

# Intraspecific variability drives diversity in food webs

Carlos J. Melián<sup>1,2</sup>, César Vilas<sup>3,4</sup>, Francisco Baldó<sup>3,5</sup>, Enrique González-Ortegón<sup>3</sup>, Pilar Drake<sup>3</sup>  
& Richard J. Williams<sup>6</sup>

<sup>1</sup>*National Center for Ecological Analysis and Synthesis, University of California, 735 State St., Suite 300, Santa Barbara, CA 93101, USA.*

<sup>2</sup>*Center for Ecology, Evolution and Biogeochemistry, Swiss Federal Institute of Aquatic Science and Technology, Seestrasse 79, Kastanienbaum CH-6047, Switzerland.*

<sup>3</sup>*Instituto de Ciencias Marinas de Andalucía (CSIC), Apdo. Oficial, 11510 Puerto Real, Cádiz, Spain.*

<sup>4</sup>*IFAPA, Centro El Toruño, Camino Tiro de Pichón s/n, 11500 El Puerto de Santa María, Cádiz, Spain.*

<sup>5</sup>*Instituto Español de Oceanografía, Centro Oceanográfico de Cádiz, Apdo. 2609, 11006 Cádiz, Spain.*

<sup>6</sup>*Microsoft Research Ltd., 7J.J. Thomson Avenue, Cambridge CB3 0FB, UK.*

**Biodiversity theories neglect individual-level variability in ecological interactions even though empirical work has revealed considerable genetic and phenotypic variation among individuals in natural populations. This impedes assessing the impact of individual-level variability on biodiversity in multi-trophic ecosystems. Here we use a density-dependent and individual-based food web model, tested against the largest individual-based food web to date, to show that non-random intraspecific variation in prey selection alters species diversity in food webs. Predators consuming many prey increase diversity by preferentially selecting common prey; predators consuming few prey inhibit diversity by preferentially selecting rare prey, putting them at risk of extinction. Thus species-level patterns cannot be explained by species-level averages, but instead must consider individual-level variation in prey selection. Individual-**

**level variation occurs in many biological and social contexts, suggesting that analyses of individual-level interaction data will be relevant in a wide range of fields.**

The paradox of low diversity being predicted by food web theory but high diversity being observed in nature has been discussed intensively for more than a half-century<sup>1-5</sup>. In recent years, a great deal of progress towards understanding the link between the structure and dynamics of food webs and its implications for species diversity has been made<sup>6-12</sup>. Despite this work, finer-grained analysis reconciling the empirical evidence of intraspecific variation<sup>13,14</sup> with diversity patterns in food webs has been lacking<sup>15-23</sup>. Long-term empirical data and competitive models of resource use predict species coexistence only if intraspecific trait variability is higher than interspecific trait variability<sup>24-26</sup>. Recent demonstrations that intraspecific variation in resource use and response to fluctuating environments exceeds the differences in species-level averages within ecological communities suggest that some individuals are specialized while others use a wide range of resources during their life cycle<sup>26-28</sup>. It also suggests that patterns found in relationships between traits of individuals may differ significantly from the patterns of relationships found between species-level means<sup>13,29-31</sup>. Intraspecific variation in resource use can enable coexistence within an ecological community, but individual variation in prey selection across prey with different abundance can lead to species extinctions in food webs. If most of the intraspecific variation in prey selection is concentrated in rare and highly profitable prey species, then we can expect multiple extinctions in the prey community and a high probability of food webs collapse<sup>15,32,33</sup>. On the other hand, if prey selection by individual predators drives a rare species advantage in which host-specific natural enemies control each species when it becomes abundant, then we can expect highly diverse food webs<sup>34-36</sup>.

To date, the lack of high resolution individual-based food web data sets, with thousands of individual diets and independent measures of prey abundance, has made it impossible to test the role of intraspecific variation in prey selection on species coexistence in complex food webs<sup>7,37</sup>.

Here we will test these ideas in a general framework using multiple years of individual diet samples and independent estimates of prey and predator abundance in different environmental conditions in three regions of the Guadalquivir river, southern Spain. The data include 47 predator and prey species with approximately 100,000 individuals sampled and have sufficient resolution and number of species to permit inference at individual- and species-levels simultaneously (“Section A” SI). This combination of individual resolution and large number of species is not available from previous data sets, which are either focused on a few thousands individuals in a few species or on a few individuals per species in food webs with a large number of species <sup>7,37–39</sup>.

We developed a suite of individual-based food web models <sup>40</sup>, shown schematically in figure 1, to quantify the effect of intraspecific variation in predator populations on diversity in food webs. From observations of prey consumption for each individual predator, and independent estimates of prey and predator abundance, we inferred two biologically plausible mechanisms to predict the variability in prey selection across individual predators and how the partitioning of this variation across prey with different abundances alters food web diversity (“Methods Summary” and “Methods”): (1) At the beginning of the simulation all individual predators have equal ability to learn from each successful experience in prey hunting in the sense that a successful encounter increases their probability of future successful encounters (Fig. S1, SI). This ability captures the speed of learning represented by  $\alpha$ . Consider the following ecologically reasonable scenario in which individuals of abundant prey species tend to occur in high-density patches but individuals from rare prey species tend to be more spatially isolated. We assume an individual predator that finds a high-density patch will then be highly connected to the abundant prey species in that patch. Conversely, a predator that never finds a patch will be weakly connected to the rare prey species, and (2) Finding a high or low density patch with individuals of abundant or rare prey species can be a consequence of chance and not an active prey selection process. In order to distinguish random encounters from active searching of common or rare prey we explore the strength of prey selection by strongly and

weakly connected individual predators by changing profitability across prey species with different abundances (“Methods Summary”). At one extreme, rare prey are at an advantage, with predators eating common prey more frequently than expected under random encounters (i.e., negative density-dependent prey selection), while at the other extreme larger and more profitable rare prey are eaten with higher probability than small and common prey (i.e., positive density-dependent prey selection).

The models generate changes over time in the number of prey items per individual predator, the strength of prey selection across strongly and weakly connected individual predators as a function of prey abundance, and the number of coexisting species in the food web as a function of the strength in prey selection. Aggregated across the whole Guadalquivir estuary food web, the distribution in the number of prey per individual predator is highly heterogeneous with most individuals having a few prey items and a few individuals acting as “hubs” containing more than  $10^3$  items (Fig. 2). The models with learning predict the variance of the number of prey items per individual predator ( $\log(\sigma^2_{data}) = 8.6$ , and the CI [ $\log(\sigma^2_{min}) = 7.3$ ,  $\log(\sigma^2_{max}) = 9.95$ ]) and most part of the distribution, but they fail to capture the lower portion of the distribution of the strongly connected predators. These distributions are qualitatively similar across predator species and in each environmental situation sampled (Figs. S2-S3, SI). The classical random encounter model without learning strongly deviates from the observed data (Fig. 2). This departure from the model without learning persists in each environmental situation for all the predators pooled and after accounting for intraspecific variability within each predator species in each environmental situation ( $p < 10^{-3}$  for all combinations, Kolmogorov-Smirnov test).

These results show that the process of previous predation success increasing an individual’s probability of future predation success is an important mechanism driving the observed variation in the number of prey per individual predator. They do not tell us how prey selection of individuals with many prey in their gut and weakly connected predators drive prey abundances and under

what situations population level means are able to generate the same dynamics as observed in the highly heterogeneous individual-based food web. For example, if the random encounter model with learning predicts the observed pattern of prey selection (frequency of diets containing rare or abundant prey species), then population level means should be an appropriate simplification to understand diversity in food webs. On the other hand, if abundant or rare prey occur in the observed predator diets significantly more or less frequently than expected with random encounters, then these deviations contain useful information for understanding the effects of density-dependent prey selection on food web diversity.

Figure 3 shows individual prey selection in the empirical data with prey abundance as a function of the number of prey items of each prey species found in each individual predator where counts of different prey species in a single individual are connected. There is substantial variation in prey selection across prey species with different abundance and across individual predators with different number of prey in the stomach content. Do weakly connected individuals (Fig. 3a-3b), preferentially select highly energetic and rare prey? Are these weakly and medium connected individuals of small size? Similarly, do the most connected individuals (Fig. 3c-3d) preferentially select the most common or rare prey? Are those strongly connected individuals of large size?

Body size is commonly used to explain patterns in predator-prey relationships<sup>41</sup>, but in these data, length of predator does not explain the variability in the number of prey items per individual predator across weakly and strongly connected predators (Fig. 4a-d, top). The model with positive density-dependent prey selection best explains the variability observed in weakly and medium connected individuals (Fig. 4a-b, bottom), while neutral prey selection best explains the variability observed in medium-strongly connected individuals (Fig. 4c, bottom) and negative density-dependent prey selection best explains the variability observed in strongly connected individuals (Fig. 4d, bottom). The positive density-dependent mechanism predicting prey selection in weakly and medium connected individuals strongly depart from the other models and it does not vary in

space and time (AIC values in Table S1, SI). Even if the mechanisms predicting prey selection in medium-strongly and strongly connected individuals vary in space and time, those mechanisms deviate in most environmental situations from the random encounter model (AIC values in Table S1, SI). The speed of learning values,  $\alpha$ , that best predict the observed data in each connectivity class at intraspecific level do not differ significantly across connectivity classes for the weakly, medium, medium-strongly and strongly connected individuals ( $p > 10^{-1}$  for all combinations, Kolmogorov-Smirnov test), but the strength in prey selection values,  $\Omega$ , between weakly-medium and medium-strongly and strongly connected individuals do differ significantly ( $p < 10^{-3}$  for all pairwise combinations, Kolmogorov-Smirnov test) and in opposite directions (Fig. 4a-d. bottom).

These patterns of prey selection have significant implications for food web diversity (Fig. 5). Negative density-dependent prey selection, or the advantage of the rare, ( $\Omega_- \ll 0$ ), predicts that most intraspecific variation in prey consumption is aggregated in the most common prey species, and thus the variability in prey consumption across prey species with different abundance is larger than in the random encounter model, ( $\Omega_o \approx 0$ ), and positive density-dependent selection model, ( $\Omega_+ \gg 0$ ), for all the classes ranging from strongly to weakly connected individuals, thus,  $\hat{\sigma}_-^2 > \hat{\sigma}_o^2 > \hat{\sigma}_+^2$ . This drives diversity to a maximum value (Fig. 5). Equalizing profitability between common and rare prey species moves the dynamics to be neutral or to a random encounter model with the strength of prey selection,  $\Omega \approx 0$ . Species richness is still high, but some extinctions of rare prey may occur. Increasing slightly the profitability of rare species to the strength of selection values that best predict the observed weakly connected predators triggers a collapse in the prey community (Figs. 4-5,  $\Omega \approx [10,1000]$ ). The nonlinear decay of species richness after a slight increase in the strength of prey selection remains qualitatively the same in space and time (Fig. S4 SI). Overall species diversity is limited by weakly connected individuals that represent in the food web studied here the 95% of the total number of individuals sampled. Weakly connected individuals drive extinctions by preferentially consuming individuals of rare species, while high

variability in the number of prey items per predator is maintained by negative frequency dependence in the most strongly connected predators leading them to consume common prey and so not drive extinctions even though they are strong consumers.

The pattern of prey selection found here could be a consequence of strongly and weakly connected predators actively foraging in a system in which prey are distributed in a spatially heterogeneous, patchy manner. Strongly connected predators preferentially search the most abundant prey species in high-density patches with a few number of prey species. A strongly connected predator that finds this kind of patch will then be highly connected to just one or a few common prey species. Conversely, weakly connected predators preferentially search low-density patches with a large number of rare prey species. A weakly connected predator will then be weakly connected to more than one rare prey species. These mechanisms are taken into account in our modeling framework and they reproduce quite well the patterns of prey selection observed in the empirical data. This implies that individual-level prey selection of spatially heterogeneously distributed prey can drive patterns of species diversity and coexistence in multi-trophic ecosystems.

This analysis of individual variation in connectivity expands on a general relation demonstrated by earlier studies of the epidemiological consequences of heterogeneity of infectiousness in contact networks<sup>42</sup>. Targeting the most highly connected individuals implies treating a small proportion of individuals, but this strategy can fail because some less-connected individuals can be highly infectious<sup>27</sup>. In the context of the large individual-based food web studied here, highly connected individual predators are preferentially selecting common prey, so their effect on prey coexistence is larger than on prey extinction and their overall effect is lower than we would expect based on their number of interactions. The opposite is true for weakly connected individuals. They preferentially select rare prey and thus their effect on extinction probability of prey species is larger than we expect based on their low number of interactions. Hence, the greater the proportion of weakly connected individuals consuming rare prey, the more pronounced their negative effect

on diversity will be.

These patterns of intraspecific variability reconcile some of the mechanisms promoting variation within natural populations with the patterns that promote or inhibit diversity in food webs. It has been shown that non-random interactions among species can increase diversity<sup>43</sup>, but the reverse is also possible if weakly connected individuals are preferentially selecting rare prey. Nestedness and compartments are two of the most general patterns in observed ecological networks that increase coexistence and diversity in food webs<sup>44,45</sup>. These two patterns can be obtained from at least two scenarios of intraspecific variability with opposite consequences for species diversity: 1) nestedness with strongly and weakly connected individuals selecting common and rare prey, respectively, and 2) the opposite scenario with strongly and weakly connected individuals selecting rare and common prey, respectively. Because the number of strongly connected individuals in large networks is orders of magnitude lower than the number of weakly connected individuals, the species-level effects on diversity and stability of these two opposite intraspecific-level patterns may differ significantly.

Current biodiversity theory can explain species abundance patterns for many groups<sup>46,47</sup>, but does not explain patterns of intraspecific variation in ecological interactions nor their implications for diversity patterns in multi-trophic ecosystems<sup>23,48</sup>. The models we have explored generate different degrees of intraspecific heterogeneity in prey selection and these models can be compared with the patterns of individual diets and species diversity using highly resolved individual-based food web data. We have shown that higher intraspecific than interspecific trait variability within one community is not sufficient to guarantee species coexistence in a food web. The same intraspecific variation in prey selection across prey species with different abundance can be structured in ways that facilitate or undermine diversity in the prey community. We have therefore determined the conditions necessary for the required changes in prey selection under similar intraspecific variability and in profitability across prey with different abundance to attain coexistence; if these are



not met, then highly profitable and rare prey go locally extinct. Several traits can explain prey selection and here we have studied only two of them, learning ability and active searching by changing profitability across prey species as a proxy for spatial heterogeneity of resources. Further analysis taking into account genetic variability and traits driving individual variability in metabolism and phenotype may be required to further disentangle the effect of multiple traits <sup>49</sup> on predator diets and their effect on species diversity in food webs across space and time.

We have developed a framework for understanding the mechanisms driving intraspecific variability in the number of prey and the strength of prey selection in natural populations and its consequences for patterns of biodiversity in multi-trophic ecosystems. Underlying this framework there are three simple birth-death models that include learning from previous feeding experience with negative, neutral and positive density-dependent prey selection. By examining these models under different parameter combinations and confronting them with data, we conclude that the factors driving prey selection in weakly and strongly connected individual predators at intraspecific level vary significantly, and thus population level means, classically used to develop food web theory, can fail to anticipate the mechanisms driving species extinction, coexistence and diversity in multi-trophic ecosystems.

## Methods Summary

Our model is a stochastic, individual-based birth and death model with  $R_1(t), R_2(t), \dots, R_{S_R}(t)$  and  $C_1(t), C_2(t), \dots, C_{S_C}(t)$  for  $t \leq 0$  the sampled population abundance of prey species- $n$  and predator species- $m$ , with  $S_R$  and  $S_C$ , the total number of prey and predator species, respectively. For  $\Delta t$  sufficiently small, a birth-death event occurs in the prey and predator community. Predator  $j$  has a probability of selecting a prey given by:

$$C_m^j(t) = \frac{K}{1 + K * e^{-\alpha\omega_j(t-1)}}, \quad (1)$$

where  $K$  defines the learning carrying capacity of individual  $j$  of species  $m$ ,  $\alpha$  is the speed at which new successful encounters increase the ability of individual  $j$  to catch a new prey item, and  $\omega$  is the number of prey items in the stomach contents of predator  $j$  at time  $t - 1$  (Fig. S1). The probability of an individual prey  $i$  of species  $n$  being selected is a function of its profitability given by:

$$P(R_n^i) = \frac{E_n}{h_n}, \quad (2)$$

where  $E_n$  and  $h_n$  define the net energy content and the handling time of prey species  $n$ . The strength of prey selection is given by the difference in profitability between the most rare,  $\psi$ , and the most common prey,  $\varphi$ . To test deviations from neutrality in prey selection among individual predators and their effect on species richness, we study the following three scenarios:

$$\Omega \begin{cases} \Omega_- = [P(R_\psi) - P(R_\varphi)] < 0 \\ \Omega_o = [P(R_\psi) - P(R_\varphi)] = 0 \\ \Omega_+ = [P(R_\psi) - P(R_\varphi)] > 0, \end{cases} \quad (3)$$

where  $\Omega_-$ ,  $\Omega_o$ , and  $\Omega_+$  represent the negative (profitability decaying linearly from common to rare prey), neutral (equal profitability for all prey species) and positive (profitability decaying from rare to common prey) density-dependent prey selection, respectively.

1. Elton, C. *Animal Ecology*. (Sidgwick Jackson) (1927).
2. MacArthur, R. Fluctuations in animal populations, and a measure of community stability. *Ecology* **36**, 533–536 (1955).
3. Hutchinson, G. E. Homage to santa rosalia or why are there so many kind of animals? *The American Naturalist* **93**, 145–159 (1959).
4. May, R. M. *Stability and complexity in model ecosystems*. Princeton University Press, Princeton. (1973).
5. Cohen, J. E., Briand, F. & Newman, C. M. *Community Food Webs: Data and Theory*. Springer-Verlag (1990).
6. Solow, A. R., Costello, C. & Beet, A. On an early result on stability and complexity. *The American Naturalist* **154**, 587–588 (1999).
7. Dunne, J. A. *The network structure of food webs (in Ecological Networks: Linking Structure to Dynamics in Food Webs, eds. Pascual, M. and Dunne, J. A.)*. (Oxford University Press, Oxford), pp. 27-86 (2005).
8. Brose, U., Williams, R. J. & Martinez, N. D. Allometric scaling enhances stability in complex food webs. *Ecology Letters* **9**, 1228–1236 (2006).
9. Rooney, N., McCann, K., Gellner, G. & Moore, J. C. Structural asymmetry and the stability of diverse food webs. *Nature* **442**, 265–269 (2006).
10. Gallet, R. *et al.* Predation and disturbance interact to shape prey species diversity. *The American Naturalist* **170**, 143–154 (2007).
11. Kondoh, M. Building trophic modules into a persistent food web. *Proceedings of the National Academy of Sciences of the USA*. **105**, 16631–16635 (2008).

12. Gross, T., Rudolf, L., Levin, S. A. & Dieckmann, U. Generalized models reveal stabilizing factors in food webs. *Science* **325**, 747–750 (2009).
13. Bolnick, D. I., Yang, L. H., Fordyce, J. A., Davis, J. M. & Svanback, R. Measuring individual-level resource specialization. *Ecology* **83**, 2936–2941 (2002).
14. Post, D. M., Palkovacs, E., Schielke, E. G. & Dodson, S. Intraspecific phenotypic variation in a predator affects community structure and cascading trophic interactions. *Ecology* **89**, 2019–2032 (2008).
15. Murdoch, W. W. Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecological Monographs* **39**, 335–354 (1969).
16. Chesson, P. L. Predator-prey theory and variability. *Annual Review of Ecology, Evolution and Systematics* **9**, 323–347 (1978).
17. May, R. M. Network structure and the biology of populations. *Trends in Ecology and Evolution* **21**, 394–399 (2006).
18. Pachepsky, E. *et al.* Consequences of intraspecific variation for the structure and function of ecological communities. Part 2: Linking diversity and function. *Ecological Modelling* **207**, 277–285 (2007).
19. Svanbäck, R., Eklöv, P., Fransson, R. & Holmgren, K. Intra-specific competition drives multiple species trophic polymorphism in fish communities. *Oikos* **117**, 114–124 (2008).
20. Ings, T. C. *et al.* Ecological networks - beyond food webs. *Journal of Animal Ecology* **78**, 253–269 (2009).
21. Stouffer, D. B. Scaling from individuals to networks in food webs. *Functional Ecology* **24**, 44–51 (2010).

22. Abrams, P. A. Implications of flexible foraging for interspecific interactions: lessons from simple models. *Functional Ecology* **24**, 7–17 (2010).
23. Bolnick, D. I. *et al.* Why intraspecific trait variation matters in community ecology. *Trends in Ecology and Evolution* **26**, 183–192 (2011).
24. Levin, S. A. Community equilibria and stability, and an extension of the competitive exclusion principle. *The American naturalist* **104**, 413–423 (1970).
25. Condit, R. S. *et al.* The importance of demographic niches to tree diversity. *Science* **313**, 98–101 (2006).
26. Clark, J. S. Individuals and the variation needed for high species diversity in forest trees. *Science* **327**, 1129–1132 (2010).
27. Lloyd-Smith, J. O. Superspreading and the impact of individual variation on disease emergence. *Nature* **438**, 293–295 (2005).
28. Araújo, M. S., Martins, E., Cruz, L. D., Fernandes, F. R. & Linhares, A. Nested diets: a novel pattern of individual-level resource use. *Oikos* **119**, 81–88 (2010).
29. Roughgarden, J. Evolution of niche width. *The American Naturalist* **106**, 683–718 (1972).
30. Cohen, J. E., Jonsson, T., Müller, C. B., Godfray, H. C. J. & Savage, V. M. Body sizes of hosts and parasitoids in individual feeding relationships. *Proceedings of the National Academy of Sciences of the USA* **102**, 684–689 (2005).
31. Biro, P. A. & Stamps, J. A. Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? *Trends in Ecology and Evolution* **25**, 653–659 (2010).

32. Holt, R. D. Predation, apparent competition, and the structure of prey communities. *Theoretical population Biology* **12**, 197–229 (1977).
33. Chesson, P. L. Variable predators and switching behavior. *Theoretical population Biology* **26**, 1–26 (1984).
34. Poulton, E. B. Notes upon, or suggested by, the colours, markings and protective attitudes of certain lepidopterous larvae and pupae, and of a phytophagous hymenopterous larva. *Transactions of the Entomological Society of London* **1884**, 27–60 (1884).
35. Clarke, B. *Balanced polymorphism and the diversity of sympatric species*. Taxonomy and Geography (Systematics Association, Oxford., 1962).
36. Janzen, D. H. Herbivores and the number of tree species in tropical forests. *The American Naturalist* **104**, 501–528 (1970).
37. Polis, G. A. Complex trophic interactions in deserts: an empirical critique of food web theory. *The American Naturalist* **138**, 123–155 (1991).
38. Cohen, J. E. *Food Web and Niche Space*. (Princeton University Press, Princeton) (1978).
39. Woodward, G. & Warren, P. *Body size and predatory interactions in freshwater: scaling from individuals to communities (in Body Size: The Structure and Function of Aquatic Ecosystems, eds. Hildrew, A. G., and Raffaelli, D. G., and Edmonds-Brown, R.)*. (Cambridge University Press, Cambridge.), pp. 98-117 (2007).
40. DeAngelis, D. L. & Mooij, W. M. Individual-based models of ecological and evolutionary processes. *Annual Review of Ecology, Evolution and Systematics* **36**, 147–168 (2005).
41. Beckerman, A. P., Petchey, O. L. & Warren, P. H. Foraging biology predicts food web complexity. *Proceedings of the National Academy of Sciences of the USA* **103**, 13745–13749 (2006).

42. Anderson, R. M. & May, R. M. *Infectious Diseases of Humans: Dynamics and Control*. (Oxford University Press, Oxford) (1991).
43. Bastolla, U. *et al.* The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature* **458**, 1018–1020 (2009).
44. Fortuna, M. A. *et al.* Nestedness versus modularity in ecological networks: two sides of the same coin? *Journal of Animal Ecology* **79**, 811–817 (2010).
45. Stouffer, D. B. & Bascompte, J. Compartmentalization increases food-web persistence. *Proceedings of the National Academy of Sciences USA* **108**, 3648–3652 (2011).
46. Allen, A. & Savage, V. M. Setting the absolute tempo of biodiversity dynamics. *Ecology Letters* **10**, 637–646 (2007).
47. Rosindell, J., Hubbell, S. P. & Etienne, R. S. The unified neutral theory of biodiversity at age ten. *Trends in Ecology and Evolution* **26**, 340–348 (2011).
48. Volkov, I., Banavar, J. R., Hubbell, S. P. & Maritan, A. Inferring species interactions in tropical forest. *Proceedings of the National Academy of Sciences of the USA* **106**, 13854–13859 (2009).
49. Allesina, S., Alonso, D. & Pascual, M. A general model for food web structure. *Science* **320**, 658–661 (2008).
50. Beaumont, M. A. Approximate Bayesian computation in evolution and ecology. *Annual Review Ecology, Evolution and Systematics* **41**, 379–406 (2010).
51. Tarantola, A. Popper, Bayes and the inverse problem. *Nature physics* **2**, 492–494 (2006).

## **Supplementary information**

See supplementary information, supplementary figures S1-S4 and Table S1.



## **Acknowledgments**

CJM was supported in part as Postdoctoral Associates at the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (Grant #EF-0553768), the University of California, Santa Barbara, and the State of California. CJM also acknowledges support from Microsoft Research Ltd., Cambridge, United Kingdom.

## **Author Information**

Correspondence and request for material should be addressed to CJM ([carlos.melian@eawag.ch](mailto:carlos.melian@eawag.ch)).

## Figure Legends

●Figure 1. Diagrams of the learning models. Right and left column of **a-c** represent the predator and prey populations, each with different abundance, respectively. Each link means a prey item is in the stomach content of an individual predator. Each individual predator is represented by a black node and the size of each node within each predator population represents the probability of catching an individual prey. This probability is a function of the number of previous successful encounters by each individual predator (see “Methods Summary”). This process generates variation at intraspecific level and it produces at least two types of individual predators: Strongly and weakly connected individuals. The same intraspecific variance in the number of prey per individual predator within each predator population from **a-c** can have different prey selection patterns across prey with different abundance and thus can lead to species extinctions in food webs. We have tested three learning models with the strength in prey selection following: **a**), Negative density-dependent prey selection or rare prey advantage: Strongly and weakly connected individual predators select preferentially the most common prey species. **b**), Random encounter model: prey selection is only a function of prey and predator abundance. Strongly and weakly connected individual predators select less common prey just by chance (orange links), and **c**), Positive density-dependent prey selection: increasing profitability of rare prey attracts strongly and weakly connected individual predators (blue and red links).

●Figure 2. The distribution in the number of prey per predator. All the  $10^5$  prey and predator individuals sampled in all environmental conditions are pooled; x-axis and y-axis represent the rank individuals in number of prey, and the absolute number of prey per individual predator, respectively. Black represents the empirical data, solid and dotted red are the mean and CI from the all the learning models. The observed distribution is highly heterogeneous with most individuals having a few prey items and a few individuals acting as “hubs” containing more than  $10^3$  items. For comparison we also plotted results from the random encounter model without learning (solid

and dotted orange are the mean and CI); this model deviates strongly from the observed data.

●Figure 3. The distribution of prey abundance of species  $k$  for each individual predator pooled across all the samplings as a function of the number of items of prey species  $k$ . Counts of different prey species in a single individual predator are connected. There are four classes of predators: **a,b**), Weakly and medium connected predators: All predator individuals with more or equal than 1 and less than 10 prey items in the stomach content, **a**, and all individuals with more or equal than 10 and less than  $10^2$  items, **b**, respectively. **c**, Medium-strongly connected predators: All individuals with more or equal than  $10^2$  and less than  $2 \times 10^2$  items, and **d**, Strongly connected predators: All individuals with more than  $2 \times 10^2$  items.

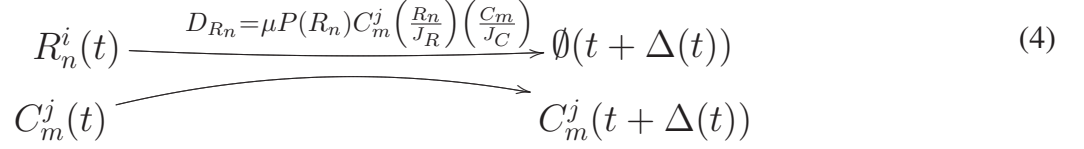
●Figure 4. The number of prey as a function of total length (**a-d**, top), and abundance of prey species  $k$  as a function of prey selection defined as the mean number of prey items of each prey species  $k$  consumed by each individual predator (**a-d**, bottom). Black dots represent the observed values and continuous and dotted red lines represent the mean and the CI from the model that best fit the data. **a-b**), Weakly, **a**, and medium, **b**, connected predators. The best fit is given by the positive density-dependent prey selection model in **a**, with  $\alpha = [0.0015]$ ,  $\Omega = [844]$ ,  $\mu_C = 0.0057$ , and  $AIC = -142$ , and **b**,  $\alpha = [0.005]$ ,  $\Omega = [101]$ ,  $\mu_C = 0.028$ , and  $AIC = -22.45$ . **c**), Medium-strongly connected predators. The best fit is given by the random encounter model with,  $\alpha = [0.0088]$ ,  $\Omega = [0]$ ,  $\mu_C = 0.044$ , and  $AIC = 20.78$ , and **d**, Strongly connected individuals. The best fit is given by the negative density-dependent prey selection model with  $\alpha = [0.0036]$ ,  $\Omega = [-805]$ ,  $\mu_C = 0.0177$ , and  $AIC = 38$ .

●Figure 5. Species richness for the prey community as a function of the strength of prey selection,  $\Omega$ , for the  $10^5$  prey and predator individuals sampled pooled across all the environmental conditions. A slight increase or decrease in the strength of prey selection generate a nonlinear decay or increase of species richness, respectively. This result remains qualitatively the same in

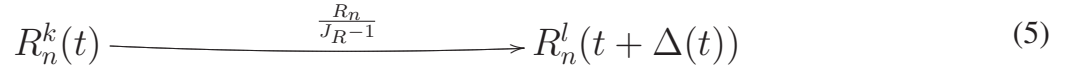
space and time (Fig. S4 SI).

## Methods

**Generalized stochastic individual-based predator-prey model** For  $\Delta t$  sufficiently small, each death event for prey species is described as:



where  $\emptyset$  is an empty site in the prey community after the death of an individual prey  $i$  of species  $n$  by an individual predator  $j$  of species  $m$  at time  $t$ . We scale time to prey dynamics,  $\mu = \mu_{R_n, C_m} = 1$  and  $P(R_n)$ ,  $C_m^j$ ,  $R_n$  and  $C_m$  are the profitability of prey species  $n$ , the probability of selecting a prey by the individual predator  $j$  of species  $m$ , and the total number of individuals of prey  $n$  and predator  $m$ , respectively.  $J_R$  and  $J_C$  are the total abundance in the prey and predator community. At the same time we have an offspring  $l$  in the prey species  $n$  given by



The death-birth process in the predator community occurs if and only if a value sampled from a uniform distribution  $[0,1]$  is smaller than the mortality rate of predator species  $m$ ,  $\mu_{C_m}$ , which is parametrized a priori by the observed number of individual predators found in the total sample. After approximately  $10^5$  prey samples, only 5% were individuals belonging to some of the 10 predator species sampled. These events are described as in eqs. (A-1) and (A-2) but with  $D_{C_n}$  and  $C_n$  instead of  $D_{R_n}$  and  $R_n$ , respectively.

The transition probabilities of the birth-death process for the individual-based prey-predator food web satisfy:

$$Pr [R_n - 1 | R_n] = D_{R_n} \left( \frac{J_R - R_n}{J_R - 1} \right) \quad (6)$$

$$Pr [R_n + 1 | R_n] = D_{R_{\neq n}} \left( \frac{R_n}{J_R - 1} \right) \quad (7)$$

$$Pr [C_n - 1|C_n] = D_{C_n} \left( \frac{J_C - C_n}{J_C - 1} \right) \quad (8)$$

$$Pr [C_m + 1|C_m] = D_{C_{\neq m}} \left( \frac{C_m}{J_C - 1} \right) \quad (9)$$

**Testing the models using ABC and AIC** Results in Figs. 2 and 4a-d bottom were obtained after sampling approximately 90,000 prey individuals per replicate after  $10^4$  replicates using the ABC method <sup>50</sup>. In Fig. 2 we simulated the distribution of the number of prey items per individual predator  $j$  (denoted as  $\mathbb{W}_s = [\omega_s^{(j)}]$ ) using  $\alpha = [10^{-4}, 10^{-2}]$ ,  $K = 100$ , and  $\mu_C = [0, 5 \times 10^{-2}]$ . In Fig. 4a-d bottom we simulated the mean number of items of prey  $k$  for four connectivity classes (denoted as  $\widehat{W}_s$ ) using the previous parameter ranges and  $\Omega = [-1000, 1000]$ . We compared these distributions with the observed data using the following general algorithm:

1. Generate  $\theta$  from  $\pi(\cdot)$ , where  $\theta = [\alpha, \mu_C, \Omega]$ .
2. Simulate  $\mathbb{W}$  and  $\widehat{W}$  from each stochastic model with parameter  $\theta$ .
3. Calculate distance for  $\mathcal{L}(\mathbb{W}_o, \mathbb{W}_s)$  and  $\mathcal{L}'(\widehat{W}_o, \widehat{W}_s)$   
between simulated  $(\mathbb{W}_s, \widehat{W}_s)$  and observed data  $(\mathbb{W}_o, \widehat{W}_o)$ .
4. Accept  $\theta$  if  $\mathcal{L} \leq \epsilon$  and  $\mathcal{L}' \leq \epsilon'$ ; return to 1,

where  $\epsilon$  and  $\epsilon'$  denote arbitrary values that satisfy a compromise between efficiency and accuracy<sup>50</sup>. We have used quite large  $\epsilon$  and  $\epsilon'$  values in the simulations so all the outcomes from the models for any parameter combination were used to compare the models with the observed data.

We implicitly assume that our predictions will not reproduce the observations exactly. Uncontrolled randomness from various unknown sources will make observations,  $\mathbb{W}_o, \widehat{W}_o$ , deviate from the theoretical model predictions,  $\mathbb{W}_s, \widehat{W}_s$ . In order to consider this inevitable mismatch, we

have used an error model. We have considered a least-absolute values criterion, which is known to be robust even when errors in the data are not normally distributed <sup>51</sup>.

We defined the following error function to model the probability of observing  $\mathbb{W}_o = [\omega_o^{(j)}]$  absolute number of items per individual predator  $j$  given a model prediction,  $\mathbb{W}_s = [\omega_s^{(j)}]$ :

$$P(\omega_o^{(j)}|\omega_s^{(j)}) \sim \exp - \left| \frac{\omega_o^{(j)} - \omega_s^{(j)}}{\omega_s^{(j)}} \right|. \quad (10)$$

To satisfy

$$\int_0^\infty P(\omega_o^{(j)}|\omega_s^{(j)})d\omega_o^{(j)} = 1, \quad (11)$$

we obtain,

$$P(\omega_o^{(j)}|\omega_s^{(j)}) = \frac{1}{\omega_s^{(j)}(2 - e^{-1})} \begin{cases} \exp(-\frac{\omega_o^{(j)} - \omega_s^{(j)}}{\omega_s^{(j)}}) : \omega_o^{(j)} > \omega_s^{(j)} \\ \exp(-\frac{\omega_s^{(j)} - \omega_o^{(j)}}{\omega_s^{(j)}}) : \omega_o^{(j)} < \omega_s^{(j)} \end{cases} \quad (12)$$

Assuming independent observational errors, it is straightforward to write a likelihood for the distribution of the number of items per individual predator for all the predators sampled,  $T$ , and identify the best fit as the one that minimizes the sum of the absolute values of the misfits as follows:

$$\mathcal{L}(\omega_o^{(1)}, \dots, \omega_o^{(T)}|\mu_C, \alpha) = \sum_{j=1}^T \log(P(\omega_o^{(j)}|\omega_s^{(j)})). \quad (13)$$

For Fig. 4a-d bottom and Table S1, we followed these additional steps: 1) sort prey abundance for all prey species,  $S_R$ , from the most rare to the most common after each replicate, and 2) identify the best fit as the one that minimizes the sum of the absolute values of the misfits for the mean value for each of the four connectivity classes,  $c$ :

$$\mathcal{L}'(\hat{\omega}_{o_c}^{(1)}, \dots, \hat{\omega}_{o_c}^{S_R}|\mu_C, \alpha, \Omega) = \sum_{i=1}^{S_R} \log(P(\hat{\omega}_{o_c}^{(i)}|\hat{\omega}_{s_c}^{(i)})), \quad (14)$$

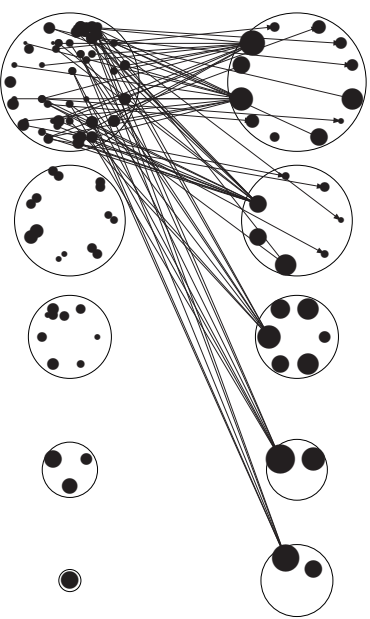
where  $\hat{\omega}_{o_c}^{(i)}$  and  $\hat{\omega}_{s_c}^{(i)}$  are the observed and the model prediction of the mean number of prey items per individual predator for each prey  $i$  for each of the four classes of individual connectivity,

respectively. We use Akaike information criteria (AIC) to compare the three models for each of the four classes. In the general case, the AIC is

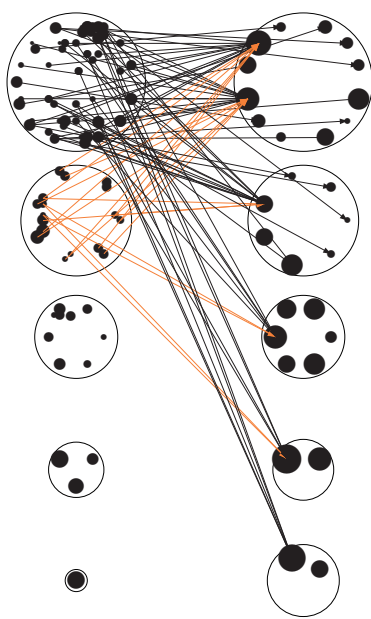
$$AIC = 2k - 2\ln(\mathcal{L}') \quad (15)$$

where  $k$  is the number of parameters in each of the models, the 2 before the  $k$  is a “penalization of parameter constant” and  $\mathcal{L}'$  is the maximum value of the likelihood function for the estimated model. Model replicates to calculate the CI taking the percentiles 0.05 and 0.95 were generated with the best parameter estimates for  $\alpha$  (Fig. 2), and  $\alpha$  and  $\Omega$ , (Fig. 4a-d, bottom) along with a family of pairs within 0.5 log-likelihood units away from the minimum. Result for Fig. 5 are obtained after  $10^4$  replicates and 1,000,000 birth-death cycles per replicate. In each replicate we randomly pick up a strength of prey selection value,  $\Omega$ , from the range  $[-10000,10000]$  and count the number of prey species with a number of individuals larger than 0.

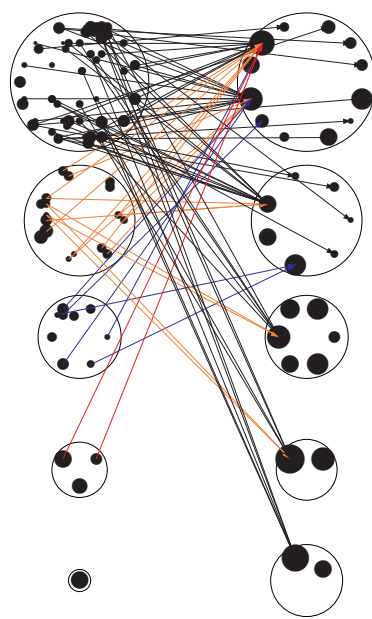




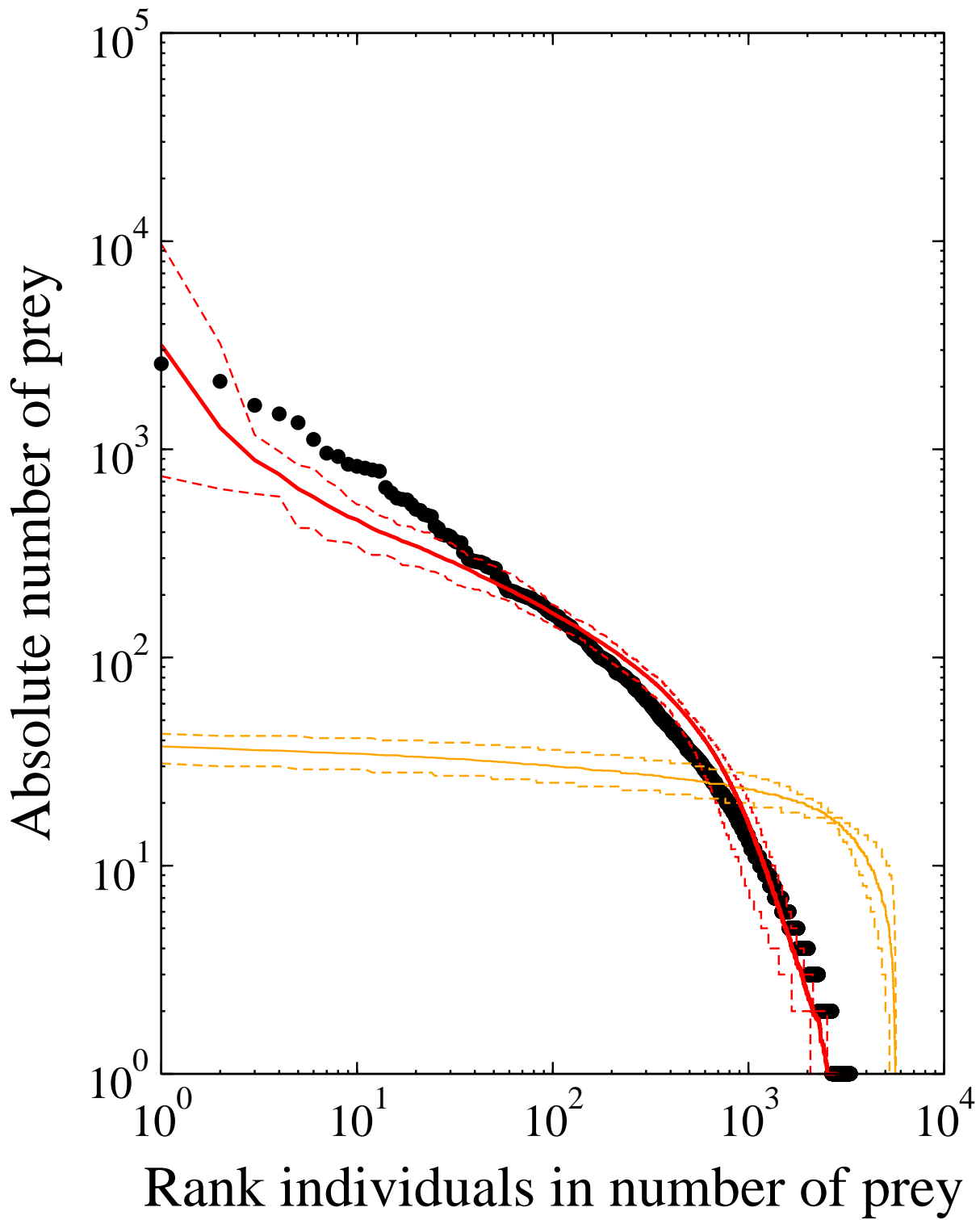
(a)

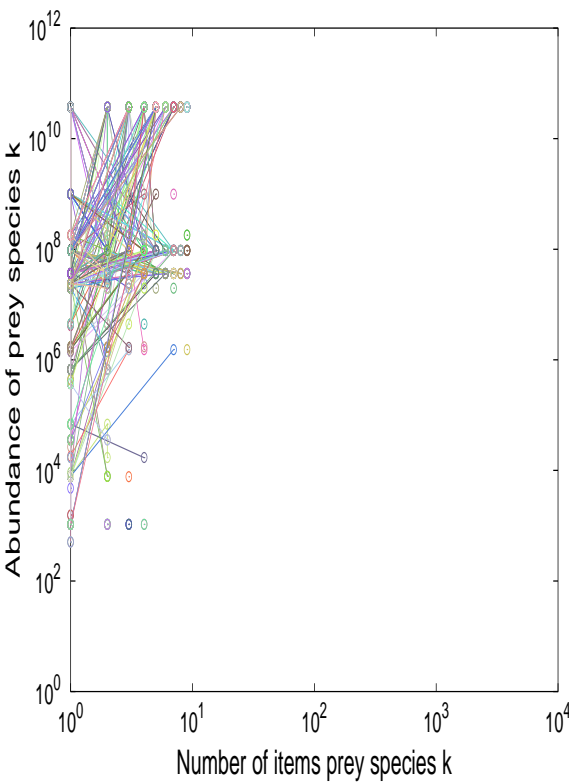


(b)

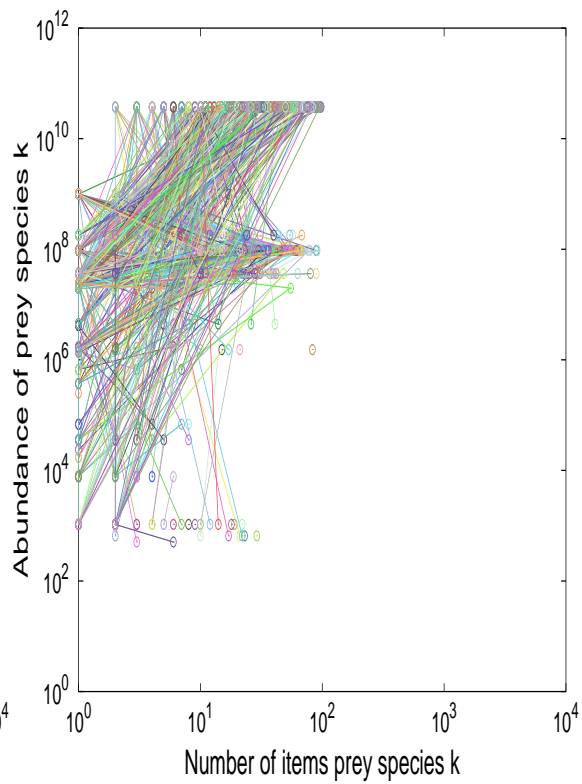


(c)

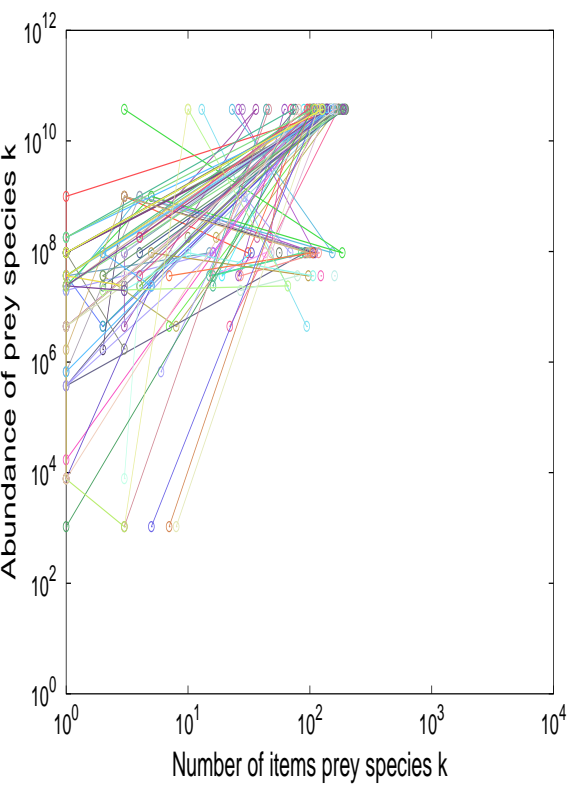




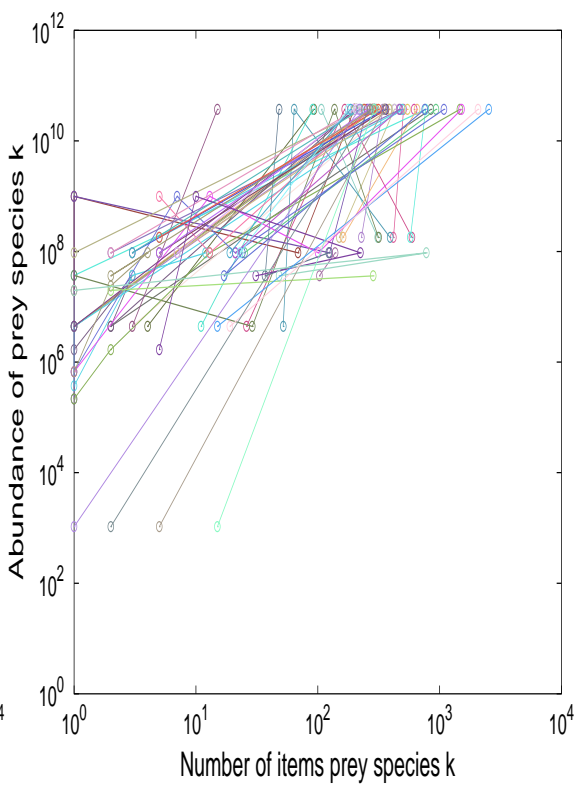
(a)



(b)



(c)



(d)

