

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 ??? and consist of 121 networks of ectoparasites infecting rodents in Central
17 Europe, collected in a range of continental ecosystems over a period of 19 years. Herbivory net-
18 works (a total of 23) were collected by ??? from various literature records. Data on mutualistic
19 interactions are the 29 “plant–pollinators” networks deposited in the *InteractionWeb* database
20 (<http://www.nceas.ucsb.edu/interactionweb/>) as of May 2012. These data are insect–plant
21 contacts, aggregated from different sources, spanning a period of over 30 years. Species with
22 no interaction were removed from the original datasets. Some networks had less than 1000
23 possible randomizations, which did not allow for efficient or meaningful randomisation [???],
24 and as such were discarded from the analysis. The final dataset has 115 parasitism networks,
25 6 herbivory networks, and 12 pollination networks. Because the sample size is unbalanced, we

1 put particular emphasis on the discussion of parasitism networks.

2 **Network analyses**

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

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

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

5 **Quantifying specificity**

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

$$9 \quad s_i = \frac{L-l_i}{L-1}$$

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

14 **Quantifying strategy diversity**

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

$$18 \quad R = \max(\mathbf{s}) - \min(\mathbf{s})$$

19 R is maximized when at least one completely specialized species k ($s_k = 1$) is found in the same
20 network as one (or more) completely generalized species l ($s_l = 0$).

21 A second measure of the distribution of specificities within a network is its evenness, denoted E .
22 We define \mathbf{s}' as all the unique values of \mathbf{s} , rounded to the second decimal place. We define U as
23 the ordered set of \mathbf{s}' values and u as each of the elements of this set. Thus $p(u)$ is the probability
24 associated to a given element of U . For example, if $\mathbf{s}' = [0.1, 1, 1, 0, 0.4]$, then $U = [0, 0.1, 0.4, 1]$,

1 $p(u = 1) = 2/5$, and $p(u = 0) = 1/5$. With this information, we calculate the self-information [??]
2 of u as $I(u) = -\ln(u)$, and based on these two sets of values, we calculate the Shannon's entropy
3 of the distribution of specificity values as

$$4 \quad H = \sum_{u \in U} [p(u)I(u)]$$

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

$$7 \quad H_{\max} = \ln(N)$$

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

$$10 \quad E = e^{H-H_{\max}}$$

11 $E = 1$ when no two organisms have the same level of specificity, and $E = 0$ when all values of \mathbf{s}'
12 are equal. Note that rounding to the second decimal place allows accounting for the fact that
13 some organisms may have very similar (but not exactly equal) specificities. Small differences
14 in the values of specificity are less important than the potential amplitude of measurement
15 error, as preliminary tests indicated that the degree to which values of \mathbf{s}' are rounded does
16 not qualitatively change observed relationships. It is also known that small differences in link
17 strength have little to no impact in larger networks [??].

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

$$19 \quad D = \frac{1}{2}(E + R)$$

20 which given that both E and R take values in $[0, 1]$, will also return values in this range. $D = 1$
21 indicates that the specificity values found in a network range from highly specialized to highly
22 generalized *and* are evenly distributed. $D = 0$ means that a network is composed entirely of
23 species sharing the same specificity values. The two advantages of D are (i) it accounts both for
24 the range of specificities and their distribution, and (ii) it is independent of the observed speci-
25 ficity values. We expect strategy diversity (D) to peak at intermediate values of connectance
26 and specificity, to increase with nestedness, and to decrease with modularity (Fig. 1). The rea-
27 soning is as follows. Interaction matrices are physically constrained objects, in that adding

1 interactions will modify their properties, and thus produce artifacts [???]. By definition, a
2 perfectly nested network maximizes strategy diversity [???], and a modular network tends to
3 minimize it. A matrix with minimal fill for a given size has all interactions on the diagonal,
4 and is therefore highly specialized, with no strategy diversity. Conversely, a completely filled
5 network is extremely generalized, and thus has no strategy diversity.

6 Results

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

16 Figure 2 presents the distributions of specificity, connectance, nestedness, and modularity in
17 networks that are either more or less functionally diverse than expected under the assumptions
18 of null model II (using the outcomes of model I yields the same qualitative results; see Table
19 1). Regardless of the baseline differences between types of network for each of the metrics con-
20 sidered, higher diversity responded in a consistent way to variation in the other metrics. Net-
21 works with higher average specificity tended to have lower average strategy diversity, higher
22 connectance, higher nestedness, and lower modularity (Table 2). Of all these, there are signifi-
23 cant interactions between all of the variables and the network having higher strategy diversity
24 than expected by chance, with the exception of modularity (Table 3). These four metrics alone
25 account for 96% of the variance of strategy diversity, and 63% of the variance in the deviation
26 of this same metric. All metrics except modularity had a significant impact on the strategy

1 diversity. Interestingly, connectance was the best predictor of strategy diversity, whereas nest-
2 edness was the best predictor of the how much strategy diversity in the empirical networks
3 deviates from random expectations. This is because by definition, null model testing removes
4 most of the effects of connectance. The type of ecological interaction was not significant; detect-
5 ing possible significance would have probably required a larger sample size for non-parasitic
6 networks.

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

16 Discussion

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

1 structure, so as to evaluate the importance of emerging properties as drivers of the maintenance
2 of species with different specificities.

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

28 In summary, although the ecological nature of an interaction (mutualistic or antagonistic) has

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

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21 Figures

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

24 **Figure 2.** Values of average specificity, nestedness, connectance, and modularity for networks
25 with more (orange) or less (purple) strategy diversity than expected by chance. The results
26 within a type of interaction are all highly consistent. For this analysis *only*, networks that were

as functionally diverse as expected (as determined by the Null Models) were removed, as their diversity of strategies can be explained only by their connectance or degree distribution.

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

Tables

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

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

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

1. Poisot T, Bever JD, Nemri A, Thrall PH, Hochberg ME (2011) A conceptual framework for the evolution of ecological specialisation. Ecology Letters 14: 841–851. Available: <http://www.ncbi.nlm.nih.gov/pubmed/21699641>.

- 1 2. Devictor V, Clavel J, Julliard R, Lavergne S, Mouillot D, et al. (2010) Defining and mea-
2 suring ecological specialization. *Journal of Applied Ecology* 47: 15–25. doi:[10.1111/j.1365-](https://doi.org/10.1111/j.1365-2664.2009.01744.x)
3 [2664.2009.01744.x](https://doi.org/10.1111/j.1365-2664.2009.01744.x).
- 4 3. Bascompte J, Jordano P, Melián CJ, Olesen JM (2003) The nested assembly of plant–animal
5 mutualistic networks. *Proceedings of the National Academy of Sciences of the United States of*
6 *America* 100: 9383–9387. Available: <http://dx.doi.org/10.1073/pnas.1633576100>.
- 7 4. Weiner J, Xiao S (2012) Variation in the degree of specialization can maintain local diversity
8 in model communities. *Theoretical Ecology* 5: 161–166. Available: [http://www.springerlink.](http://www.springerlink.com/content/34113763815g4j04/http://www.springerlink.com/index/10.1007/s12080-011-0153-)
9 [com/content/34113763815g4j04/http://www.springerlink.com/index/10.1007/s12080-011-0153-](http://www.springerlink.com/content/34113763815g4j04/http://www.springerlink.com/index/10.1007/s12080-011-0153-)
- 10 5. Diaz S, Cabido M (2001) Vive la différence: plant functional diversity matters to ecosystem
11 processes. *Trends in Ecology and Evolution* 16: 646–655. Available: [http://linkinghub.](http://linkinghub.elsevier.com/retrieve/pii/S0169534701022832)
12 [elsevier.com/retrieve/pii/S0169534701022832](http://linkinghub.elsevier.com/retrieve/pii/S0169534701022832).
- 13 6. Petchey OL, Gaston KJ (2002) Functional diversity (FD), species richness and community
14 composition. *Ecology Letters* 5: 402–411. Available: [http://doi.wiley.com/10.1046/j.](http://doi.wiley.com/10.1046/j.1461-0248.2002.00339.x)
15 [1461-0248.2002.00339.x](http://doi.wiley.com/10.1046/j.1461-0248.2002.00339.x).
- 16 7. Ackerly DD, Cornwell WK (2007) A trait-based approach to community assembly: partition-
17 ing of species trait values into within- and among-community components. *Ecology Letters* 10:
18 135–145. Available: <http://www.ncbi.nlm.nih.gov/pubmed/17257101>.
- 19 8. Wilson DS, Yoshimura J (1994) On the coexistence of specialists and generalists. *The Amer-*
20 *ican Naturalist* 144: 692–707. Available: [http://www.journals.uchicago.edu/doi/abs/10.](http://www.journals.uchicago.edu/doi/abs/10.1086/285702)
21 [1086/285702](http://www.journals.uchicago.edu/doi/abs/10.1086/285702).
- 22 9. Hochberg ME, Hassell MP, May RM (1990) The dynamics of host-parasitoid-pathogen in-
23 teractions. *The American Naturalist* 135: 74–94. Available: [http://www.jstor.org/stable/](http://www.jstor.org/stable/2462139)
24 [2462139](http://www.jstor.org/stable/2462139).
- 25 10. De Meeûs T, Hochberg ME, Renaud F (1995) Maintenance of two genetic entities by habitat
26 selection. *Evolutionary Ecology* 9: 131–138.

- 1 11. Egas M, Dieckmann U, Sabelis MW (2004) Evolution restricts the coexistence of specialists
2 and generalists: the role of trade-off structure. *The American Naturalist* 163: 518–531.
- 3 12. Abrams PA (2006) The prerequisites for and likelihood of generalist-specialist coexistence.
4 *The American Naturalist* 167: 329–342.
- 5 13. Ravigné V, Dieckmann U, Olivieri I (2009) Live where you thrive: Joint evolution of habitat
6 choice and local adaptation facilitates specialization and promotes diversity. *The American*
7 *Naturalist* 174: 141–169.
- 8 14. Forister ML, Dyer LA, Singer MS, Stireman III JO, Lill JT (2012) Revisiting the evolution
9 of ecological specialization, with emphasis on insect–plant interactions. *Ecology* 93: 981–991.
10 Available: <http://www.esajournals.org/doi/abs/10.1890/11-0650.1>.
- 11 15. Poisot T, Lounnas M, Hochberg ME (2013) The structure of natural microbial enemy-victim
12 networks. *Ecological Processes*.
- 13 16. Stouffer DB, Bascompte J (2009) Understanding food-web persistence from local to global
14 scales. *Ecology Letters* 13: 154–161.
- 15 17. Proulx S, Promislow D, Phillips P (2005) Network thinking in ecology and evolution.
16 *Trends in Ecology and Evolution* 20: 345–353. Available: [http://www.sciencedirect.com/](http://www.sciencedirect.com/science/article/pii/S0169534705000881)
17 [science/article/pii/S0169534705000881](http://www.sciencedirect.com/science/article/pii/S0169534705000881).
- 18 18. Poisot T, Canard E, Mouquet N, Hochberg ME (2012) A comparative study of ecological
19 specialization estimators. *Methods in Ecology and Evolution* 3: 537–544. doi:[10.1111/j.2041-](https://doi.org/10.1111/j.2041-210X.2011.00174.x)
20 [210X.2011.00174.x](https://doi.org/10.1111/j.2041-210X.2011.00174.x).
- 21 19. Otto SB, Rall BC, Brose U (2007) Allometric degree distributions facilitate food-web stabil-
22 ity. *Nature* 450: 1226–1229. Available: <http://www.ncbi.nlm.nih.gov/pubmed/18097408>.
- 23 20. Thrall PH, Hochberg ME, Burdon JJ, Bever JD (2007) Coevolution of symbiotic mutualists
24 and parasites in a community context. *Trends in Ecology and Evolution* 22: 120–126.
- 25 21. Ferry-Graham LA, Bolnick DI, Wainwright PC (2002) Using functional morphology to
26 examine the ecology and evolution of specialization. *Integrative and Comparative Biology* 42:

1 265–277.

2 22. Hassell M, May R (1986) Generalist and specialist natural enemies in insect predator-prey
3 interactions. The Journal of Animal Ecology 55: 923–940. Available: [http://www.jstor.org/
4 stable/10.2307/4425](http://www.jstor.org/stable/10.2307/4425).