

## Notes and Comments

### Food Web Laws or Niche Theory? Six Independent Empirical Tests

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Over the past 2 decades, empirical food webs have been shown to possess regular patterns of various kinds. Some of the first food web patterns were reported as "food web laws," the most notable being the link-species scaling law. This empirically derived law described an inverse relationship between community species richness and web connectance (Cohen and Briand 1984; Cohen and Newman 1985). Subsequent evaluation of food webs constructed with more detailed data falsified (Warren 1989; Winemiller 1989*a*, 1990; Hall and Raffaelli 1991; Polis 1991) and modified (Warren 1990; Martinez 1991, 1992; Pimm et al. 1991; Martinez et al. 1999) many of the early food web generalizations. Martinez (1991) estimated the presence and absence of feeding links (web topology) among species recorded for Little Rock Lake and proposed a new food web pattern called "constant connectance." Subsequent examination of other topological webs reinforced the constant connectance pattern (Martinez 1992).

Connectance ( $C$ ) is the number of observed trophic

links ( $L$ ) divided by the total possible number of trophic links ( $S^2$ ), where  $S$  is the number of species in the community. The link-species scaling law predicts two predator-prey interactions per species across all values of  $S$ . In contrast, if connectance is constant, then the number of predator-prey interactions per species increases as species richness increases (Martinez 1992; Williams and Martinez 2000). Of course, this relationship also implies that average niche breadth increases as the number of sympatric species increases, a prediction exactly opposite the prediction of species packing (MacArthur and Levins 1967; Pianka 1976). Under the species packing model, interspecific competition is reduced when niche breadth and interspecific overlap in resource use decline. Much literature supports the idea that similar species (i.e., guild members) reduce interspecific competition by subdividing their use of available resources (Pianka 1974, 1976, 1986; Schoener 1974, 1982; Winemiller and Pianka 1990). Reduction in niche breadth with increasing species richness has been shown via field experiments (Werner and Hall 1976) and comparative research (Werner 1977; Fox 1981). Under species packing, the average number of predator-prey interactions per species should decline with increasing  $S$ .

Thus, three alternative predictions can be tested with empirical data on consumer diets from communities containing different numbers of species. Except for the simplest communities, reliable and detailed diet data for every consumer species, from microbes to vertebrates, cannot be obtained. However, one can perform detailed studies of diets of consumer guilds or taxocenes from locations that vary in species richness. Another advantage of studying diets of a community subset is that consumption of food items can be quantified rather than reported as mere presence or absence of a feeding link. In this way, predictions about connectance (number of observed links) and diet breadth (taking into account relative amounts consumed) both can be examined.

Here we compare relationships between niche breadth and consumer resource links in relation to species richness of consumer taxocenes for six data sets: desert lizards (three continental data sets), Neotropical lizards; Neo-

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tropical fishes, and North American grassland grasshoppers. Each lizard data set was compiled by a single field researcher. In the case of desert lizards, three data sets compiled by Pianka (1986) were analyzed separately (North America, Kalahari, Australia). The Neotropical fish data set contained Winemiller's (1990) data from Venezuela and Costa Rica and also included eight assemblages from Knöppel's (1970) study of Amazonian stream fish diets, which used very similar food categories and methods. The grasshopper data set consisted of Joern's data plus data from four other studies that used the same methods and criteria (Mulkern et al. 1969; Ueckert and Hansen 1971; Sheldon and Rogers 1978; Bergman 1983). By reducing the number of researchers involved in data collection, we greatly reduce subjective methodological variation that has been shown to be so damaging to large-scale, comparative, food web studies (Winemiller 1990; Polis 1991; Martinez 1992; Hall and Raffaelli 1993; Martinez et al. 1999).

In drawing comparisons between community and assemblage trophic networks, we are mindful of potential sources of systematic bias. Taxonomic assemblages are subsets of communities that might not reflect species richness patterns in their respective communities. Although we could not obtain community-wide species richness data for our study sites (from microbes to mammals), available evidence suggests that species richness of our consumer assemblages scales closely with total species richness at the community level. Species richness of grasshoppers and plants is strongly correlated among 22 North American desert and grassland sites ( $r = 0.71$  and  $P < .0001$ , based on Otte's [1976] estimates from standardized plot surveys). Species richness of lizards and birds is correlated across Pianka's study sites both within and among continents (North America:  $r = 0.945$ ,  $P < .01$ ,  $N = 10$ ; Kalahari:  $r = 0.69$ ,  $P < .05$ ,  $N = 10$ ; Australia:  $r = 0.82$ ,  $P < .01$ ,  $N = 9$ ; all sites:  $r = 0.78$ ,  $P < .01$ ,  $N = 29$ ). Lizard and frog species richness is correlated across Vitt's study sites ( $r = 0.54$ ,  $P < .05$ ,  $N = 15$ ), and more species of amphibians, reptiles, and piscivorous birds were recorded at Winemiller's Neotropical study sites with more fish species.

Any food web analysis is influenced by arbitrary decisions and methods for designating community boundaries, spatial scale, temporal scale, taxonomic groupings, and trophic links (Hall and Raffaelli 1993, 1997; Winemiller and Polis 1996). Variation in taxonomic/trophic units reported in food webs has been addressed through use of the "trophospecies" concept. Species that share the same list of predators and prey are grouped as a trophospecies (Cohen 1978). None of the comparative studies demonstrating food web patterns explicitly showed how species were aggregated into trophospecies, and a recent empirical

test of objective rules for creating trophic aggregations revealed serious problems with the trophospecies concept (Yodzis and Winemiller 1999). Thus, bias associated with species aggregation is likely to be as great or greater than that associated with focusing on trophic interactions at the level of species assemblages (see also Hall and Raffaelli 1997; Sugihara et al. 1997).

Methods for dietary analysis and sample sizes are reported in Pianka (1986), Vitt and Zani (1998a, 1998b), Winemiller (1990), and Joern (1979a, 1979b, 1983). In each case, dietary proportions of prey categories were based on volumes in stomach contents. Because rare species with small samples can bias estimates of diet breadth, our analysis includes only species in which  $\geq 10$  individuals contained stomach contents. Rarefaction analysis with abundant species with broad diets (e.g., *Astyanax bimaculatus*, *Triporthus angulatus*, and other omnivorous characid fishes) revealed that a sample of 10 individuals generally was sufficient to reveal  $>90\%$  of dietary diversity documented in the complete data set. In most cases, sample sizes were 30–300, with samples for several species exceeding 300. Although some food items could have been undersampled, these six data sets were collected with greater methodological consistency, precision, accuracy, and effort than data sets used for broad food web comparisons. The latter data sets were compiled using diverse published and unpublished sources, expert opinion, and even guesswork to record presence or absence of trophic links (Briand and Cohen 1984; Martinez 1992).

We performed six independent comparisons of relationships between species richness, diet breadth, and number of trophic links, and we made no quantitative analysis of values across these data sets. Number of food resource categories designated by each investigator (North American desert lizards = 19, Kalahari lizards = 20, Australian lizards = 19, Neotropical lizards = 29, Neotropical fishes = 119, grassland grasshoppers = 17–75 depending on local plant diversity) was based on the greatest level of taxonomic resolution and precision that could be consistently obtained based on examination of stomach contents. The same methods and criteria were used across all sites for each taxonomic data set. Diet breadth was calculated from proportional volumetric diet data using Levins's (1968) index. Number of links per consumer species was the number of food categories recorded for a given species at an individual survey site, without regard for volumetric proportions. Mean number of links per consumer was the mean for all species at a survey site. Least squares linear regression was performed on untransformed data.

No consistent pattern of diet breadth in relation to species richness was observed (fig. 1). Diet breadth was not significantly associated with species richness in four of six cases (North American lizards, Kalahari lizards, Neotrop-

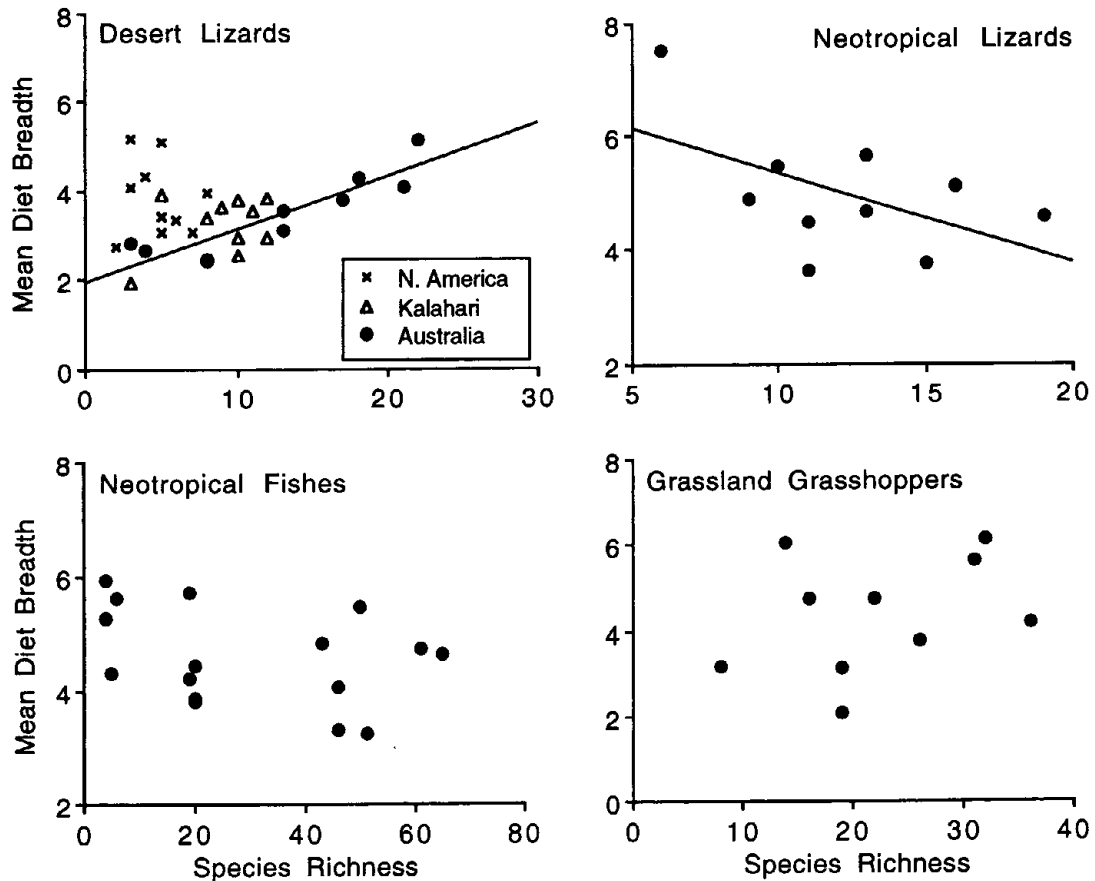


Figure 1: Mean diet breadth for desert lizards, Neotropical lizards, Neotropical fishes, and grassland grasshoppers as a function of species richness. Significant regressions ( $P < .05$ ) were for Australian lizards ( $y = 0.12x + 1.91$ ,  $r^2 = 0.80$ ) and Neotropical lizards ( $y = -0.16x + 6.91$ ,  $r^2 = 0.28$ ).

ical fishes, grassland grasshoppers;  $r^2 < 0.14$ ,  $P \gg .05$ ). Diet breadth of Australian desert lizards increased with species richness, and diet breadth of Neotropical lizards decreased with species richness; however, the proportion of variance explained by linear regressions was low. Thus, one case weakly supports constant connectance, one weakly supports species packing, and four support none of the three theories.

In four of six cases, mean number of links per consumer revealed no significant association with species richness (fig. 2;  $r^2 < 0.12$ ,  $P \gg .05$ ). Two of the desert lizard data sets (Kalahari, Australia) revealed a positive relationship with species richness, a pattern generally consistent with constant connectance (even so, about 70% of the variation between  $C$  and  $S$  remains unexplained for the Kalahari). According to constant connectance,  $L = 0.14S^2$ . For Kalahari lizards,  $L = 0.18S^2$ , and for Australian lizards,  $L = 0.235S^2$ . Although these data sets appear to conform to the constant connectance model, they actually fit poorly when one considers that relatively few instances of sau-

rophagy are included in our assemblage data sets. In a food web, average number of links per consumer includes both prey links (denoting prey taxa consumed) and predator links (denoting predator-prey interactions in which a consumer itself is eaten by a predator). In Winemiller's (1990) analysis of four tropical aquatic webs, mean number of consumer links to prey nodes was actually greater than mean number of predator links to consumer nodes by about four to one. Because they have comparatively little vertical structure, our lizard and grasshopper assemblages probably slightly underestimate total number of links per species. Thus, our analysis supports neither link-species scaling nor constant connectance relationships. Nor does it support the species packing model. Why?

All three theories predict a linear relationship between  $L/S$  and  $S$  (with no slope for link-species scaling, positive slope for constant connectance, and negative slope for species packing). The low correlation between  $L/S$  and  $S$  that we documented would be expected if variation in local environmental conditions, both biotic and abiotic, causes

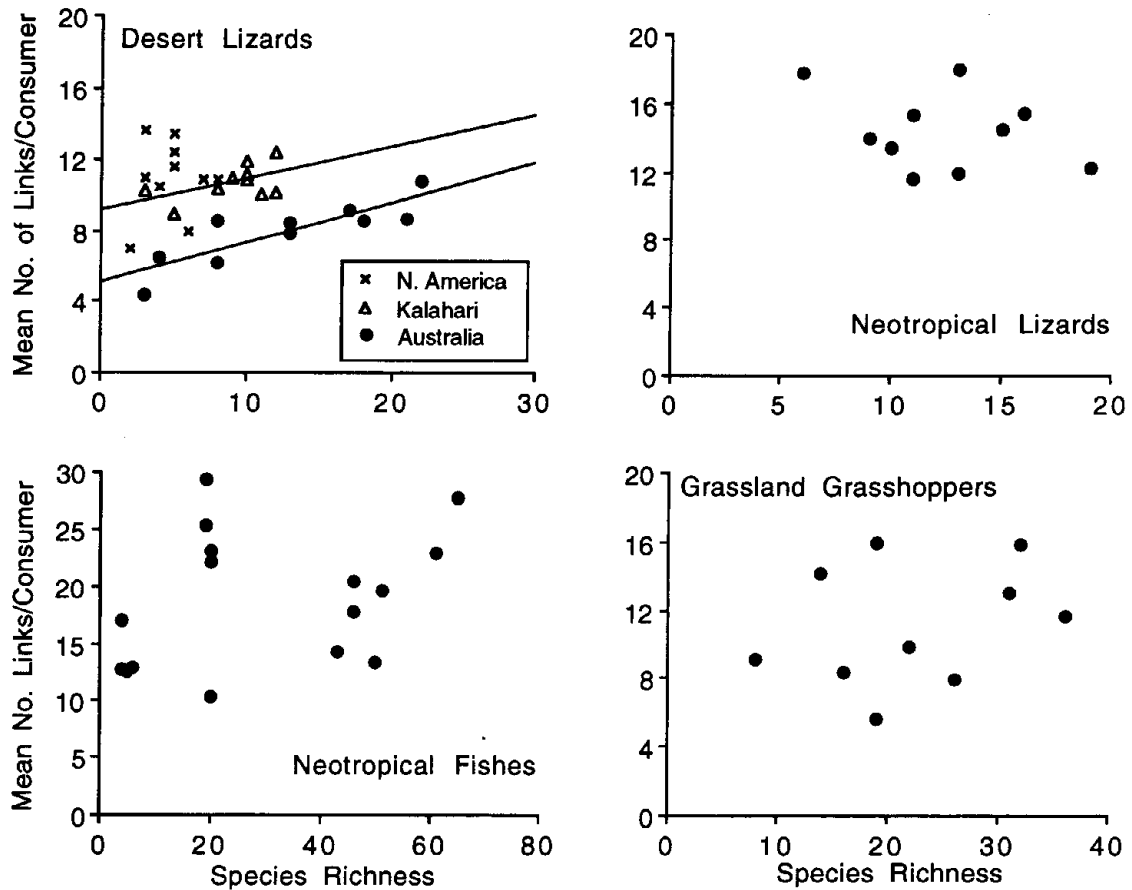


Figure 2: Mean number of trophic links per consumer for desert lizards, Neotropical lizards, Neotropical fishes, and grassland grasshoppers as a function of species richness. Significant regressions ( $P < .05$ ) were for Kalahari lizards ( $y = 0.18x + 9.15$ ,  $r^2 = 0.29$ ) and Australian lizards ( $y = 0.23x + 5.03$ ,  $r^2 = 0.72$ ).

between-site intraspecific diet variation. Warren (1990) explained how the relationship of  $L/S$  to  $S$  could be influenced by niche partitioning in response to resource competition or apparent competition for enemy-free space in more species-rich communities. Warren obtained  $L = 0.24S^2$  for food webs estimated from different areas of a pond during different seasons. This relationship is the same as that obtained for Australian desert lizards and may reflect constraints imposed by morphology and behavior on predator-prey interactions, which in turn vary in response to spatiotemporal environmental variation (Warren 1990).

Implicit in all three alternative theories is the premise that all other factors are held constant. In reality, all other factors are highly variable when performing between-site comparisons, as is done in food web comparisons and as we have done here. Therefore, low correlations between mean niche breadth and the mean number of links per consumer are expected with species richness. This expect-

ation reveals the major failure of food web comparisons based on different ecosystems, time periods, and studies that employ different methods and criteria. Repeated pleas to standardize methods used for empirical food web comparisons (Winemiller 1990; Polis 1991; Cohen et al. 1993; Hall and Raffaelli 1993, 1997; Murtaugh 1994; Bersier et al. 1999) continue to go unheeded (e.g., Williams and Martinez 2000).

Average number of links per consumer varied within and between assemblages, with a low of eight for Australian desert lizards and a high of 19 for Neotropical fishes. Some of this variation between data sets reflects biology (fishes may have broader diets than lizards), and some reflects different criteria for erecting food categories. Even when we considered methodological bias and the fact that our data sets only counted prey links (with no accounting for predator links to our consumers), average number of links per consumer greatly exceeded the value of 2 predicted by the link-species scaling law. If we compare the

significant linear relationship of the two desert lizard assemblages with the predictions of constant connectance, the number of links per consumer is uniformly underestimated. With the exception of the Australian assemblage in which saurophagy by *Varanus eremius* was common, the lizard data sets tended to contain two to three consumer trophic levels, so underestimation also could be attributed to the lack of vertical structure in our data sets compared with the food webs analyzed by Martinez (1992). Again, this source of bias is probably no greater than a variety of other potential sources of bias in food web comparisons, such as bias in taxonomic aggregation (lumping into trophospecies), variable resolution and precision in dietary analyses, subjective definition of community membership, and variable spatial and temporal resolution.

A variety of factors probably obviate the trend predicted by species packing theory. These include resolution of diet categories, niche complementarity, and spatiotemporal variation in resource demand/supply ratios that affect patterns of niche partitioning and that may not be reflected in mean diet breadth of a local assemblage integrated over a growing season (temperate climates) or year (Tropics). For example, piscivorous Neotropical fishes display seasonal patterns of niche compression and resource partitioning that corresponded to shifts in prey abundance (Winemiller 1989b), and fish assemblages show greater niche partitioning during the dry period (Winemiller and Pianka 1990). Australian desert lizards showed significant microhabitat partitioning but not significant food resource partitioning when the analysis was based on 19 prey categories (Winemiller and Pianka 1990). When we used a finer scale of resolution for food resources (200 prey categories), significant food resource partitioning was revealed in the same data set. Grasshopper assemblages also reveal significant resource partitioning. In all three grasshopper assemblages examined by Joern and Lawlor (1980), observed niche overlap was significantly less than overlap generated from random patterns of resource utilization.

Failure to detect a species packing pattern in more species-rich communities could be caused by an interaction between effects of interspecific competition and greater resource diversity. All other factors being equal, greater resource diversity should yield broader diets. In more species-rich communities, greater prey diversity could counter the effect of diffuse competition resulting in a pattern that reveals little net change in diet breadth in relation to  $S$ .

In conclusion, our analysis of dietary data for six guild/assemblage data sets, obtained with a high degree of sampling effort and methodological consistency, provided little or no support for the theory of link-species scaling or constant connectance of food webs. Only one of six cases supported species packing theory. The lack of congruence be-

tween our data sets and food web theories probably reflects intersite and temporal variance in abiotic and biotic factors plus methodological biases in our data sets, especially in earlier food web compilations from which these theories were derived. Even when we exclude trophic links with predators, species in our data sets interacted with far more than the two taxa predicted by the link-species scaling law, and, with the possible exception of two desert lizard assemblages, mean number of links per consumer exceeded predictions of the constant connectance model. A variety of environmental factors drive temporal variation in population density and structure, community structure, and species interactions. Standardization of methods and metrics for comparisons of properties at the highest levels of biological organization is no trivial task. Recent efforts to achieve greater standardization, precision, and accuracy in food web research (Deb 1995; Tavares-Cromar and Williams 1996; Townsend et al. 1998; Thompson and Townsend 1999; Memmott et al. 2000) have revealed more, not less, variation. Whereas these studies have not yielded universal patterns, they have provided valuable new insights into ecological dynamics and interrelationships.

#### Literature Cited

- Bergman, D. J. 1983. Ecology of grasshopper communities of Ozark cedar glades. M.S. thesis. University of Missouri, Columbia.
- Bersier, L.-F., P. Dixon, and G. Sugihara. 1999. Scale-invariant or scale-dependent behavior of the link density property in food webs: a matter of sampling effort? *American Naturalist* 153:676–682.
- Briand, F., and J. E. Cohen. 1984. Community food webs have scale-invariant structure. *Nature (London)* 307: 264–266.
- Cohen, J. E. 1978. Food webs and niche space. Princeton University Press, Princeton, N.J.
- Cohen, J. E., and F. Briand. 1984. Trophic links of community food webs. *Proceedings of the National Academy of Sciences of the USA* 81:4105–4109.
- Cohen, J. E., and C. M. Newman. 1985. A stochastic theory of community food webs. I. Models and aggregated data. *Proceedings of the Royal Society of London B, Biological Sciences* 224:421–448.
- Cohen, J. E., R. A. Beaver, S. H. Cousins, D. L. DeAngelis, L. Goldwasser, K. L. Heong, R. Holt, et al. 1993. Improving food webs. *Ecology* 74:252–258.
- Deb, D. 1995. Scale-dependence of food web structures: tropical ponds as paradigm. *Oikos* 72:245–262.
- Fox, B. J. 1981. Niche parameters and species richness. *Ecology* 62:1415–1425.
- Hall, S. J., and D. G. Raffaelli. 1991. Food web patterns:

- lessons from a species-rich web. *Journal of Animal Ecology* 60:823–839.
- . 1993. Food webs: theory and reality. *Advances in Ecological Research* 24:187–237.
- . 1997. Food web patterns: what do we really know? Pages 395–417 in A. C. Gange and V. K. Brown, eds. *Multitrophic interactions in terrestrial systems*. Blackwell Science, Oxford.
- Joern, A. 1979a. Feeding patterns in grasshoppers (Orthoptera: Acrididae): factors influencing diet specialization. *Oecologia* 38:325–347.
- . 1979b. Resource utilization and community structure in arid grassland grasshopper assemblages. *Transactions of the American Entomological Society* 105:253–300.
- . 1983. Host plant utilization by grasshoppers (Orthoptera: Acrididae) in a sandhills prairie. *Journal of Range Management* 36:793–797.
- Joern, A., and L. R. Lawlor. 1980. Arid grassland grasshopper community: comparisons with neutral models. *Ecology* 61:591–599.
- Knöppel, H.-A. 1970. Food of central Amazonian fishes: contribution to the nutrient-ecology of Amazonian rain-forest streams. *Amazoniana* 2:257–352.
- Levins, R. 1968. *Evolution in changing environments*. Princeton University Press, Princeton, N.J.
- MacArthur, R. H., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist* 101:377–385.
- Martinez, N. D. 1991. Artifacts or attributes? effects of resolution on the Little Rock Lake food web. *Ecological Monographs* 61:367–392.
- . 1992. Constant connectance in community food webs. *American Naturalist* 140:1208–1218.
- Martinez, N. D., B. A. Hawkins, H. A. Dawah, and B. P. Feifarek. 1999. Effects of sampling effort on characterization of food-web structure. *Ecology* 80:1044–1055.
- Memmott, J., N. D. Martinez, and J. E. Cohen. 2000. Predators, parasitoids and pathogens: species richness, trophic generality and body sizes in a natural food web. *Journal of Animal Ecology* 2000:1–15.
- Mulkern, G. B., K. P. Pruess, H. Knutson, A. F. Hagen, J. B. Campbell, and J. D. Lambley. 1969. Food habits and preferences of grassland grasshoppers of the North Central Great Plains. *North Dakota State University Experiment Station Bulletin* 481. Fargo.
- Murtaugh, P. A. 1994. Statistical analysis of food webs. *Biometrics* 50:1199–1202.
- Otte, D. 1976. Species patterns of New World desert grasshoppers in relation to plant diversity. *Journal of Biogeography* 3:197–209.
- Pianka, E. R. 1974. Niche overlap and diffuse competition. *Proceedings of the National Academy of Sciences of the USA* 71:2141–2145.
- . 1976. Competition and niche theory. Pages 114–141 in R. M. May, ed. *Theoretical ecology: principles and applications*. Blackwell Science, Oxford.
- . 1986. *Ecology and natural history of desert lizards*. Princeton University Press, Princeton, N.J.
- Pimm, S. L., J. H. Lawton, and J. E. Cohen. 1991. Food web patterns and their consequences. *Nature (London)* 350:669–674.
- Polis, G. A. 1991. Complex trophic interactions in deserts: an empirical critique of food-web theory. *American Naturalist* 138:123–155.
- Schoener, T. W. 1974. Resource partitioning in ecological communities. *Science (Washington, D.C.)* 185:27–39.
- . 1982. The controversy over interspecific competition. *American Scientist* 70:586–595.
- Sheldon, J. K., and L. E. Rogers. 1978. Grasshopper food habits within a shrub-steppe community. *Oecologia* 32:85–92.
- Sugihara, G., L.-F. Bersier, and K. Schoenly. 1997. Effects of taxonomic and trophic aggregation on food web properties. *Oecologia* 112:272–284.
- Tavares-Cromar, A. F., and D. D. Williams. 1996. The importance of temporal resolution in food web analysis: evidence from a detritus-based stream. *Ecological Monographs* 66:91–113.
- Thompson, R. M., and C. R. Townsend. 1999. The effect of seasonal variation on the community structure and food-web attributes of two streams: implications for food-web science. *Oikos* 87:75–88.
- Townsend, C. R., R. M. Thompson, A. R. McIntosh, C. Kilroy, E. Edwards, and M. R. Scarsbrook. 1998. Disturbance, resource supply, and food-web architecture in streams. *Ecology Letters* 1:200–209.
- Ueckert, D. N., and R. M. Hansen. 1971. Dietary overlap of grasshoppers on sandhill rangeland in northeastern Colorado. *Oecologia* 8:276–295.
- Vitt, L. J., and P. A. Zani. 1998a. Ecological relationships among sympatric lizards in a transitional forest in the northern Amazon of Brazil. *Journal of Tropical Ecology* 12:63–86.
- . 1998b. Prey use among sympatric lizard species in lowland rain forest of Nicaragua. *Journal of Tropical Ecology* 14:537–559.
- Warren, P. H. 1989. Spatial and temporal variation in the structure of a freshwater food web. *Oikos* 55:299–311.
- . 1990. Variation in food web structure: the determinants of connectance. *American Naturalist* 136:689–700.
- Werner, E. E. 1977. Species packing and niche complementarity in three sunfishes. *American Naturalist* 111:553–578.

- Werner, E. E., and D. J. Hall. 1976. Niche shifts in sunfishes: experimental evidence and significance. *Science* (Washington, D.C.) 191:404–406.
- Williams, R. J., and N. D. Martinez. 2000. Simple rules yield complex food webs. *Nature* (London) 404: 180–183.
- Winemiller, K. O. 1989*a*. Must connectance decrease with species richness? *American Naturalist* 134:960–968.
- . 1989*b*. Ontogenetic diet shifts and resource partitioning among piscivorous fishes in the Venezuelan llanos. *Environmental Biology of Fishes* 26:177–199.
- . 1990. Spatial and temporal variation in tropical fish trophic networks. *Ecological Monographs* 60: 331–367.
- Winemiller, K. O., and E. R. Pianka. 1990. Organization in natural assemblages of desert lizards and tropical fishes. *Ecological Monographs* 60:27–55.
- Winemiller, K. O., and G. A. Polis. 1996. Food webs: what can they tell us about the world? Pages 1–22 in G. A. Polis and K. O. Winemiller, eds. *Food webs: integration of patterns and dynamics*. Chapman & Hall, New York.
- Yodzis, P., and K. O. Winemiller. 1999. In search of operational trophospecies in a tropical aquatic food web. *Oikos* 87:327–340.

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