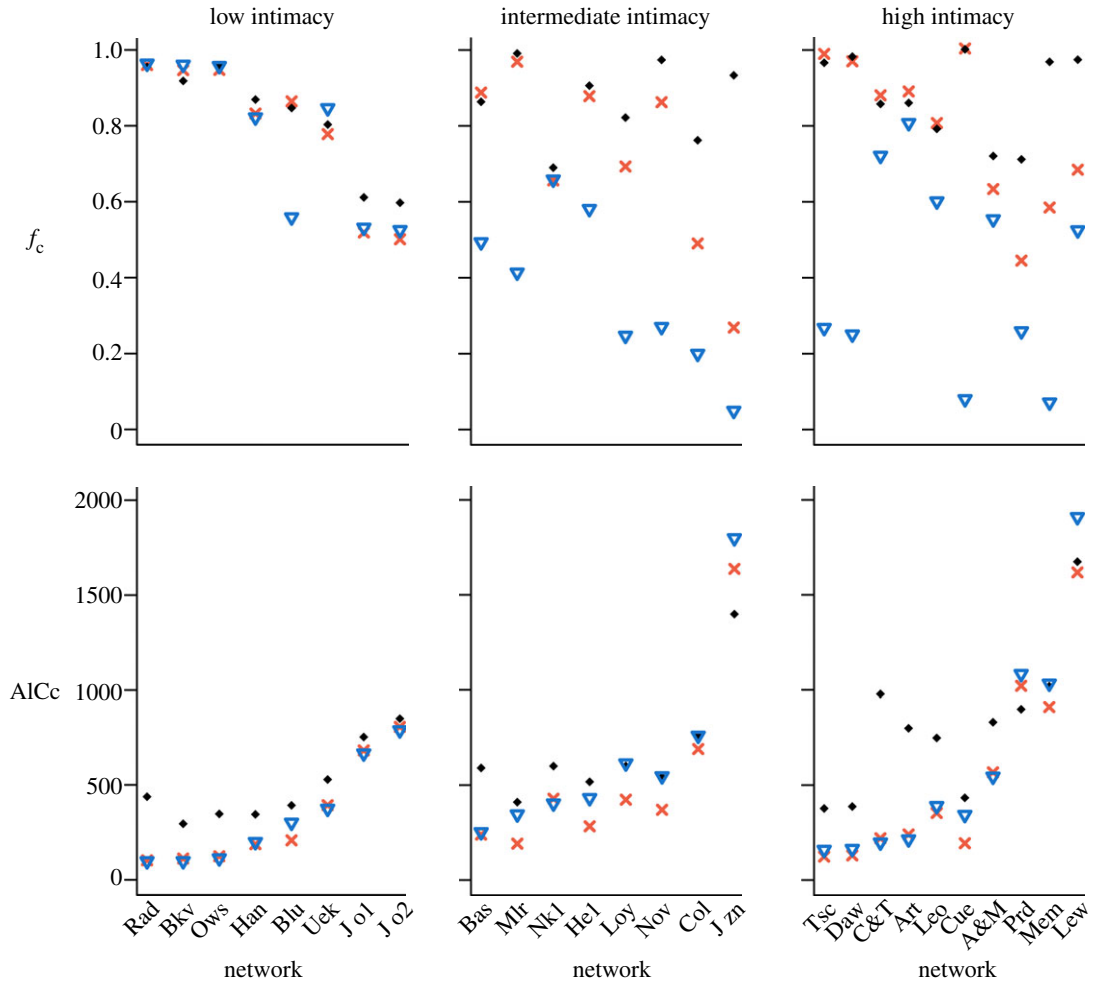


Figure 2. Fraction of correctly predicted links,  $f_c$ , and AICc values of each model for two-mode networks with different levels of intimacy. Networks are ordered from the smallest to the largest to highlight the effect of network size. Triangles represent the values for the cascade model, crosses for the one-dimensional PNM, and diamonds for the two-dimensional PNM. The name codes for each network can be found in the electronic supplementary material, appendix A. (Online version in colour.)

shape interaction patterns might be similar for systems with similar levels of intimacy despite these systems representing antagonisms or mutualisms. Nestedness partially emerges due to differences in population abundances among potential partners [6], probably a key component shaping both mutualisms and antagonisms with low intimacy. In addition, it has been proposed that grazing and free-living mutualisms might be much alike in the evolutionary processes shaping specialization [11], whereas symbiotic mutualisms might be similar to symbiotic antagonisms in the evolutionary processes shaping their patterns of interaction [33]. Moreover, our results suggest that interaction intimacy might have strong implications for the stability of species interactions. Nested patterns of resource use may have a destabilizing effect on antagonisms, as suggested by numerical simulations [7] and qualitative stability analysis [2], whereas the lower connectance and higher modularity of intimate antagonisms are associated with higher stability at the community level [2,7]. Future studies should investigate if antagonisms with low-interaction intimacy in fact tend to be more unstable to ecological perturbations than intimate antagonisms. Overall, our analyses using food web models contribute in three principal ways to our

understanding of the organization of antagonisms involving multiple interacting species.

First, our results show that simple models are capable of reproducing different types of antagonistic, two-mode networks. Therefore, large differences in network structure can be reproduced by a set of simple models assuming that antagonistic interactions are determined by a few dimensions in the niche space. Because two-mode networks are the building blocks of more complex ecological networks [34], a promising avenue for research is to explore how ecological networks formed by different types of interactions [10] can be reproduced by merging assembly rules in different ways.

Second, model performance differed among two-mode networks with different levels of interaction intimacy. The mechanisms underlying intimate interactions can be very complex. Organisms, such as leaf-mining and gall-forming insects and parasites need very specific host-recognition systems and mechanisms to avoid the mechanical and chemical defences of the hosts, in addition to specific morphology and physiology that allow these organisms to live within their hosts in such a close relationship [13,33,35]. Similar trends are observed in interactions with intermediate levels of intimacy, such as those formed by caterpillars and their host plants, in which complex

defence/counter defence complementarities play a key role [36,37]. Thus, the assembly mechanisms of intimate interactions are in general much more complex than the mechanisms structuring low-intimacy trophic interactions, such as body size [14,32], feeding apparatus constraints [38] or phenological matching and abundance effects [39]. These differences were mirrored by differences in model performance. The cascade model, the simplest in the set of models we tested in this study, can reproduce a great percentage of the interactions in low-intimacy networks, but it performs poorly in reproducing networks depicting interactions with intermediate and high levels of intimacy. These results generalize recent findings [22] that the cascade model shows good performance in reproducing low-intimacy mutualistic networks, pointing out for general mechanisms shaping low-intimacy mutualisms and antagonisms.

The cascade model tends to generate networks that are more nested than modular [22] and was thus unable to reproduce the highly modular structure of networks of interactions with higher intimacy. Conversely, the two versions of the PNM were much more successful in reproducing the high-intimacy networks. The addition of one dimension to the niche space was only advantageous for the largest networks analysed. This finding agrees with previous results for whole food webs [27]. Therefore, the simple assumptions of the niche model appear to successfully capture the essential assembly rules of networks representing intimate interactions. The versatility of the rules of the niche model facilitates the reproduction of the patterns of interaction of consumers with very narrow diet ranges, allowing each consumer to explore a small portion of the feeding axis such that niche overlap is minimal. These results corroborate the view [40] that one-dimensional niche generalization may be a useful simplification in models used to reproduce the structure of food webs. Although this property certainly does not mean that only one characteristic of consumers and resources is important in determining who interacts with whom in a given locality [16], it does suggest that the core of the network of interactions is well represented by considering one dimension that can, in turn, represent a combination of traits. The current challenge is to find an approach allowing the different traits shaping high-intimacy interactions to be combined in estimates of the parameters. A next step in this analysis would be to parametrize these minimal two-mode models with biological information on species traits, as in the recently introduced body size-based models for entire food webs [28,32].

Third, in addition to the insights that they yield into the assembly processes of ecological communities, food web models furnish the possibility of building ensembles of networks that share the same realistic structural backbone but encompass the uncertainty of the occurrence of each pairwise interaction. For this reason, food web models have been used to build ensembles of food webs with a similar realistic structure. This approach allowed tests of the general properties of the structure and dynamics of study systems [2,41]. In this paper, we expanded the range of the types of ecological networks that can be reproduced by food web models.

One key problem that still requires a solution is the extent of the applicability of the one-dimensional niche simplification results to all species and all their interactions. By probing into each network, future studies could provide an assessment of the species whose interactions are well predicted by food web models and the species for which food web models often fail. This assessment will allow us to improve our understanding of the generality of simple assembly rules and the complementary mechanisms generating the diversity of patterns of interaction in nature.

We thank S. Allesina for suggestions related to the likelihood approach, and two anonymous reviewers for their comments and suggestions. M.M.P. and P.R.G. were supported by FAPESP grants.

## REFERENCES

- May, R. M. 1972 Will a large complex system be stable. *Nature* **238**, 413–414. (doi:10.1038/238413a0)
- Allesina, S. & Tang, S. 2012 Stability criteria for complex ecosystems. *Nature* **483**, 205–208. (doi:10.1038/nature10832)
- Thébault, E. & Loreau, M. 2003 Food-web constraints on biodiversity–ecosystem functioning relationships. *Proc. Natl Acad. Sci. USA* **100**, 14 949–14 954. (doi:10.1073/pnas.2434847100)
- Guimarães Jr, P. R., Jordano, P. & Thompson, J. N. 2011 Evolution and coevolution in mutualistic networks. *Ecol. Lett.* **14**, 877–885. (doi:10.1111/j.1461-0248.2011.01649.x)
- Vázquez, D. P., Melián, C. J., Williams, N. M., Blüthgen, N., Krasnov, B. R. & Poulin, R. 2007 Species abundance and asymmetric interaction strength in ecological networks. *Oikos* **116**, 1120–1127. (doi:10.1111/j.0030-1299.2007.15828.x)
- Krishna, A., Guimarães Jr, P. R., Jordano, P. & Bascompte, J. 2008 A neutral-niche theory of nestedness in mutualistic networks. *Oikos* **117**, 1609–1618. (doi:10.1111/j.1600-0706.2008.16540.x)
- Thébault, E. & Fontaine, C. 2010 Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* **329**, 853–856. (doi:10.1126/science.1188321)
- Ollerton, J. 2006 ‘Biological barter’: patterns of specialization compared across different mutualisms. In *Plant–pollinator interactions: from specialization to generalization* (eds N. M. Waser & J. Ollerton), pp. 411–435. Chicago, IL: University of Chicago Press.
- Guimarães Jr, P. R., Rico-Gray, V., Oliveira, P., Izzo, T., dos Reis, S. F. & Thompson, J. N. 2007 Interaction intimacy affects structure and coevolutionary dynamics in mutualistic networks. *Curr. Biol.* **17**, 1–7. (doi:10.1016/j.cub.2007.09.059)
- Fontaine, C., Guimarães Jr, P. R., Kefi, S., Loeuille, N., Memmott, J., van der Putten, W. H., van Veen, F. J. F. & Thébault, E. 2011 The ecological and evolutionary implications of merging different types of networks. *Ecol. Lett.* **14**, 1170–1181. (doi:10.1111/j.1461-0248.2011.01688.x)
- Thompson, J. N. 2005 *The geographic mosaic of coevolution*. Chicago, IL: University of Chicago Press.
- Combes, C. 2001 *Parasitism: the ecology and evolution of intimate interactions*. Chicago, IL: University of Chicago Press.
- Hespenheide, H. A. 1991 Bionomics of leaf-mining insects. *Annu. Rev. Entomol.* **36**, 535–560. (doi:10.1146/annurev.en.36.010191.002535)

- 14 Sinclair, A. R. E., Mduma, S. & Brashares, J. S. 2003 Patterns of predation in a diverse predator–prey system. *Nature* **425**, 288–290. (doi:10.1038/nature01934)
- 15 Blüthgen, N., Menzel, F., Hovestadt, T., Fiala, B. & Blüthgen, N. 2007 Specialization, constraints, and conflicting interests in mutualistic networks. *Curr. Biol.* **17**, 341–346. (doi:10.1016/j.cub.2006.12.0)
- 16 Dunne, J. A. 2006 The network structure of food webs. In *Ecological networks: linking structure to dynamics in food webs* (eds M. Pascual & J. A. Dunne), pp. 27–86. New York, NY: Oxford University Press.
- 17 Cohen, J. E. 1990 A stochastic-theory of community food webs 0.6. Heterogeneous alternatives to the cascade model. *Theor. Popul. Biol.* **37**, 55–90. (doi:10.1016/0040-5809(90)90027-S)
- 18 Williams, R. J. & Martinez, N. D. 2000 Simple rules yield complex food webs. *Nature* **404**, 180–183. (doi:10.1038/35004572)
- 19 Allesina, S., Alonso, D. & Pascual, M. 2008 A general model for food web structure. *Science* **320**, 658–661. (doi:10.1126/science.1156269)
- 20 Stouffer, D. B. 2010 Scaling from individuals to networks in food webs. *Funct. Ecol.* **24**, 44–51. (doi:10.1111/j.1365-2435.2009.01644.x)
- 21 Saavedra, S., Reed-Tsochas, F. & Uzzi, B. 2009 A simple model of bipartite cooperation for ecological and organizational networks. *Nature* **457**, 463–466. (doi:10.1038/nature07532)
- 22 Pires, M. M., Prado, P. I. & Guimarães Jr, P. R. 2011 Do food web models reproduce the structure of mutualistic networks? *PLoS ONE* **6**, e27280. (doi:10.1371/journal.pone.0027280)
- 23 Lewinsohn, T. M., Prado, P. I., Jordano, P. & Bascompte, J. 2006 Structure in plant–animal interaction assemblages. *Oikos* **113**, 174–184. (doi:10.1111/j.0030-1299.2006.14583.x)
- 24 Tilmon, K. J. 2008 *Specialization, speciation, and radiation: the evolutionary biology of herbivorous insects*. Los Angeles, CA: University of California Press.
- 25 Almeida-Neto, M., Guimarães, P., Guimarães Jr, P. R., Loyola, R. D. & Ulrich, W. 2008 A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* **117**, 1227–1239. (doi:10.1111/j.0030-1299.2008.16644.x)
- 26 Olesen, J. M., Bascompte, J., Dupont, Y. L. & Jordano, P. 2007 The modularity of pollination networks. *Proc. Natl Acad. Sci. USA* **104**, 19 891–19 896. (doi:10.1073/pnas.0706375104)
- 27 Williams, R. J. & Purves, D. W. 2011 The probabilistic niche model reveals substantial variation in the niche structure of empirical food webs. *Ecology* **92**, 1849–1857. (doi:10.1890/11-0200.1)
- 28 Williams, R. J., Anandanadesan, A. & Purves, D. 2010 The probabilistic niche model reveals the niche structure and role of body size in a complex food web. *PLoS ONE* **5**, e12092. (doi:10.1371/journal.pone.0012092)
- 29 Kirkpatrick, S., Gelatt, C. D. & Vecchi, M. P. 1983 Optimization by simulated annealing. *Science* **220**, 671–680. (doi:10.1126/science.220.4598.671)
- 30 McKay, M. D., Beckman, R. J. & Conover, W. J. 1979 A comparison of three methods for selecting values of input variables in the analysis of output from a computer code. *Technometrics* **21**, 239–245. (doi:10.2307/1268522)
- 31 Burnham, K. P. & Anderson, D. R. 2002 *Model selection and multimodel inference: a practical information-theoretic approach*. New York, NY: Springer.
- 32 Petchey, O. L., Beckerman, A. P., Riede, J. O. & Warren, P. H. 2008 Size, foraging, and food web structure. *Proc. Natl Acad. Sci. USA* **105**, 4191–4196. (doi:10.1073/pnas.0710672105)
- 33 Sachs, J. L., Essenberg, C. J. & Turcotte, M. M. 2011 New paradigms for the evolution of beneficial infections. *Trends Ecol. Evol.* **26**, 202–209. (doi:10.1016/j.tree.2011.01.010)
- 34 Kondoh, M., Kato, S. & Sakato, Y. 2010 Food webs are built up with nested subwebs. *Ecology* **91**, 3123–3130. (doi:10.1890/09-2219.1)
- 35 Harris, M. O., Stuart, J. J., Mohan, M., Nair, S., Lamb, R. J. & Rohfritsch, O. 2003 Grasses and gall midges: plant defense and insect adaptation. *Annu. Rev. Entomol.* **48**, 549–577. (doi:10.1146/annurev.ento.48.091801.112559)
- 36 Coley, P. D. & Barone, J. A. 1996 Herbivory and plant defenses in tropical forests. *Annu. Rev. Ecol. Syst.* **27**, 305–335. (doi:10.1146/annurev.ecolsys.27.1.305)
- 37 Poelman, E. H., van Loon, J. J. A. & Dicke, M. 2008 Consequences of variation in plant defense for biodiversity at higher trophic levels. *Trends Plant Sci.* **13**, 534–541. (doi:10.1016/j.tplants.2008.08.003)
- 38 Jordano, P. 1995 Angiosperm fleshy fruits and seed dispersers: a comparative analysis of adaptation and constraints in plant–animal interactions. *Am. Nat.* **145**, 163–191. (doi:10.1086/285735)
- 39 Cates, R. G. 1981 Host plant predictability and the feeding patterns of monophagous, oligophagous, and polyphagous insect herbivores. *Oecologia* **48**, 319–326. (doi:10.1007/BF00346961)
- 40 Cohen, J. 1978 *Food webs and niche space*. Princeton, NJ: Princeton University Press.
- 41 Dunne, J. A. & Williams, R. J. 2009 Cascading extinctions and community collapse in model food webs. *Phil. Trans. R. Soc. B* **364**, 1711–1723. (doi:10.1098/rstb.2008.0219)