

# A continuum of specialists and generalists in empirical communities

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1 Understanding the persistence of specialists and generalists within ecological communities is  
2 a topical research question, with far-reaching consequences for the maintenance of functional  
3 diversity. Although theoretical studies indicate that restricted conditions may be necessary  
4 to achieve coexistence between specialists and generalists, analyses of larger empirical (and  
5 species-rich) communities reveal the pervasiveness of coexistence. In this paper, we analyze 175  
6 ecological bipartite networks of three interaction types (animal hosts-parasite, plant-herbivore  
7 and plant-pollinator), and measure the extent to which these communities are composed of  
8 species with different levels of specificity in their biotic interactions. We find a continuum from  
9 specialism to generalism. Furthermore, we demonstrate that diversity tends to be greatest in  
10 networks with intermediate connectance, and argue this is because of physical constraints in  
11 the filling of networks.

12 **Keywords:** bipartite networks; specificity; nestedness; modularity; food webs; parasites; polli-  
13 nators; herbivores

## 14 Introduction

15 The functional diversity of ecological communities emerges through the simultaneous occur-  
16 rence of species with contrasted resource use [1], habitat selection [2], and interactions [3,4].  
17 Both empirical and theoretical studies have shown how different degrees of niche partitioning  
18 can promote functional diversity [5–7]. However, the co-occurrence of specialist and generalist  
19 species has received considerably less attention. The majority of studies seeking to understand  
20 the conditions for co-occurrence between populations of specialists and generalists in both  
21 biotic (*e.g.* predator–prey, host–parasite) and abiotic (*e.g.* habitat choice) interactions have fo-  
22 cused on small communities [8–13]. Approaches based on model analysis or controlled experi-  
23 ments have two features impeding their generalization to large communities. First, the number  
24 of interacting organisms is often kept low, either to facilitate model analysis or because of ex-  
25 perimental constraints. In practice, this means that studies investigating the co-occurrence of  
26 species with contrasted specificities assume no intermediate situations between the endpoints

1 of specialism and generalism, whereas natural systems exhibit more of a continuum [14,15].  
2 Second, it is unclear to what extent results can be scaled up to more realistic communities.  
3 Stouffer and colleagues [16] showed that because adding species and interactions increases the  
4 potential for complex population dynamical feedbacks, complete, realistic networks tend to  
5 exhibit different behaviors than simple modules (*i.e.* those typically used in models or experi-  
6 ments), begging for an analysis of co-occurrence in empirical communities.

7 Network theory offers powerful tools to characterize the complexity of ecological communities  
8 [17] and the degree of specialisation of the species within them [18]. In a species interaction  
9 network, each species is a node, and each interaction is an edge, connecting a pair of nodes.  
10 From a network perspective, measuring the specificity of a species can be performed by count-  
11 ing the number of links it has with other species, or to study the distribution of the strengths  
12 of such links [18]. Previous work described the degree-distribution of empirical networks, *i.e.*  
13 the fact that there is a continuum of species, ranging from highly specialized to generalists  
14 [19]. While much is known about the factors (*e.g.* biotic [20], abiotic [13,14], developmen-  
15 tal and physiological [21]) driving the specialization of single species, less is known about the  
16 spectrum of specificities and niche-overlaps that can co-occur in large ecological networks, and  
17 reasons for different spectra. As the co-occurrence and interactions between specialized and  
18 generalized species is key to maintaining functional diversity [2], promoting community sta-  
19 bility [22], and ensuring network persistence [3], there is a need to investigate the exact extent  
20 of this co-occurrence.

21 In a previous paper [1], we argued that the mechanisms shaping the evolution of specificity  
22 were similar for both antagonistic and mutualistic interactions, which implies that relation-  
23 ships between specificity, the co- occurrence of specialists and generalists, and other metrics  
24 of community structure should be similar across different types of ecological interaction, de-  
25 spite each category of network having different structural properties. One central result of the  
26 analyses presented in the present contribution is that empirical data show consistently more  
27 variation in specificities of all species on the upper trophic level (hereafter called “strategy di-  
28 versity”) than predicted by two contrasting null models. This suggests that organisms with

1 very different levels of specificity can co-occur in most natural systems.

2 In this paper, we use a large dataset of species interaction networks spanning three contrasted  
3 types of ecological interactions (herbivory, parasitism, and mutualism), to characterize to what  
4 extent species with different specificities can co- occur within the same community. Impor-  
5 tantly, we find a continuum from networks of mostly-specialized to mostly-generalized species,  
6 with the potential for specialist/generalist co-occurrence being greater at intermediate points.

7 Strategy diversity is contingent upon network properties, including nestedness (a measure of  
8 niche overlap between species with different specificities), modularity (the fact that species in-  
9 teract within loosely connected clusters), and connectance (the proportion of realized links),  
10 emphasizing the need to adopt a network-oriented methodology in the study of biotic interac-  
11 tions at the community level.

## 12 **Methods**

### 13 **Datasets**

14 We employ three datasets: two for antagonistic (ectoparasite–animal host and insect herbivore–  
15 plant) interactions, and one for mutualistic (pollinator–plant) interactions. Parasitism networks  
16 were collected by Stanko and colleagues [23] and consist of 121 networks of ectoparasites in-  
17 fecting rodents in Central Europe, collected in a range of continental ecosystems over a period  
18 of 19 years. Herbivory networks (a total of 23) were collected by Thébault and Fontaine [24]  
19 from various literature records. Data on mutualistic interactions are the 29 “plant–pollinators”  
20 networks deposited in the *InteractionWeb* database (<http://www.nceas.ucsb.edu/interactionweb/>)  
21 as of May 2012. These data are insect–plant contacts, aggregated from different sources, span-  
22 ning a period of over 30 years. Species with no interaction were removed from the original  
23 datasets. Some networks had less than 1000 possible randomizations, which did not allow for  
24 efficient or meaningful randomisation [25], and as such were discarded from the analysis. The  
25 final dataset has 115 parasitism networks, 6 herbivory networks, and 12 pollination networks.

1 Because the sample size is unbalanced, we put particular emphasis on the discussion of para-  
2 sitism networks.

### 3 **Network analyses**

4 Each bipartite network is represented by its adjacency matrix  $\mathbf{M}$  with  $T$  rows (for the upper  
5 level, *i.e.* ectoparasites, herbivores, and pollinators) and  $L$  columns (for the lower level, *i.e.* an-  
6 imal hosts and plants being eaten or pollinated). In each network,  $\mathbf{M}_{ij}$  represents the existence  
7 of an interaction between species  $i$  and species  $j$  [26]. For each network, we calculate its size  
8 ( $Z = L \times T$ ), and connectance ( $Co$ , the proportion of established interactions). We focus our  
9 analyses on the upper level, since we have more knowledge of specialization mechanisms for  
10 these organisms [27]. Nestedness is calculated using the NODF (Nestedness based on Overlap  
11 and Decreasing Fill) measure [28], which is insensitive to network shape (asymmetry in the  
12 number of species at each of the two trophic levels) and size. Modularity is estimated using the  
13 LP-BRIM method [29], which both increases modularity detection compared to the adaptive  
14 BRIM method, and is less computationally intensive [30]. For each network, we retained the  
15 highest modularity  $Q_{bip}$  [31] observed in a total of 1000 replicate runs.

16 We contrast empirical observations with the predictions of two different null models, each  
17 based on the impact of different aspects of network structure (connectance, and degree distri-  
18 bution in the whole network). For each null model, we filled a network through a Bernoulli pro-  
19 cess, in which the probability of each pairwise species interaction occurring ( $P_{ij}$ ) is determined  
20 in one of the following ways. Null model I [32] is connectance based and assigns the same  
21 probability to each interaction,  $P_{ij} = Co$ . Compared to the empirical network on which they are  
22 based, simulated networks can have the same connectance, but a potentially different degree  
23 distribution. Null model II [3] uses information about species degree to calculate the proba-  
24 bility that a particular interaction will occur. This probability is  $P_{ij} = (T \times G_i + L \times V_j) / (2 \times Z)$ ,  
25 where  $G_i$  and  $V_j$  are, respectively, the generality (number of interactions) of upper level species  
26  $i$ , and the vulnerability (number of interactions) of lower level species  $j$  [33]. Simply put, the  
27 probability of the interaction occurring is the mean of the degrees (ranged in 0–1) of the two

1 species involved. Note that the first null model is nested into the second.  
 2 Each of these models was applied to each network in the dataset, so as to generate 1000 random  
 3 networks (meaning that each empirical network was fed into the model to generate a total of  
 4 2000 randomizations). Each of these networks was analyzed in the same way as empirical  
 5 networks.

## 6 **Quantifying specificity**

7 We quantify specificity based on the proportion of available species with which a focal species  
 8 interacts [18], using a ranged version of Schoener’s generality. For each species  $i$  of the upper  
 9 level (*e.g.* parasites), its specificity is given by

$$10 \mathbf{s}_i = \frac{L-l_i}{L-1}$$

11 where  $L$  is the number of lower level species (*e.g.* hosts) found in the network, and  $l_i$  is the  
 12 number of interaction partners of species  $i$ . The vector  $\mathbf{s}$  is the distribution of specificities at  
 13 the network scale. Values of 1 indicate complete specialism (single partner), and values of 0  
 14 indicate complete generalism (all possible partners).

## 15 **Quantifying strategy diversity**

16 We quantify two aspects of the co-occurrence of specialists and generalists (*i.e.* “strategy di-  
 17 versity”). First, “specificity range” or  $R$ , is simply the difference between the specificity of the  
 18 most and least specialized organisms, such that

$$19 R = \max(\mathbf{s}) - \min(\mathbf{s})$$

20  $R$  is maximized when at least one completely specialized species  $k$  ( $\mathbf{s}_k = 1$ ) is found in the same  
 21 network as one (or more) completely generalized species  $l$  ( $\mathbf{s}_l = 0$ ).

22 A second measure of the distribution of specificities within a network is its evenness, denoted  $E$ .  
 23 We define  $\mathbf{s}'$  as all the unique values of  $\mathbf{s}$ , rounded to the second decimal place. We define  $U$  as  
 24 the ordered set of  $\mathbf{s}'$  values and  $u$  as each of the elements of this set. Thus  $p(u)$  is the probability

associated to a given element of  $U$ . For example, if  $\mathbf{s}' = [0.1, 1, 1, 0, 0.4]$ , then  $U = [0, 0.1, 0.4, 1]$ ,  $p(u = 1) = 2/5$ , and  $p(u = 0) = 1/5$ . With this information, we calculate the self-information [34] of  $u$  as  $I(u) = -\ln(u)$ , and based on these two sets of values, we calculate the Shannon's entropy of the distribution of specificity values as

$$H = \sum_{u \in U} [p(u)I(u)]$$

If  $U$  takes on  $N$  possible values, then the theoretical maximum of  $H$  (attained when all values of  $\mathbf{s}'$  are unique, *i.e.* no two species share the same degree of specificity) is

$$H_{\max} = \ln(N)$$

To eliminate any scaling effect that might occur due to different network sizes, we take the exponentials of these values [35], such that the standardized value of  $E$  is

$$E = e^{H-H_{\max}}$$

$E = 1$  when no two organisms have the same level of specificity, and  $E = 0$  when all values of  $\mathbf{s}'$  are equal. Note that rounding to the second decimal place allows accounting for the fact that some organisms may have very similar (but not exactly equal) specificities. Small differences in the values of specificity are less important than the potential amplitude of measurement error, as preliminary tests indicated that the degree to which values of  $\mathbf{s}'$  are rounded does not qualitatively change observed relationships. It is also known that small differences in link strength have little to no impact in larger networks [36].

Finally, we present a simple summary statistic that we call “strategy diversity” ( $D$ ),

$$D = \frac{1}{2}(E + R)$$

which given that both  $E$  and  $R$  take values in  $[0, 1]$ , will also return values in this range.  $D = 1$  indicates that the specificity values found in a network range from highly specialized to highly generalized *and* are evenly distributed.  $D = 0$  means that a network is composed entirely of species sharing the same specificity values. The two advantages of  $D$  are (i) it accounts both for the range of specificities and their distribution, and (ii) it is independent of the observed specificity values. We expect strategy diversity ( $D$ ) to peak at intermediate values of connectance



1 and specificity, to increase with nestedness, and to decrease with modularity (Fig. 1). The rea-  
2 soning is as follows. Interaction matrices are physically constrained objects, in that adding  
3 interactions will modify their properties, and thus produce artifacts [25,37]. By definition, a  
4 perfectly nested network maximizes strategy diversity [28], and a modular network tends to  
5 minimize it. A matrix with minimal fill for a given size has all interactions on the diagonal,  
6 and is therefore highly specialized, with no strategy diversity. Conversely, a completely filled  
7 network is extremely generalized, and thus has no strategy diversity.

## 8 Results

9 All types of networks tend to have more strategy diversity and to be composed of more spe-  
10 cialized species than expected by chance. For each empirical network, we measure whether  
11 its structural properties (strategy diversity, nestedness, modularity) are higher or lower than  
12 expected by chance using the two null models. Our results are reported in Table 1. Both null  
13 models gave consistent results regarding whether the empirical networks represented a devia-  
14 tion from the random expectations. Host-parasite networks are on average less modular than  
15 expected, herbivory networks are more, and there is no clear trend in pollination networks.  
16 There is a marked tendency towards higher than expected nestedness in all types of interac-  
17 tions.

18 Figure 2 presents the distributions of specificity, connectance, nestedness, and modularity in  
19 networks that are either more or less functionally diverse than expected under the assumptions  
20 of null model II (using the outcomes of model I yields the same qualitative results; see Table  
21 1). Regardless of the baseline differences between types of network for each of the metrics con-  
22 sidered, higher diversity responded in a consistent way to variation in the other metrics. Net-  
23 works with higher average specificity tended to have lower average strategy diversity, higher  
24 connectance, higher nestedness, and lower modularity (Table 2). Of all these, there are signifi-  
25 cant interactions between all of the variables and the network having higher strategy diversity  
26 than expected by chance, with the exception of modularity (Table 3). These four metrics alone

1 account for 96% of the variance of strategy diversity, and 63% of the variance in the deviation  
2 of this same metric. All metrics except modularity had a significant impact on the strategy  
3 diversity. Interestingly, connectance was the best predictor of strategy diversity, whereas nest-  
4 edness was the best predictor of the how much strategy diversity in the empirical networks  
5 deviates from random expectations. This is because by definition, null model testing removes  
6 most of the effects of connectance. The type of ecological interaction was not significant; detect-  
7 ing possible significance would have probably required a larger sample size for non-parasitic  
8 networks.

9 We finally look at the relationships between network metrics and strategy diversity (Fig. 3).  
10 Strategy diversity increases with connectance (it is expected to be 0 for a connectance of 1, but  
11 no network in our dataset is densely connected), decreases with average specificity (as before,  
12 strategy diversity is 0 if the average specificity is 0), increases linearly with nestedness, and  
13 decreases with modularity. An interesting result in this analysis is that the trend is the same  
14 for all three types of interaction considered, with the exception that herbivory and pollination  
15 networks tended to occupy the “low connectance” end of the gradient; they behave in the same  
16 way as do parasitism networks, reinforcing the idea that structural constraints such as that  
17 introduced by connectance may be driving emergent network properties.

## 18 Discussion

19 Several mechanisms have been proposed to explain the co-occurrence of potentially competing  
20 species, including behavior [???], spatial or temporal heterogeneity [???], and trade-offs associ-  
21 ated with species interactions [???,??,??]. Ecological factors such as environmental and spatial  
22 heterogeneity and evolutionary processes such as niche partitioning may permit the coexis-  
23 tence between competing species with similar and/or different number of resources [???,??].  
24 However, most of these results were obtained in systems of low complexity, and the extent to  
25 which specialists and generalists co-occur in natural communities remains to be evaluated. By  
26 analyzing three bipartite network datasets covering a range of both ecological and structural

1 situations, we show how co-occurrence can be linked with other topological network proper-  
 2 ties. This calls for a better integration of network methodology to the analysis of community  
 3 structure, so as to evaluate the importance of emerging properties as drivers of the maintenance  
 4 of species with different specificities.

5 ??? showed that most emergent network properties could be predicted based on connectance.  
 6 This included, notably, components of the degree distribution involved in determining nested-  
 7 ness. The results presented here suggest that although the relationship between connectance,  
 8 emergent metrics (such as nestedness and modularity), and strategy diversity is conserved  
 9 across types of ecological interactions (the strength of this assertion being tempered by the low  
 10 sample size for herbivory and mutualism networks), the differences between interaction types  
 11 stemmed mostly from networks having different connectances. Specifically, host-parasite net-  
 12 works were more connected than the other types, but all three types of interaction had an equal  
 13 proportion (approximately two-thirds) of networks with more strategy diversity than expected  
 14 by chance. Overall, we report that networks with higher nestedness and lower modularity,  
 15 also had more strategy diversity than expected under the assumptions of the two null models.  
 16 This observation offers promising new research perspectives. If the main difference between  
 17 interaction types is their connectance, then the different mechanisms involved must be studied  
 18 alongside their impacts on network structure. Species specialization is regulated by differences  
 19 in life-history traits [???], competition for access to resources [???,?], or phylogenetic conser-  
 20 vatism in attack/defense strategies [???]. Through their impact on species range of resources  
 21 used, these factors are likely to be involved in driving network structure, and connectance in  
 22 particular. For example, in herbivorous systems, plants may employ multiple defenses against  
 23 enemies, including the release of toxic compounds [???] and/or attraction of a herbivore's natu-  
 24 ral enemies [???,??,??,??]. The simultaneous existence of different levels of defense such as those  
 25 mentionned above may promote lower connectance. It can also result in the faster diversifi-  
 26 cation of exploitation strategies at the upper level (in the sense that enemies specialize on a  
 27 *defense mechanism* rather than on the set of defended species) than in other types of interac-  
 28 tions relying on narrower sets of mechanisms [???]. This may result in the maintenance of high

1 strategy diversity relative to connectance in some antagonistic interactions.

2 In summary, although the ecological nature of an interaction (mutualistic or antagonistic) has  
3 an impact on network structure, strategy diversity that is higher than expected by chance seems  
4 to be a conserved property in bipartite ecological networks. The particular position occupied  
5 by a network along a continuum of, *e.g.* connectance or nestedness, can emerge because of  
6 the life-history traits of species establishing interactions {{ref}}, and we suggest that increased  
7 attention should be given to understanding how fine- scale mechanisms at the individual or  
8 population level drive the structure of community-level networks. It is nonetheless clear that  
9 despite theoretical predictions, generalists and specialists are often found together in nature.  
10 Understanding this gap between predictions and observations will be a major challenge, one  
11 that should be addressed by understanding the mechanisms of coexistence and co-occurrence  
12 in large multi-species communities.

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## 23 Figures

24 **Figure 1.** Cartoon depiction of the expected relationships between connectance and other met-  
25 rics.

26 **Figure 2.** Values of average specificity, nestedness, connectance, and modularity for networks

1 with more (orange) or less (purple) strategy diversity than expected by chance. The results  
2 within a type of interaction are all highly consistent. For this analysis *only*, networks that were  
3 as functionally diverse as expected (as determined by the Null Models) were removed, as their  
4 diversity of strategies can be explained only by their connectance or degree distribution.

5 **Figure 3.** Scatterplot of strategy diversity versus other network metrics. It is clear that regard-  
6 less of the interaction type, diversity of strategies responds in a similar way to other network  
7 metrics. Points are colored as in Figure 2. Triangles are host-parasite systems, squares are  
8 plants-herbivores, and circles are plants-pollinators.

## 9 Tables

10 **Table 1.** Results of the null models analyses. For each network metric, and for each null  
11 model, we indicate the proportion of networks that had significantly larger or smaller values  
12 of this metric than expected by chance. A network has a significantly different value from the  
13 prediction when the empirical value falls outside of the 95% confidence interval for the value  
14 as measured on the randomized networks [???].

15 **Table 2.** Analysis of the results presented in Fig. 2. We used a two-sampled t-test to determine  
16 differences from chance expectations for metric networks with either, less, as much, or more  
17 strategy diversity. We observe that all metrics are different for parasitism networks, but not for  
18 other interaction types (although our failure to report an effect is most likely due to the small  
19 sample size, as attested by some extremely large confidence intervals).

20 **Table 3.** Analysis of variance partitioning (ANOVA on a linear additive models) of the effects  
21 of connectance, nestedness, average specificity, and modularity, on strategy diversity, and the  
22 excess diversity of strategy (deviation of empirical values from simulated networks as assessed  
23 by the Null Model analysis). Preliminary analyses showed no impact of the interaction type on  
24 these relationships, so this was not included as a covariate.

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