

Research article

Uneven abundances determine nestedness in climbing plant-host interaction networks



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ABSTRACT

Nestedness is a common pattern in interaction networks. However, its ecological and evolutionary meaning is under debate. Evidence shows that nestedness in mutualistic networks may be just a consequence of the species–abundance distribution. This has been questioned as abundance itself could be influenced by differences in generalism between species. Host-parasite networks in plant communities also show nested patterns, but their relationship with abundance has been seldom addressed. Importantly, an assessment of the potentially different effect of the number of interacting species (*i.e.* generalism levels) on the size of parasite and host populations can help understanding the role of abundance in determining both generalism and nestedness. Here we show that nestedness follows abundance expectations in an interaction network of climbing plants (*i.e.* structural parasites) and their tree and shrub hosts. Our results also point to a direct effect of abundance on both nestedness and generalism levels because species degree does not deviate from abundance expectations for both climbing plants and their hosts. Further, we found a similar level of discordance between generalization (a generalism measure independent of species abundance) and abundance for both parties. Our findings provide evidence that the factors underlying uneven abundance distributions can induce nestedness in interaction networks. We stress the importance of neutral processes related to species dominance as major determinants of nestedness in host-parasite networks.

1. Introduction

A central tenet in Ecology is to identify the mechanisms through which species interactions determine community properties in space and time. A common way to address this issue is conceiving species interactions between two guilds (*e.g.* hosts and parasites or plants and pollinators) as bipartite networks, whose architectures reveal invariant interaction patterns across different ecosystems (Jordano *et al.*, 2003), latitudinal gradients (Morris *et al.*, 2014) or interaction types (Joppa *et al.*, 2010). This has led to numerous studies trying to unravel the causes (*e.g.* Vázquez *et al.*, 2009a) and consequences (*e.g.* Bastolla *et al.*, 2009) of these interaction structures. Among the potential set of patterns emerging from interaction networks, nestedness (*i.e.*, the

tendency of specialist species to interact with proper subsets of those interacting with generalist species; Bascompte *et al.*, 2003) has received considerable attention. Nestedness has been reported in a number of interaction networks from different ecosystems, including both mutualistic and host-parasite interactions (*e.g.* Joppa *et al.*, 2010). Yet, despite its pervasiveness, the ecological and evolutionary significance of this pattern is still under debate.

Three main hypotheses have been proposed to account for the eco-evolutionary causes of this pattern (Fontaine, 2013; Ulrich *et al.*, 2009). The first suggests that nested interaction patterns enhance both community resilience (*i.e.* the speed to recover the equilibrium state after a disturbance; Okuyama and Holland, 2008; Thébaud and Fontaine, 2010) and persistence (*i.e.* the number of existing species at

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equilibrium; Bastolla et al., 2009; Rohr et al., 2014; Saavedra and Stouffer, 2013; Thébault and Fontaine, 2010). However, little agreement has been reached about this possibility since no positive effects of nestedness on community resilience and persistence were recorded after accounting for other significant factors such as interaction strength, the number of mutualistic partners or interaction frequencies (Allesina and Tang, 2012; James et al., 2012; Staniczenko et al., 2013; but see also Rohr et al., 2014). The second hypothesis points to (co) evolutionary processes as responsible for nested patterns. Evidence for this argument comes from communities where the number of mutualistic partners appears to be evolutionary conserved (Rezende et al., 2007), and simulations based on adaptive dynamics (McQuaid and Britton, 2013). Alternatively, some authors have claimed for “non-adaptive community selection” to explain the preponderance of nestedness patterns (Borrelli et al., 2015). However, no precise evolutionary mechanisms have been directly related to the appearance and preponderance of nestedness (Fontaine, 2013). The third hypothesis attributes the origin of this pattern to neutral processes, where interactions would be mainly governed by the relative abundance of the species present in the community (neutral abundance hypothesis, e.g. Krishna et al., 2008; Vázquez et al., 2009a). Here, the log-normal abundance distributions commonly found in many communities would generate patterns of nested interactions (i.e. rare species would be more likely to interact with the most abundant ones, which in turn would form a core of highly-connected generalists). Despite the substantial evidence in this respect (Canard et al., 2012; Dáttilo et al., 2013; Krishna et al., 2008; Sáyo et al., 2013; Vázquez et al., 2009a), some authors cast doubts on this hypothesis due to the difficulty in distinguishing whether a species is generalist due to its abundance or vice versa (e.g. Fontaine, 2013; Krishna et al., 2008). Note that, in the domain of ecological networks, generalism refers to a high number of interacting species, regardless of whether these species act as resources or consumers (e.g. a host attacked by many parasite species is considered a generalist).

The work on nestedness in ecological interactions has been developed mainly on mutualistic networks. This calls for questioning whether the proposed causes of nested patterns hold for host-parasite networks (Graham et al., 2009; Lima et al., 2012; Sfair et al., 2010). Among the three general hypotheses described above, only the neutral-abundance hypothesis would hold for any interaction type (e.g. Canard et al., 2012). In fact, nestedness –or any of its associated features– can be explained by the distribution of species abundance in both host-parasite (Lima et al., 2012; Vázquez et al., 2005; Vázquez et al., 2007) and mutualistic networks (e.g. Canard et al., 2012; Dáttilo et al., 2013; Sáyo et al., 2013; Vázquez et al., 2009a). Notably, the problem of causality between abundance and generalism does not necessarily apply to host-parasite networks. That is, while parasite species may increase their abundance by increasing the number of host species used (i.e. their generalism), host species abundance does not necessarily have to be positively influenced by the number of parasite species using them. Such decoupled relationship between generalism and abundance makes host-parasite networks suitable study models to assess whether there is any direct effect of abundance on interaction nestedness.

In this work we investigate whether abundance may determine interaction nestedness in host-parasite networks using a climbing plant–host tree network. Despite climbing plants constitute important elements for the functioning and structure of forest ecosystems (Schnitzer et al., 2015), their interaction networks have been scarcely studied (Blick and Burns, 2009, 2011; Sfair et al., 2010). Climbing plants are “structural parasites” of trees and shrubs (Stevens, 1987; Hegarty, 1991), so they use (consume) the structural support resource provided by them, but may differ in the range of hosts that they are able to use (Carrasco-Urra and Gianoli, 2009; Gianoli, 2015; Hegarty, 1991; Putz and Holbrook, 1991). Importantly, while generalism may enhance the abundance of climbing plant species, it should have the opposite

effect on host species (Hegarty, 1991; Ingwell et al., 2010). This allowed us to delve into the abundance–generalism causality problem. We firstly analyzed the consistency between observed and expected nestedness based on abundance in the studied climbing plant–host community. Secondly, given that the consequences of generalism are different for parasite and host species, we also attempted to infer causality in the relation between abundance and generalism. If abundance determines the realized generalism in the local interactions, a strong and positive abundance–generalism correlation for both hosts and climbing plants should be expected. On the contrary, if generalism determines local abundance, the correlation between abundance and generalism should be positive and strong for climbers but null (or even negative) for their hosts.

2. Material and methods

2.1. Study site and sampling design

The study area is located in the Northern Central Iberian Plateau, Spain, within a remnant temperate forest located at the margins of the Cega River (ETRS89 UTM 30N coordinate: x 394682.55; y 4579316.17). This forest is included as a protected area in the Natura Network 2000 (LIC-ES4180070). Although the area has a typical cool-Mediterranean climate with 12 °C annual average temperature and 480 mm annual precipitation, microclimate conditions associated with valley topography has allowed the relict temperate vegetation to persist since the end of the last glacial period (Soriano et al., 2002). The studied forest harbors over 50 species of trees, shrubs, and climbing plants, including temperate shrubs such as *Lonicera xylosteum*, *Viburnum opulus*, *Crataegus monogyna*, *Rhamnus cathartica*, *Cornus sanguinea*, *Prunus spinosa* and *Rubus ulmifolius*, trees like *Corylus avellana*, *Populus nigra*, *Frangula alnus*, *Fraxinus angustifolia* and *Alnus glutinosa*, and climbing plants such as *Hedera helix*, *Lonicera peryclimenum*, *Humulus lupulus*, *Dioscorea communis* and *Bryonia dioica* (Cuesta-Cano et al., 2007).

To characterize the network of interactions between climbing plants and their host trees and shrubs, we haphazardly established forty plots (10 m length, 5 m width) along the riparian forest of the Cega River; plots were 200 m apart from each other. In each plot climber–host interactions were recorded. An interaction between a climbing plant and a host species was considered to occur when the attachment was evident, beyond the mere physical contact between them. Interaction frequency was determined as the number of plots where a species pair interacted. We used this measure of interaction frequency instead of the number of interacting individuals because the difficulty in counting individuals for some species could lead to skewed estimations (see Appendix S1 for photographs of the community that illustrate this point). Accordingly, the number of plots where a given species occurred was used as a surrogate for species abundance in the community. We preferred this proxy for abundance because: 1) estimates based on species cover would lead to misleading estimations of the total surface available for climbing among hosts (mainly due to differences in branch height between trees and shrubs); 2) estimations based on the observed number of interactions could lead to overestimation of the effects of abundance (Vizentin-Bugoni et al., 2014); and 3) interaction frequency was calculated as the number of plots where an interaction occurred, hence a suitable and realistic abundance measure to contrast neutral expectations would be the number of plots where species occur.

2.2. Abundance and nestedness

To explore the effect of species abundance on nestedness we projected the observed number of interactions into a probability matrix based on species abundance, following Vázquez et al. (2009a). The probability matrix was derived as the product of the vectors of host and climbing plant abundance, with the host i and the climbing plant j

receiving an interaction with a probability based on the product of their relative abundance. The randomization algorithm was run 1000 times, measuring nestedness using four different indices, based on different definitions of nestedness. This approach allowed us to consider the different aspects of nestedness due to the lack of a consensual definition for this concept (Almeida-Neto et al., 2008; Ulrich et al., 2009). We employed two commonly used nestedness indices for binary matrices: Temperature index (Temp) as implemented in “BINMATNEST” (Rodríguez-Gironés and Santamaría, 2006) and “NODF” (Almeida-Neto et al., 2008). For an easy comparison between indices, Temp values were transformed as $N_{tm} = (100 - \text{Temp})/100$ (Bascompte et al., 2003). Weighted networks (i.e. those using interaction frequencies) have been found to be less affected by unevenness in the sampling effort (Blüthgen, 2010). Therefore, two measures of nestedness for quantitative matrices were also employed: “WINE” (Galeano et al., 2009) and “Weighted NODF” (Almeida-Neto and Ulrich, 2011). Finally, since the indices used can be related to matrix fill (or connectance; Almeida-Neto et al., 2008) the procedure was repeated modifying the randomization algorithm to maintain the observed matrix fill. This algorithm starts reassembling interactions until the observed matrix fill is reached. Then, it allocates the remaining interactions within pairs of species that have already received an interaction, also based on abundance probabilities (Appendix B).

We assumed that nestedness deviated from abundance expectations if observed nestedness values were either below 5% or above 95% of the values obtained using null models based on abundance. Observed values above the 95% of null model values would point to other causes contributing to generate the nested pattern, while below the 5% threshold would indicate other mechanisms counteracting the effects of species abundance (e.g. reciprocal specialization).

2.3. Abundance vs. generalism

Levels of generalism can be measured in several ways (Dormann, 2011). Among these, the number of interaction partners (i.e. species degree; Jordano et al., 2003) is the measure more directly related to nestedness patterns (at least in their binary form). Thus, we firstly investigated whether the abundance–species degree relationship differs for climbing plants and their hosts. However, if only this measure is considered, the abundance–generalism causality problem might still apply in the case of climbing plants. Further, even under a non-neutral scenario, host degree can be related to abundance simply because more abundant hosts would have an increased probability to encounter climbing plants capable to infest them (although this would also point to important effects of abundance). Hence, we also explored the relationship between abundance and the d' specialization index (Blüthgen et al., 2006), a measure of specialism independent of abundance. This index is a normalization between 0 and 1 of the Kullback-Leibler relative entropy index (Kullback and Leibler, 1951):

$$d_i = \sum_{j=1} \left(p'_{ij} \cdot \ln \frac{p'_{ij}}{q_j} \right)$$

where p'_{ij} represents the frequency of interaction between species i and species j divided by the total number of interactions of species i , and q_j denotes the availability of species j , in our case calculated as its relative abundance (see Blüthgen et al., 2006 for details of the normalization procedure). Therefore, the index measures the deviation between species use and species availability, regardless of the number of interactions and, in turn, the effects of abundance. Species showing high deviations (i.e. specialists) have values tending to 1, whilst those showing low deviations (i.e. generalists) have values tending to 0. For the sake of simplicity we subtracted this index to 1 (i.e. $1 - d'$; hereafter generalization), to obtain higher values as the generalization level increases.

The Spearman's correlation coefficient was used to measure the

correlation among variables (i.e. between abundance and both species degree and generalization). Further, as correlation does not imply causality, the observed correlation coefficients were also compared with those obtained in the null models based on abundance. A significantly lower correlation was assumed if observed values fell below the lowest 5% correlations of the null models. If generalism determines species abundance we should find that the relationship between species generalization and abundance is positive and stronger than abundance expectations for climbing plants. In the case of hosts this relationship should be similar or even lower than null model expectations based on abundance – assuming that host fitness is either unaffected or strongly affected by climbing plant infestations, respectively. On the contrary, a low correlation between generalization and abundance, together with a high correlation between species degree and abundance (although matching abundance expectations) in both parties, would be indicative of abundance as determinant of generalism.

All analyses were carried out in R environment (R Core and Team, 2015). The indices of nestedness, together with the d' index, were computed using the “bipartite” package (Dormann et al., 2009), and the abundance-based null models were created using the script provided in Vázquez et al. (2009a) and a modified version of it to keep constant matrix fill.

3. Results

We recorded a total of 26 potential host tree and shrub species, of which 24 (11 trees, 11 shrubs and two treelets) had associated climbing plants (Fig. 1). The only two species that were not infested by climbers (*Pinus pinaster* and *Pyrus pyraister*) were actually rare species – only occurring in one plot – and were thus excluded from the subsequent analyses. On the other hand, ten climbing plant species were recorded, six herbaceous vines and four woody climbers (Fig. 1).

Observed nestedness did not significantly deviate from the null models based on abundance for all nestedness indices except NODF ($N_{tm} = 0.75$, $P = 0.40$; WINE = 0.52, $P = 0.39$; and Weighted NODF = 18.1, $P = 0.48$; Fig. 2). NODF values fell below the 5% of null model values (NODF = 55.20, $P = 0.004$), which suggests that other factors counteract the effects of abundance. However, this index was the most sensitive to matrix fill. When matrix fill was accounted for, the observed NODF did not significantly deviate from abundance-based null expectations ($P = 0.15$, Appendix B).

Abundance and species degree were highly correlated for both parties (Spearman's $\rho = 0.84$ and 0.88 , for climbing plants and host respectively, Fig. 3a and b). In both cases the abundance–species degree correlations did not significantly deviate from those obtained with the abundance-based null models (climbing plants: mean null Spearman's $\rho = 0.91$, SD = 0.05, $P = 0.892$; host species: mean null Spearman's $\rho = 0.85$, SD = 0.05, $P = 0.226$). Generalization levels were considerably high in both cases (mean = 0.91, SD = 0.05 and mean = 0.85, SD = 0.12; for climbing plants and hosts, respectively). However, this index was weakly related to abundance for both parties, being its relationship even negative in the case of climbing plants (Spearman's $\rho = -0.1$ and 0.10 , for climbing plants and hosts respectively, Fig. 3c and d). The correlation coefficients were considerably lower than those obtained from the null models based on abundance (climbing plants: mean null Spearman's $\rho = 0.71$, SD = 0.18, $P = 1$; host species: mean null Spearman's $\rho = 0.46$, SD = 0.18, $P = 0.961$). Finally, generalization and species degree were not significantly correlated for both climbing plants (Spearman's $\rho = 0.30$, $P = 0.40$) and their hosts (Spearman's $\rho = 0.22$, $P = 0.31$).

4. Discussion

Our results show that species abundance has a strong effect on the nestedness structure of the studied parasite-host network. This relationship has been previously found for mutualistic networks (Krishna et al.,

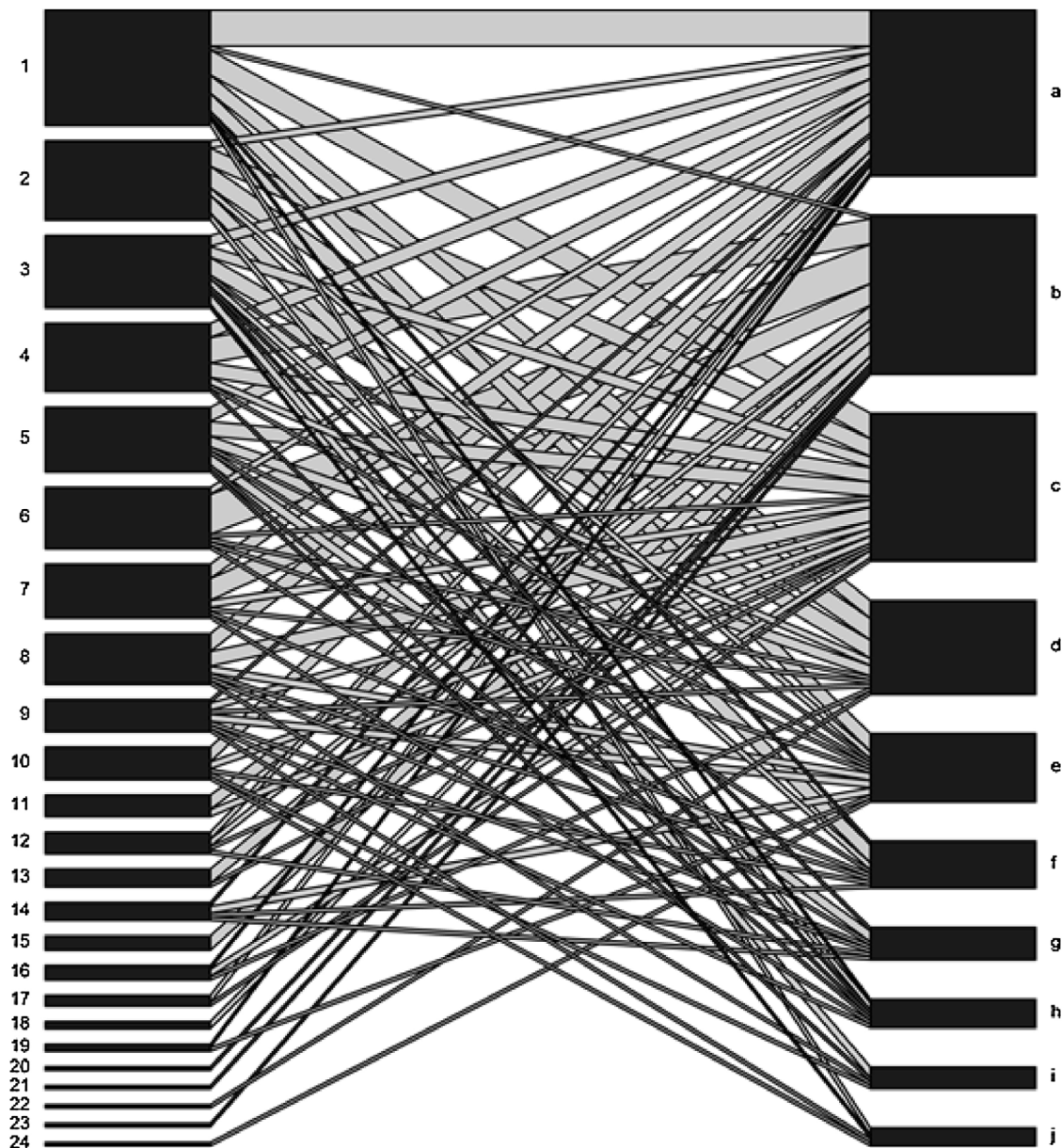


Fig. 1. Climbing plant-host tree/shrub interaction network. Black boxes represent species and their width corresponds to the number of single interactions (i.e. species strength). Grey lines represent species interactions and line thickness indicates the interaction frequency for each pair of interacting species. On the left, tree and shrub host species are depicted by numbers (tr = tree, sh = shrub, tl = treelet). 1: *Ligustrum vulgare* (sh), 2: *Pteridium aquilinum* (sh), 3: *Lonicera xylosteum* (sh), 4: *Crataegus monogyna* (tl), 5: *Viburnum opulus* (sh), 6: *Populus nigra* (tr), 7: *Corylus avellana* (tr), 8: *Cornus sanguinea* (sh), 9: *Prunus spinosa* (sh), 10: *Rhamnus cathartica* (sh), 11: *Fraxinus angustifolia* (tr), 12: *Salix atrocinerea* (tr), 13: *Alnus glutinosa* (tr), 14: *Rubus ulmifolius* (sh), 15: *Betula pendula* (tr), 16: *Salix purpurea* (tl), 17: *Rosa canina* (sh), 18: *Quercus faginea* (tr), 19: *Frangula alnus* (tr), 20: *Alnus incana* (tr), 21: *Euonymus europaeus* (tr), 22: *Juniperus communis* (sh), 23: *Salix fragilis* (tr), 24: *Cytisus scoparius* (sh). On the right, climbing plants are depicted by letters (hv = herbaceous vine, vv = woody vine). a: *Lonicera periclymenum* (vv), b: *Hedera helix* (vv), c: *Humulus lupulus* (hv), d: *Galium aparine* (hv), e: *Vicia villosa* (hv), f: *Dioscorea communis* (hv), g: *Solanum dulcamara* (vv), h: *Vitis vinifera* (vv), i: *Bryonia dioica* (hv), j: *Lathyrus sativus* (hv).

2008; Vázquez et al., 2009a; Verdú and Valiente-Banuet, 2011; Olito and Fox, 2014). However, the causality problem between species abundance and generalism has complicated the identification of the factor actually driving the patterns of interaction nestedness in these networks (Krishna et al., 2008; Fontaine, 2013). Parasite-host networks do not have this problem, at least in the case of hosts, which allows delving into the causality of the abundance-generalism relationship.

Parasites can certainly benefit from being generalist by increasing the chance of finding a suitable host, while hosts attacked by more species should not necessarily show higher abundance or fitness. In this context, similar high correlations between abundance and species degree for climbing plants and their hosts were recorded, both being clearly within the expected range that was derived from our null models based on abundance. These similarities between parasites and hosts

suggest that abundance is the main determinant of generalism in the studied interaction network. It could be argued, however, that the abundance-generalism causality problem still holds for the (structural) parasites. Yet, we found complementary evidence supporting species abundance as the driver of generalism. Neither climbing plants nor their hosts showed a significant relationship between generalization and both abundance and species degree. Firstly, our results suggest that generalization levels do not have a positive impact on the abundance of climbing plants, as it is expected if abundance determines generalism. Secondly, our results also show that species degree (which is the measure of generalism most directly related to nestedness) is more strongly determined by abundance than by generalization levels. The cases of *V. vinifera* and *H. helix* clearly illustrate these findings. The former is one of the species with highest generalization levels in the

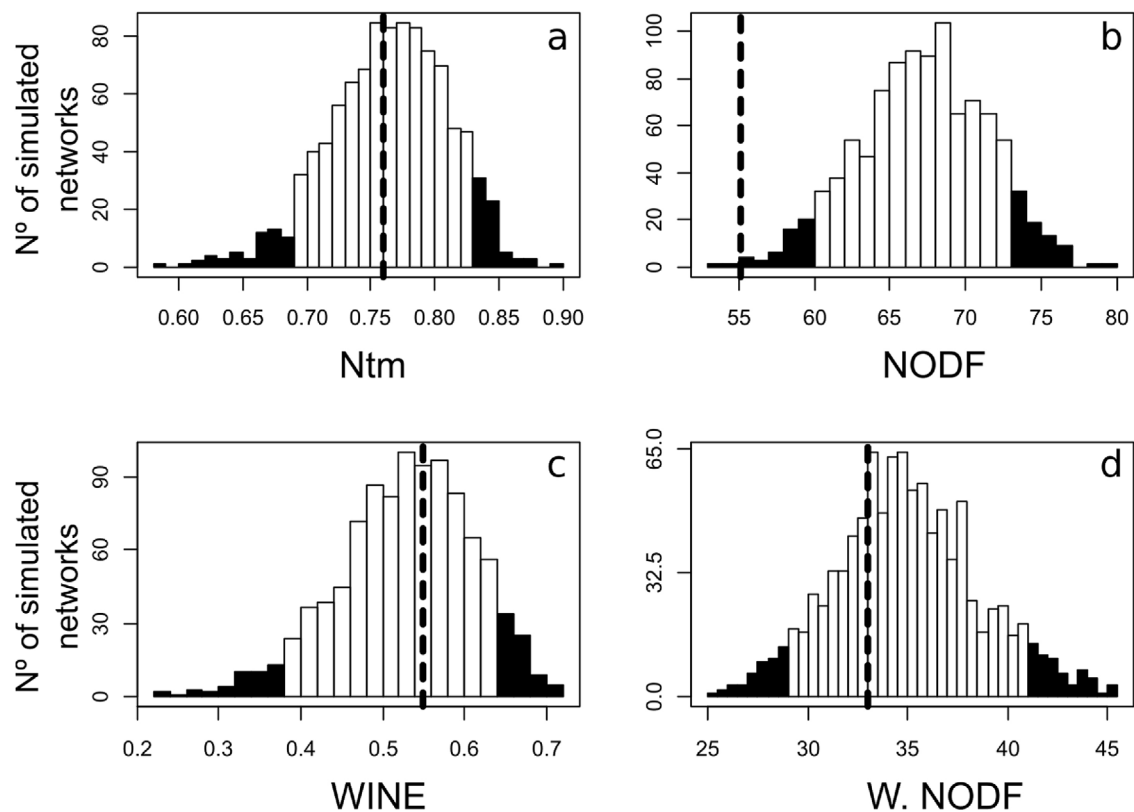


Fig. 2. Distribution of nestedness based on species abundance among 1000 simulated networks for the four indices of nestedness used: a) N_{tm} , b) NODF, c) WINE and d) weighted NODF. The observed values (dotted lines) are above the lowest 5% and below the highest 95% of the nestedness values derived from the abundance-based null models (depicted in black). The only exception is NODF, where the observed values are below the lowest 5% null values (but see also Appendix 2).

study site, showing nevertheless one of the lowest values for both species degree and abundance (see Fig. 3). Conversely, *H. helix* shows the lowest generalization level, although it is one of the species with highest values of species degree and abundance (see Fig. 3). This implies that the probability of infestation by a climbing plant depends on host abundance. Climbing plants are in general opportunistic (Blick and Burns, 2011), being able to colonize new hosts as long as they have access to them, regardless of their different levels of generalization. In any case, these results confirm the role of abundance as a key factor for network properties in the study system at both the species and structural levels (*i.e.*, generalism and nestedness, respectively). Recent evidence of abundance as a cause of generalism for mutualistic networks provides additional support for our findings (Fort et al., 2016).

Opposing the hypothesis of abundance as determinant of nestedness patterns, Suweis et al. (2013) found that increases in species abundance – accompanied by increases in dominance – lead to increases in nestedness as a consequence of positive interactions. Therefore they proposed that nestedness in mutualistic networks could be a consequence of optimizing species abundance across all species present in the community. However, our results do not support such interpretation – at least for host-parasite networks, since we found both that empirical nestedness values are consistent with those obtained assuming neutral interactions, and that abundance determines species degree. In fact, Blüthgen et al. (2008) found that higher degrees of dominance lead to higher degrees of nestedness simply through neutral processes in the allocation of interactions. This would apply to either mutualistic or antagonistic networks. It could be argued that the mechanisms underlying the interaction patterns in mutualistic and antagonistic networks are fundamentally different, so the agreement between abundance and nestedness would result from contrasting mechanisms in different types of networks. However, following the principle of parsimony (Sober, 1981; see also Blüthgen et al., 2008), it seems more likely that the effect

of abundance on nestedness is a direct result of the neutral distribution of interactions throughout all the individuals present in the community. A number of studies in several types of networks have found similar effects of species abundance on nestedness (Vázquez et al., 2009a; Verdú and Valiente-Banuet, 2011; Lima et al., 2012; Dáttilo et al., 2013; Sáyago et al., 2013; Olito and Fox, 2014; but see Canard et al., 2014; Vizentin-Bugoni et al., 2014), thus supporting the general validity of this hypothesis for explaining the nestedness structure of interaction networks.

Contrary to our findings, Canard et al. (2014) found that abundance did not explain nestedness variation in ectoparasite-rodent networks. Nevertheless, it is important to note that these results were based on the NODF index. In fact, the results of the present study using such index were similar to those of Canard et al. (2014), but we have also shown that they were strongly affected by matrix fill. When controlling for matrix filling, nestedness did not significantly deviate from abundance expectations. Thus, it is likely that the lack of relationship found by Canard et al. (2014) resulted from the particular index they used. Indeed, these authors found good agreement between abundance and network properties related to nestedness, such as levels of specialization. Alternatively, there are clear biological differences between their study system and ours, which could also partly explain the contrasting results. Ectoparasite-rodent interactions are more intimate than climbing plant-host interactions, and interaction intimacy may influence network structure significantly (Guimarães et al. 2007; Pires and Guimarães, 2013).

It is important to note that other factors besides species dominance and neutral allocation of interactions could influence network properties, such as the abovementioned interaction intimacy. In this sense, we do not argue that abundance is the sole factor determining network structure. Other factors are known to contribute to network properties, such as the spatio-temporal overlapping of individuals from different levels (*e.g.* Vázquez et al., 2009a; Olito and Fox, 2014), trait matching

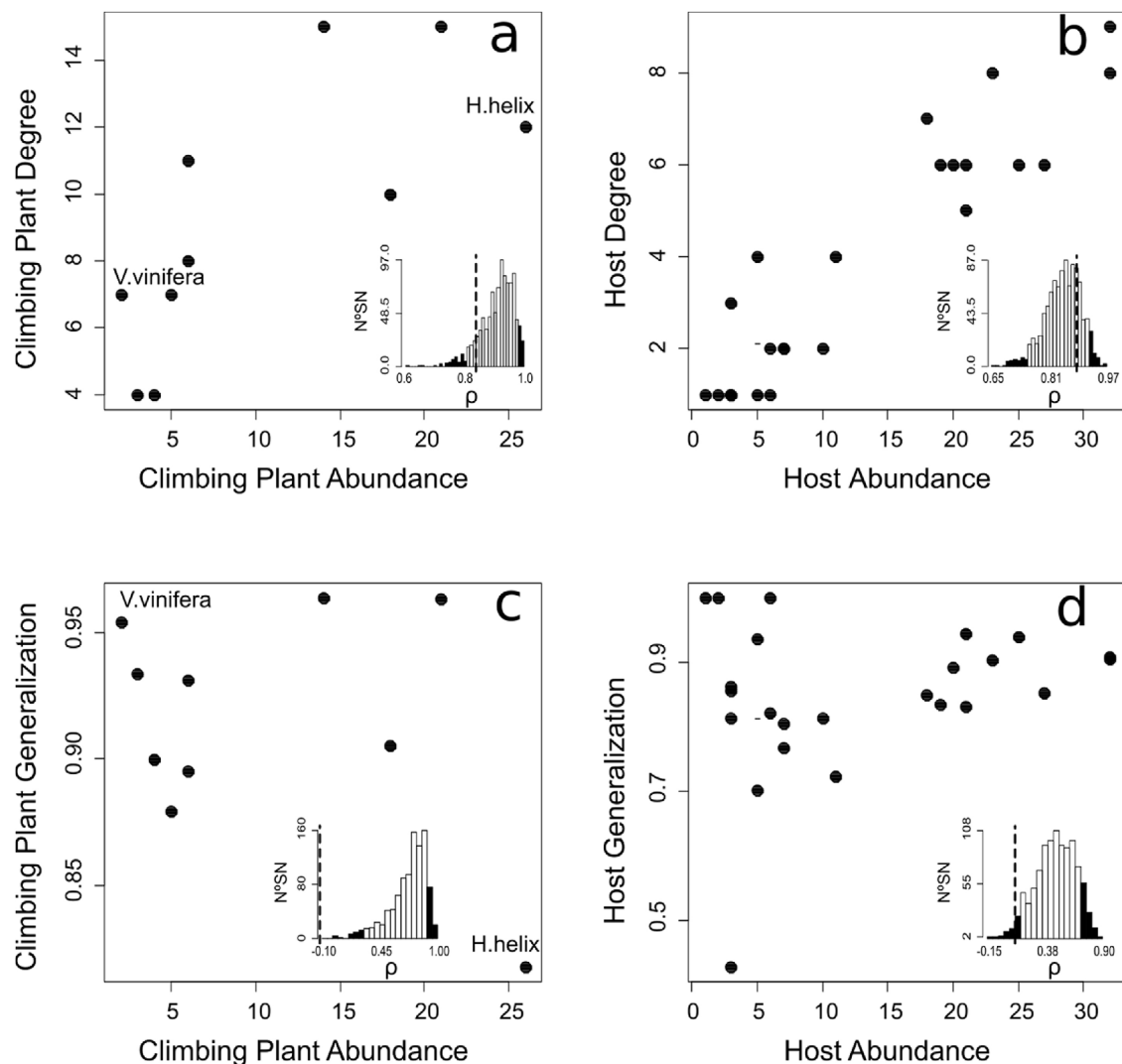


Fig. 3. Relationships between abundance and both species degree (a and b, for climbing plants and hosts respectively) and generalization (c and d, for climbing plants and hosts respectively). The points corresponding to *H. helix* and *V. vinifera* are labeled as examples showing low and high generalization levels, respectively, but high and low values of abundance and species degree, respectively (see main text). The histogram on the bottom of each scatterplot represents the distribution of Spearman's ρ correlation coefficients between abundance and generalism estimates based on species abundance among 1000 simulated networks (N°SN). The observed values (dotted lines) are above the lowest 5% of the coefficients derived from the null models (depicted in black) in the case of species degree, whereas observed values are below the lowest 5% null values for generalization level.

(e.g. Vizentin-Bugoni et al., 2014) or trait mismatching (Verdú and Valiente-Banuet, 2011). Hence, it seems clear that both neutral and niche processes act together as drivers of interaction patterns. In fact, current efforts are focused on disentangling the relative contribution of both types of processes to network structure (Vázquez et al., 2009a; Verdú and Valiente-Banuet, 2011; Sáyo et al., 2013; Olito and Fox, 2014; Vizentin-Bugoni et al., 2014). Here, we argue that future research efforts should also pay attention to which combinations of the intrinsic conditions of ecological communities boost either neutral or niche-based processes. As we have shown, these intrinsic conditions include uneven abundance distributions, but spatial heterogeneity, intimacy levels, functional trait diversity, phylogenetic diversity and even the diversity on the species geographic affinities (Calatayud et al., 2016) should also be considered when analyzing interaction networks. Detailed information from a diverse array of study systems is yet required to determine the hierarchical contribution of all these factors to neutral or niche-based processes (Vázquez et al., 2009b). Before such data are available, we propose that the species-abundance distribution plays a major role in promoting different levels of nestedness through the neutral allocation of species interactions.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ppees.2017.04.003>.

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