

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] and species persistence [8]. However, the co-occurrence
19 of specialist and generalist species has received considerably less attention. The majority of
20 studies seeking to understand the conditions for co-occurrence between populations of spe-
21 cialists and generalists in both biotic (*e.g.* predator–prey, host–parasite) and abiotic (*e.g.* habitat
22 choice) interactions have focused on small communities [9–14]. Approaches based on model
23 analysis or controlled experiments have two features impeding their generalization to large
24 communities. First, the number of interacting organisms is often kept low, either to facilitate
25 model analysis or because of experimental constraints. In practice, this means that studies in-
26 vestigating the co-occurrence of species with contrasted specificities assume no intermediate

1 situations between the endpoints of specialism and generalism, whereas natural systems ex-
2 hibit more of a continuum [15,16]. Second, it is unclear to what extent results can be scaled
3 up to more realistic communities. Stouffer and colleagues [17] showed that because adding
4 species and interactions increases the potential for complex population dynamical feedbacks,
5 complete, realistic networks tend to exhibit different behaviors than simple modules (*i.e.* those
6 typically used in models or experiments), begging for an analysis of co-occurrence in empirical
7 communities.

8 Network theory offers powerful tools to characterize the complexity of ecological communities
9 [18] and the associated degree of species specialisation within them [19]. In a species interac-
10 tion network, each species is a node, and each interaction is an edge, connecting a pair of nodes.
11 From a network perspective, measuring the specificity of a species can be performed by count-
12 ing the number of links it has with other species, or to study the distribution of the strengths
13 of such links [19]. Previous work described the degree-distribution of empirical networks, *i.e.*
14 the fact that there is a continuum of species, ranging from highly specialized to generalists
15 [20]. While much is known about the factors (*e.g.* biotic [21], abiotic [14,15], developmen-
16 tal and physiological [22]) driving the specialization of single species, less is known about the
17 spectrum of specificities and niche-overlaps that can co-occur in large ecological networks, and
18 reasons for different spectra. As the co-occurrence and interactions between specialized and
19 generalized species is key to maintaining functional diversity [2], promoting community sta-
20 bility [23], and ensuring network persistence [3], there is a need to investigate the extent and
21 properties of this co-occurrence.

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

1 two contrasting null models. This suggests that organisms with very different levels of speci-
2 ficity can co-occur in most natural systems.

3 In this paper, we use a large dataset of species interaction networks spanning three contrasted
4 types of ecological interactions (herbivory, parasitism, and mutualism), to characterize to what
5 extent species with different specificities can co- occur within the same community. Import-
6 tantly, we find a continuum from networks of mostly-specialized to mostly-generalized species,
7 with the potential for specialist/generalist co-occurrence being greater at intermediate points.
8 Strategy diversity is contingent upon network properties, including nestedness (a measure of
9 niche overlap between species with different specificities), modularity (the fact that species in-
10 teract within loosely connected clusters), and connectance (the proportion of realized links),
11 emphasizing the need to adopt a network-oriented methodology in the study of biotic interac-
12 tions at the community level.

13 **Methods**

14 **Datasets**

15 We employ three datasets: two for antagonistic (ectoparasite–animal host and insect herbivore–
16 plant) interactions, and one for mutualistic (pollinator–plant) interactions. Parasitism networks
17 were collected by Stanko and colleagues [24] and consist of 121 networks of ectoparasites in-
18 fecting rodents in Central Europe, collected in a range of continental ecosystems over a period
19 of 19 years. Herbivory networks (a total of 23) were collected by Thébault and Fontaine [25]
20 from various literature records. Data on mutualistic interactions are the 29 “plant–pollinators”
21 networks deposited in the *InteractionWeb* database (<http://www.nceas.ucsb.edu/interactionweb/>)
22 as of May 2012. These data are insect–plant contacts, aggregated from different sources, span-
23 ning a period of over 30 years. Species with no interaction were removed from the original
24 datasets. Some networks had less than 1000 possible randomizations, which did not allow for
25 efficient or meaningful randomisation [26], and as such were discarded from the analysis. The

1 final dataset has 115 parasitism networks, 6 herbivory networks, and 12 pollination networks.
2 Because the sample size is unbalanced, we put particular emphasis on the discussion of para-
3 sitism networks.

4 **Network analyses**

5 Each bipartite network is represented by its adjacency matrix \mathbf{M} with T rows (for the upper
6 level, *i.e.* ectoparasites, herbivores, and pollinators) and L columns (for the lower level, *i.e.*
7 animal hosts and plants being consumed or pollinated). In each network, \mathbf{M}_{ij} represents the
8 existence of an interaction between species i and species j [27]. For each network, we calculate
9 its size ($Z = L \times T$), and connectance (Co , the proportion of established interactions). We focus
10 our analyses on the upper level, since we have more knowledge of specialization mechanisms
11 for these organisms [28]. Nestedness is calculated using the NODF (Nestedness based on Over-
12 lap and Decreasing Fill) measure [29], which is insensitive to network shape (asymmetry in the
13 number of species at each of the two trophic levels) and size. Modularity is estimated using the
14 LP-BRIM method [30], which both increases modularity detection compared to the adaptive
15 BRIM method, and is less computationally intensive [31]. For each network, we retained the
16 highest modularity Q_{bip} [32] observed in a total of 1000 replicate runs.

17 We contrast empirical observations with the predictions of two different null models, each
18 based on the impact of different aspects of network structure (connectance, and degree distri-
19 bution in the whole network). For each null model, we filled a network through a Bernoulli pro-
20 cess, in which the probability of each pairwise species interaction occurring (P_{ij}) is determined
21 in one of the following ways. Null model I [33] is connectance based and assigns the same
22 probability to each interaction, $P_{ij} = Co$. Compared to the empirical network on which they are
23 based, simulated networks can have the same connectance, but a potentially different degree
24 distribution. Null model II [3] uses information about species degree to calculate the proba-
25 bility that a particular interaction will occur. This probability is $P_{ij} = (T \times G_i + L \times V_j) / (2 \times Z)$,
26 where G_i and V_j are, respectively, the generality (number of interactions) of upper level species
27 i , and the vulnerability (number of interactions) of lower level species j [34]. Simply put, the

1 probability of the interaction occurring is the mean of the degrees (ranged in 0–1) of the two
2 species involved. Note that the first null model is nested into the second.

3 Each of these models was applied to each network in the dataset, so as to generate 1000 random
4 networks (meaning that each empirical network was fed into the model to generate a total of
5 2000 randomizations). Each of these networks was analyzed in the same way as empirical
6 networks.

7 **Quantifying specificity**

8 We quantify specificity based on the proportion of available species with which a focal species
9 interacts [19], using a ranged version of Schoener’s generality. For each species i of the upper
10 level (*e.g.* parasites), its specificity is given by

$$11 \quad \mathbf{s}_i = \frac{L-l_i}{L-1}$$

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

16 **Quantifying strategy diversity**

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

$$20 \quad R = \max(\mathbf{s}) - \min(\mathbf{s})$$

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

23 A second measure of the distribution of specificities within a network is its evenness, denoted E .

24 We define \mathbf{s}' as all the unique values of \mathbf{s} , rounded to the second decimal place. We define U as

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 [35] 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 [36], 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 [37].

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 [26,38]. By definition, a
4 perfectly nested network maximizes strategy diversity [29], 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 network tend to have more strategy diversity and to be composed of more spe-
10 cialized species than expected by chance (Table 1). For each empirical network, we mea-
11 sure whether its structural properties (strategy diversity, nestedness, modularity) are higher
12 or lower than expected by chance using the two null models. Our results are reported in Table
13 1. Both null models gave consistent results regarding whether the empirical networks repre-
14 sented a deviation from the random expectations. Host-parasite networks are on average less
15 modular than expected, herbivory networks are more, and there is no clear trend in pollination
16 networks. There is a marked tendency towards higher than expected nestedness in all types of
17 interactions.

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 1).
21 Regardless of the baseline differences between types of network for each of the metrics consid-
22 ered, higher diversity responded in a consistent way to variation in the other metrics. Networks
23 with higher average specificity tended to have lower average strategy diversity, higher con-
24 nectance, higher nestedness, and lower modularity (Table 2). There are significant interactions
25 between all of the variables and the network having higher strategy diversity than expected
26 by chance, with the exception of modularity (Table 3). These four metrics alone account for

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

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

17 Discussion

18 Several mechanisms have been proposed to explain the co-occurrence of potentially competing
19 species, including behavior [13], spatial or temporal heterogeneity [9], and trade-offs associ-
20 ated with species interactions [1,12,39]. Ecological factors such as environmental and spatial
21 heterogeneity and evolutionary processes such as niche partitioning may permit the coexis-
22 tence between competing species with similar and/or different number of resources [40,41].
23 However, most of these results were obtained in systems of low complexity, and the extent to
24 which specialists and generalists co-occur in natural communities remains to be evaluated. By
25 analyzing three bipartite network datasets covering a range of both ecological and structural
26 situations, we show how co-occurrence can be linked with other topological network proper-

1 ties. This calls for a better integration of network methodology to the analysis of community
2 structure, with the aim of understanding the co-occurrence of species with different specific-
3 ties.

4 Most emergent network properties could be predicted based on connectance alone [26]. This
5 included, notably, components of the degree distribution involved in determining nestedness.
6 The results presented here suggest that although the relationship between connectance, emer-
7 gent metrics (such as nestedness and modularity), and strategy diversity is conserved across
8 types of ecological interactions (the strength of this assertion being tempered by the low sam-
9 ple size for herbivory and mutualism networks), the differences between interaction types
10 stemmed mostly from networks having different connectances. Specifically, host-parasite net-
11 works were more connected than the other types, but all three types of interaction had an equal
12 proportion (approximately two-thirds) of networks with more strategy diversity than expected
13 by chance. Overall, we report that networks with higher nestedness and lower modularity,
14 also had more strategy diversity than expected under the assumptions of the two null models.
15 This observation offers promising new research perspectives. If the main difference between
16 interaction types is their connectance, then the different mechanisms involved must be studied
17 alongside their impacts on network structure. Species specialization is regulated by differences
18 in life-history traits [1], competition for access to resources [40,42], or phylogenetic conser-
19 vatism in attack/defense strategies [43]. Through their impact on species range of resources
20 used, these factors are likely to be involved in driving network structure, and connectance in
21 particular. For example, in herbivorous systems, plants may employ multiple defenses against
22 enemies, including the release of toxic compounds [44] and/or attraction of a herbivore's nat-
23 ural enemies [45–48]. The simultaneous existence of different levels of defense such as those
24 mentionned above may promote lower connectance. It can also result in the faster diversifi-
25 cation of exploitation strategies at the upper level (in the sense that enemies specialize on a
26 *defense mechanism* rather than on the set of defended species) than in other types of interac-
27 tions relying on narrower sets of mechanisms [15]. This may result in the maintenance of high
28 strategy diversity relative to connectance in some antagonistic interactions.

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

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14 computational support. We thank É. Thébault and C. Fontaine for sharing data for plants
15 and herbivores systems. The bipy package used for the analyses, and the C99 program used
16 for the generation of random networks under the three null models are available at <http://github.com/tpoisot/bipy> and <http://github.com/tpoisot/CNullModels>. # Figures

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

20 **Figure 2.** Values of average specificity, nestedness, connectance, and modularity for networks
21 with more (orange) or less (purple) strategy diversity than expected by chance. The results
22 within a type of interaction are all highly consistent. For this analysis *only*, networks that
23 were as functionally diverse as expected (as determined by the Null Models) were removed,
24 since their diversity of strategies can be explained solely by either their connectance or degree
25 distribution.

26 **Figure 3.** Scatterplot of strategy diversity versus other network metrics. Regardless of the in-
27 teraction type, diversity of strategies responds in a similar way to other network metrics. Points
28 are colored as in Figure 2. Triangles are host-parasite systems, squares are plants-herbivores,

1 and circles are plants-pollinators.

2 Tables

3 **Table 1.** Results of the null models analyses. For each network metric, and for each null model,
4 we indicate the proportion of networks that had significantly larger or smaller values than
5 expected by chance. A network has a significantly different value from the prediction when
6 the empirical value falls outside of the 95% confidence interval for the value as measured on
7 randomized networks [49].

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

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

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