

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 [poisot2011a], habitat selection [devictor2010],
17 and interactions [bascompte2003; weiner2012]. Both empirical and theoretical studies have
18 shown how different degrees of niche partitioning can promote functional diversity [diaz2001;
19 @petchey2002; @ackerly2007]. However, the co-occurrence of specialist and generalist species
20 has received considerably less attention. The majority of studies seeking to understand the
21 conditions for co-occurrence between populations of specialists and generalists in both bi-
22 otic (e.g. predator-prey, host-parasite) and abiotic (e.g. habitat choice) interactions have fo-
23 cused on small communities [wilson1994; hochberg1990a; demeeus1995; egas2004;
24 @abrams2006; @ravigne2009]. Approaches based on model analysis or controlled experiments
25 have two features impeding their generalization to large communities. First, the number of
26 interacting organisms is often kept low, either to facilitate model analysis or because of ex-

1 perimental constraints. In practice, this means that studies investigating the co-occurrence of
2 species with contrasted specificities assume no intermediate situations between the endpoints
3 of specialism and generalism, whereas natural systems exhibit more of a continuum [foris-
4 ter_revisiting_2012; @poisot_structure_2013]. Second, it is unclear to what extent results can be
5 scaled up to more realistic communities. @stouffer_understanding_2009 showed that because
6 adding species and interactions increases the potential for complex population dynamical feed-
7 backs, complete, realistic networks tend to exhibit different behaviors than simple modules (*i.e.*
8 those typically used in models or experiments), begging for an analysis of co-occurrence in em-
9 pirical communities.

10 Network theory offers powerful tools to characterize the complexity of ecological commu-
11 nities [proulx_network_2005] and the degree of specialisation of the species within them
12 [poisot_mee]. In a species interaction network, each species is a node, and each interaction is
13 an edge, connecting a pair of nodes. From a network perspective, measuring the specificity of a
14 species can be performed by counting the number of links it has with other species, or to study
15 the distribution of the strengths of such links [poisot_comparative_2012]. Previous work de-
16 scribed the degree-distribution of empirical networks, *i.e.* the fact that there is a continuum
17 of species, ranging from highly specialized to generalists [otto_allometric_2007]. While much
18 is known about the factors (*e.g.* biotic [thrall_coevolution_2007], abiotic [ravigne_live_2009;
19 forister_revisiting_2012], developmental and physiological [ferry-graham_using_2002]) driv-
20 ing the specialization of single species, less is known about the spectrum of specificities and
21 niche-overlaps that can co-occur in large ecological networks, and reasons for different spec-
22 tra. As the co-occurrence and interactions between specialized and generalized species is key
23 to maintaining functional diversity [devictor_defining_2010], promoting community stabil-
24 ity [hassell_generalist_1986], and ensuring network persistence [bascompte_2003], there is
25 a need to investigate the exact extent of this co-occurrence.

26 In a previous paper [poisot_conceptual_2011], we argued that the mechanisms shaping the
27 evolution of specificity were similar for both antagonistic and mutualistic interactions, which
28 implies that relationships between specificity, the co- occurrence of specialists and generalists,

1 and other metrics of community structure should be similar across different types of ecolog-
2 ical interaction, despite each category of network having different structural properties. One
3 central result of the analyses presented in the present contribution is that empirical data show
4 consistently more variation in specificities of all species on the upper trophic level (hereafter
5 called “strategy diversity”) than predicted by two contrasting null models. This suggests that
6 organisms with very different levels of specificity can co-occur in most natural systems.

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

17 **Methods**

18 **Datasets**

19 We employ three datasets: two for antagonistic (ectoparasite–animal host and insect herbivore–
20 plant) interactions, and one for mutualistic (pollinator–plant) interactions. Parasitism networks
21 were collected by @stanko_mammal_2002 and consist of 121 networks of ectoparasites infect-
22 ing rodents in Central Europe, collected in a range of continental ecosystems over a period of 19
23 years. Herbivory networks (a total of 23) were collected by @thebault_stability_2010 from vari-
24 ous literature records. Data on mutualistic interactions are the 29 “plant–pollinators” networks
25 deposited in the *InteractionWeb* database (<http://www.nceas.ucsb.edu/interactionweb/>) as

1 of May 2012. These data are insect–plant contacts, aggregated from different sources, spanning
2 a period of over 30 years. Species with no interaction were removed from the original datasets.
3 Some networks had less than 1000 possible randomizations, which did not allow for efficient
4 or meaningful randomisation [poisot_when_2013], and as such were discarded from the anal-
5 ysis. The final dataset has 115 parasitism networks, 6 herbivory networks, and 12 pollination
6 networks. Because the sample size is unbalanced, we put particular emphasis on the discussion
7 of parasitism networks.

8 **Network analyses**

9 Each bipartite network is represented by its adjacency matrix \mathbf{M} with T rows (for the upper
10 level, *i.e.* ectoparasites, herbivores, and pollinators) and L columns (for the lower level, *i.e.*
11 animal hosts and plants being eaten or pollinated). In each network, \mathbf{M}_{ij} represents the ex-
12 istence of an interaction between species i and species j [dunne_network_2006]. For each
13 network, we calculate its size ($Z = L \times T$), and connectance (Co, the proportion of established
14 interactions). We focus our analyses on the upper trophic level, since we have more knowledge
15 of specialization mechanisms for these organisms [*e.g.* futuyma_evolution_1988]. Nested-
16 ness is calculated using the NODF (Nestedness based on Overlap and Decreasing Fill) mea-
17 sure [almeida-neto-consistent_2008], which is insensitive to network shape (asymmetry in
18 the number of species at each of the two trophic levels) and size. Modularity is estimated
19 using the LP-BRIM method [liu_community_2010], which both increases modularity detec-
20 tion compared to the adaptive BRIM method, and is less computationally intensive [bar-
21 ber_detecting_2009]. For each network, we retained the highest modularity [Q_{bip} *sensu*
22 barber_modularity_2007] observed in a total of 1000 replicate runs.

23 We contrast empirical observations with the predictions of two different null models, each
24 based on the impact of different aspects of network structure (connectance, and degree distri-
25 bution in the whole network). For each null model, we filled a network through a Bernoulli
26 process, in which the probability of each pairwise species interaction occurring (P_{ij}) is deter-
27 mined in one of the following ways. Null model I [*e.g.* fortuna_habitat_2006] is connectance

1 based and assigns the same probability to each interaction, $P_{ij} = C_o$. Compared to the empiri-
2 cal network on which they are based, simulated networks can have the same connectance, but a
3 potentially different degree distribution. Null model II [bascompte_nested_2003] uses infor-
4 mation about species degree to calculate the probability that a particular interaction will occur.
5 This probability is $P_{ij} = (T \times G_i + L \times V_j) / (2 \times Z)$, where G_i and V_j are, respectively, the generality
6 (number of interactions) of upper level species i , and the vulnerability (number of interactions)
7 of lower level species j [schoener_food_1989]. Simply put, the probability of the interaction
8 occurring is the mean of the degrees (ranged in 0–1) of the two species involved. Note that the
9 first null model is nested into the second.

10 Each of these models was applied to each network in the dataset, so as to generate 1000 random
11 networks (meaning that each empirical network was fed into the model to generate a total of
12 2000 randomizations). Each of these networks was analyzed in the same way as empirical
13 networks.

14 **Quantifying specificity**

15 We quantify specificity based on the proportion of available species with which a focal species
16 interacts [poisot_comparative_2012 and references therein], using a ranged version of Schoener's
17 generality. For each species i of the upper level (*e.g.* parasites), its specificity is given by

$$18 \quad s_i = \frac{L - l_i}{L - 1}$$

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

1 Quantifying strategy diversity

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

$$5 \quad R = \max(\mathbf{s}) - \min(\mathbf{s})$$

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

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

9 We define \mathbf{s}' as all the unique values of \mathbf{s} , rounded to the second decimal place. We define U as
10 the ordered set of \mathbf{s}' values and u as each of the elements of this set. Thus $p(u)$ is the probability
11 associated to a given element of U . For example, if $\mathbf{s}' = [0.1, 1, 1, 0, 0.4]$, then $U = [0, 0.1, 0.4, 1]$,
12 $p(u = 1) = 2/5$, and $p(u = 0) = 1/5$. With this information, we calculate the self-information
13 [shannon_mathematical_1948] of u as $I(u) = -\ln(u)$, and based on these two sets of values, we
14 calculate the Shannon’s entropy of the distribution of specificity values as

$$15 \quad H = \sum_{u \in U} [p(u)I(u)]$$

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

$$18 \quad H_{\max} = \ln(N)$$

19 To eliminate any scaling effect that might occur due to different network sizes, we take the
20 exponentials of these values [bersier_quantitative_2002], such that the standardized value of
21 E is

$$22 \quad E = e^{H-H_{\max}}$$

23 $E = 1$ when no two organisms have the same level of specificity, and $E = 0$ when all values of \mathbf{s}'
24 are equal. Note that rounding to the second decimal place allows accounting for the fact that
25 some organisms may have very similar (but not exactly equal) specificities. Small differences
26 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 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 [berlow_interaction_2004].

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 and specificity, to increase with nestedness, and to decrease with modularity (Fig. 1). The reasoning is as follows. Interaction matrices are physically constrained objects, in that adding interactions will modify their properties, and thus produce artifacts [miklos_randomization_2004;poisot_when_2013]. By definition, a perfectly nested network maximizes strategy diversity [almeida-neto_consistent_2008], and a modular network tends to minimize it. A matrix with minimal fill for a given size has all interactions on the diagonal, and is therefore highly specialized, with no strategy diversity. Conversely, a completely filled network is extremely generalized, and thus has no strategy diversity.

Results

All types of networks tend to have more strategy diversity and to be composed of more specialized species than expected by chance. For each empirical network, we measure whether its structural properties (strategy diversity, nestedness, modularity) are higher or lower than expected by chance using the two null models. Our results are reported in Table 1. Both null models gave consistent results regarding whether the empirical networks represented a deviation from the random expectations. Host-parasite networks are on average less modular than

1 expected, herbivory networks are more, and there is no clear trend in pollination networks.
2 There is a marked tendency towards higher than expected nestedness in all types of interac-
3 tions.

4 Figure 2 presents the distributions of specificity, connectance, nestedness, and modularity in
5 networks that are either more or less functionally diverse than expected under the assumptions
6 of null model II (using the outcomes of model I yields the same qualitative results; see Table
7 1). Regardless of the baseline differences between types of network for each of the metrics con-
8 sidered, higher diversity responded in a consistent way to variation in the other metrics. Net-
9 works with higher average specificity tended to have lower average strategy diversity, higher
10 connectance, higher nestedness, and lower modularity (Table 2). Of all these, there are signifi-
11 cant interactions between all of the variables and the network having higher strategy diversity
12 than expected by chance, with the exception of modularity (Table 3). These four metrics alone
13 account for 96% of the variance of strategy diversity, and 63% of the variance in the deviation
14 of this same metric. All metrics except modularity had a significant impact on the strategy
15 diversity. Interestingly, connectance was the best predictor of strategy diversity, whereas nest-
16 edness was the best predictor of the how much strategy diversity in the empirical networks
17 deviates from random expectations. This is because by definition, null model testing removes
18 most of the effects of connectance. The type of ecological interaction was not significant; detect-
19 ing possible significance would have probably required a larger sample size for non-parasitic
20 networks.

21 We finally look at the relationships between network metrics and strategy diversity (Fig. 3).
22 Strategy diversity increases with connectance (it is expected to be 0 for a connectance of 1, but
23 no network in our dataset is densely connected), decreases with average specificity (as before,
24 strategy diversity is 0 if the average specificity is 0), increases linearly with nestedness, and
25 decreases with modularity. An interesting result in this analysis is that the trend is the same
26 for all three types of interaction considered, with the exception that herbivory and pollination
27 networks tended to occupy the “low connectance” end of the gradient; they behave in the same
28 way as do parasitism networks, reinforcing the idea that structural constraints such as that

1 introduced by connectance may be driving emergent network properties.

2 **Discussion**

3 Several mechanisms have been proposed to explain the co-occurrence of potentially competing
4 species, including behavior [abrams_prerequisites_2006], spatial or temporal heterogeneity
5 [wilson_coexistence_1994], and trade-offs associated with species interactions [mcpeek_trade-
6 offs_1996; egas_evolution_2004; poisot_conceptual_2011]. Ecological factors such as envi-
7 ronmental and spatial heterogeneity and evolutionary processes such as niche partitioning may
8 permit the coexistence between competing species with similar and/or different number of re-
9 sources [bascompte_asymmetric_2006; poullain_evolution_2008]. However, most of these
10 results were obtained in systems of low complexity, and the extent to which specialists and
11 generalists co-occur in natural communities remains to be evaluated. By analyzing three bi-
12 partite network datasets covering a range of both ecological and structural situations, we show
13 how co-occurrence can be linked with other topological network properties. This calls for a
14 better integration of network methodology to the analysis of community structure, so as to
15 evaluate the importance of emerging properties as drivers of the maintenance of species with
16 different specificities.

17 poisot_when_2013 showed that most emergent network properties could be predicted based
18 on connectance. This included, notably, components of the degree distribution involved in
19 determining nestedness. The results presented here suggest that although the relationship
20 between connectance, emergent metrics (such as nestedness and modularity), and strategy di-
21 versity is conserved across types of ecological interactions (the strength of this assertion being
22 tempered by the low sample size for herbivory and mutualism networks), the differences be-
23 tween interaction types stemmed mostly from networks having different connectances. Specif-
24 ically, host-parasite networks were more connected than the other types, but all three types of
25 interaction had an equal proportion (approximately two-thirds) of networks with more strat-
26 egy diversity than expected by chance. Overall, we report that networks with higher nestedness

1 and lower modularity, also had more strategy diversity than expected under the assumptions
2 of the two null models. This observation offers promising new research perspectives. If the
3 main difference between interaction types is their connectance, then the different mechanisms
4 involved must be studied alongside their impacts on network structure. Species specialization
5 is regulated by differences in life-history traits [@poisot_conceptual_2011], competition for ac-
6 cess to resources [@bascompte_asymmetric_2006; @bascompte_plant-animal_2007], or phylo-
7 genetic conservatism in attack/defense strategies [@cavender-bares_merging_2009]. Through
8 their impact on species range of resources used, these factors are likely to be involved in
9 driving network structure, and connectance in particular. For example, in herbivorous sys-
10 tems, plants may employ multiple defenses against enemies, including the release of toxic
11 compounds [@Arimura2005] and/or attraction of a herbivore's natural enemies [@Ode2006;
12 @Wei2007; @Van-Nouhuys2003; @Singer2012]. The simultaneous existence of different levels
13 of defense such as those mentioned above may promote lower connectance. It can also result
14 in the faster diversification of exploitation strategies at the upper level (in the sense that ene-
15 mies specialize on a *defense mechanism* rather than on the set of defended species) than in other
16 types of interactions relying on narrower sets of mechanisms [@Forister2012]. This may re-
17 sult in the maintenance of high strategy diversity relative to connectance in some antagonistic
18 interactions.

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

1 in large multi-species communities.

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12 Figures

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

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

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

1 Tables

2 **Table 1.** Results of the null models analyses. For each network metric, and for each null
3 model, we indicate the proportion of networks that had significantly larger or smaller values
4 of this metric than expected by chance. A network has a significantly different value from the
5 prediction when the empirical value falls outside of the 95% confidence interval for the value
6 as measured on the randomized networks [see *e.g.* @flores_statistical_2011].

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

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