CAN STABLE ISOTOPE RATIOS PROVIDE FOR COMMUNITY-WIDE MEASURES OF TROPHIC STRUCTURE?

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Abstract. Stable isotope ratios (typically of carbon and nitrogen) provide one representation of an organism's trophic niche and are widely used to examine aspects of food web structure. Yet stable isotopes have not been applied to quantitatively characterize community-wide aspects of trophic structure (i.e., at the level of an entire food web). We propose quantitative metrics that can be used to this end, drawing on similar approaches from ecomorphology research. For example, the convex hull area occupied by species in $\delta^{13}C$–$\delta^{15}N$ niche space is a representation of the total extent of trophic diversity within a food web, whereas mean nearest neighbor distance among all species pairs is a measure of species packing within trophic niche space. To facilitate discussion of opportunities and limitations of the metrics, we provide empirical and conceptual examples drawn from Bahamian tidal creek food webs. These examples illustrate how this methodology can be used to quantify trophic diversity and trophic redundancy in food webs, as well as to link individual species to characteristics of the food web in which they are embedded. Building from extensive applications of stable isotope ratios by ecologists, the community-wide metrics may provide a new perspective on food web structure, function, and dynamics.

Key words: biodiversity; diet; ecomorphology; food webs; functional groups; niche; predator–prey interactions; trophic guild; trophic redundancy.

INTRODUCTION

Charles Elton defined a species' "niche" as the sum of all the interactions (especially trophic) that link it to other species in an ecosystem (Elton 1927). In other words, the niche represents the overall trophic role of that species (Leibold 1995). Since stable isotope ratios in an organism's tissues derive from all trophic pathways culminating in that individual, they can be used as one means to depict the trophic niche. Applications of stable isotope ratios (typically of carbon and nitrogen) in food web ecology take advantage of natural variation in stable isotope ratios, and the underlying aspects of a species' trophic niche, which the variation reflects. For nitrogen, ratios of ^{15}N to ^{14}N (expressed as $\delta^{15}N$) exhibit stepwise enrichment with trophic transfers, and are powerful tools for estimating trophic position of organisms. Ratios of carbon isotopes ($\delta^{13}C$) vary substantially among primary producers with different photosynthetic pathways (e.g., C_3 vs. C_4 plants), but change little with trophic transfers. Therefore, $\delta^{13}C$ can be used to determine ultimate sources of dietary carbon (DeNiro and Epstein 1981, Peterson and Fry 1987, Post 2002*b*). Because of these (and other) insights into trophic

niches conferred by isotope ratios, they have become one of the most common tools employed in the study of trophic structure.

Since the earliest applications of stable isotope ratios by food web ecologists, a common approach has been to present $\delta^{13}C$–$\delta^{15}N$ bi-plots with species (or individuals, populations) plotted based on their mean stable isotope signatures. Relative position of species in this bi-plot space is used to infer aspects of food web structure. Although qualitative insights from $\delta^{13}C$–$\delta^{15}N$ bi-plots can be informative in some instances, recent research has sought to provide more quantitative measures based on these data. For example, they can be used to calculate trophic positions (Vander Zanden et al. 1997, Post et al. 2000, Post 2002*a*, Layman et al. 2005), relative contribution of prey items to consumers (Vander Zanden and Vadeboncoeur 2002), niche shifts (Post 2003), and intraspecific diet variability (Bolnick et al. 2003, Bearhop et al. 2004, Matthews and Mazumder 2004). Each of these quantitative applications focuses on the specific energy flow pathways leading to one (or a few) consumer species of interest.

We propose a novel analytical approach to calculate "community-wide" measures of trophic structure using stable isotope ratios. This approach draws on techniques frequently applied in ecomorphology literature, where metrics defining trophic characteristics are calculated based on two-dimensional representations of species' morphological characteristics (Ricklefs and Miles 1994).

Such studies have quantified position of species in "morphospace" (typically derived from principal components analysis of a suite of morphological characteristics), and analyzed these positional data using quantitative metrics. We propose a similar approach based on the stable isotope representations of species' niches. This application differs from traditional ecomorphology approaches in that it is not restricted to a specific taxonomic group with similar morphologies (e.g., fish or bats), and it is based on a representation of realized trophic niches (sensu Post 2002a) instead of presumed trophic roles derived from phenotypic characteristics (e.g., Winemiller 1991). We review specific quantitative metrics that can be used to analyze stable isotope representations of trophic niches, and provide empirical and conceptual examples using food webs from Bahamian tidal creeks. We discuss potential opportunities and limitations of this approach, and suggest the circumstances under which the metrics will most likely yield meaningful insights into food web structure, function (e.g., energy flow among species), and dynamics.

General Methodology

The first step in applying community-wide metrics is to clearly define the food web of interest (for recent discussions on delineating food webs see Winemiller and Layman 2005 and Post et al., in press). Following Elton's (1927) conception of the consumer trophic niche, we describe analyses that focus on consumer species only, although stable isotope ratios of basal resource pools may provide additional insight into metric variation (see Discussion). Stable isotope ratios most commonly employed by ecologists are $\delta^{13}C$ and $\delta^{15}N$, and we discuss metrics based on these two ratios. Hereafter, we refer to the $\delta^{13}C$–$\delta^{15}N$ space in which species are plotted as "niche space." Other stable isotopes may be incorporated into this general framework, e.g., sulfur in marine food webs (see Connolly et al. 2004), thereby expanding to a third dimension and providing additional resolution of species' position within an expanded niche space. Community-wide isotope metrics described herein are calculated based on mean $\delta^{13}C$–$\delta^{15}N$ values of multiple individuals for each species in a food web, although it is acknowledged that there is important intraspecific variation that this particular level of analysis will not account for (see Discussion).

We describe six community-wide metrics that reflect important aspects of trophic structure. The first four metrics are measures of the total extent of spacing within $\delta^{13}C$–$\delta^{15}N$ bi-plot space, i.e., community-wide measures of trophic diversity. The final two metrics reflect relative position of species to each other within niche space and can be used to estimate the extent of trophic redundancy. These and other metrics have been widely discussed and applied within the ecomorphology literature (Findley 1973, Ricklefs and Travis 1980, Winemiller 1991,

Ricklefs and Miles 1994), and such sources provide details of underlying theory, mathematics, and methodological considerations.

1) $\delta^{15}N$ Range (NR): Distance between the two species with the most enriched and most depleted $\delta^{15}N$ values (i.e., maximum $\delta^{15}N$ – minimum $\delta^{15}N$). NR is one representation of vertical structure within a food web. Trophic position of organisms must be calculated in relation to the $\delta^{15}N$ values of a standardized baseline (Post 2002b) but, generally, a larger range in $\delta^{15}N$ among consumers suggests more trophic levels and thus a greater degree of trophic diversity.

2) $\delta^{13}C$ range (CR): Distance between the two species with the most enriched and most depleted $\delta^{13}C$ values (i.e., maximum $\delta^{13}C$ – minimum $\delta^{13}C$). Increased CR would be expected in food webs in which there are multiple basal resources with varying $\delta^{13}C$ values, providing for niche diversification at the base of a food web.

3) Total area (TA): Convex hull area encompassed by all species in $\delta^{13}C$–$\delta^{15}N$ bi-plot space. This represents a measure of the total amount of niche space occupied, and thus a proxy for the total extent of trophic diversity within a food web. TA is influenced by species with extreme positions on either the $\delta^{13}C$ or $\delta^{15}N$ axis (or both), and thus typically will be correlated to some degree with these two metrics. Details on calculating convex hull area (and volumes) can be found in Cornwell et al. (2006).

4) Mean distance to centroid (CD): Average Euclidean distance of each species to the $\delta^{13}C$–$\delta^{15}N$ centroid, where the centroid is the mean $\delta^{13}C$ and $\delta^{15}N$ value for all species in the food web. This metric provides a measure of the average degree of trophic diversity within a food web. In cases where a few outlier species may differentially affect TA, this measure may better reflect the overall degree of trophic diversity in the food web. However, this measure also is a function of the degree of species spacing (see following metric).

5) Mean nearest neighbor distance (NND): Mean of the Euclidean distances to each species' nearest neighbor in bi-plot space, and thus a measure of the overall density of species packing. Food webs with a large proportion of species characterized by similar trophic ecologies will exhibit a smaller NND (increased trophic redundancy) than a web in which species are, on average, more divergent in terms of their trophic niche.

6) Standard deviation of nearest neighbor distance (SDNND): A measure of the evenness of species packing in bi-plot space that is less influenced than NND by sample size. Low SDNND values suggest more even distribution of trophic niches.

We present empirical data to illustrate how individual species' niches, and dispersion of those niches, drive variation in community-wide metric values. The data are from Bahamian tidal creek food webs (see Layman and Silliman 2002, Layman et al. 2004; Valentine et al., in press), with the webs delineated based on all macro-

consumer species resident to the creek systems. Replicate individuals for all species were collected using nets, traps, and by hand over a 3–5 day period for each creek system. Stable isotope analyses were conducted on individuals using standard isotopic preparation and analysis for estuarine samples (e.g., Peterson and Fry 1987, Post 2002b, Connolly et al. 2004, Jacob et al. 2005). Analyses were conducted on 2–9 individuals of each macroconsumer species, mean values for each species are plotted based in $\delta^{13}C$ and $\delta^{15}N$ space, and community-wide metrics calculated from the species' mean values. We discuss a general framework for applying the community-wide metrics, but this is only a foundation from which a variety of statistical approaches (e.g., incorporation of null models as in Cornwell et al. 2006) can be developed to provide for rigorous tests of ecological patterns and theory.

RESULTS AND DISCUSSION

Community-wide metrics reflect specific aspects of trophic structure within a food web, with trophic niches of individual species (and relative position of those niches) determining metric values. As an example, Fig. 1 provides data from a Bahamian tidal creek food web, with the convex hull used to calculate TA outlined. The TA value is influenced by those species with extreme values along the $\delta^{13}C$- and/or $\delta^{15}N$-axes. For example, the chicken liver sponge (*Chondrilla nucula*; $\delta^{13}C$ = −13.6‰, $\delta^{15}N$ = −3.5‰; solid circle) has a distinct $\delta^{15}N$ value because of its unique (within this food web) trophic niche in which it utilizes small size classes of seston (and thus has a depleted $\delta^{15}N$ value). Loss of this species would result in a decrease in overall trophic diversity in the food web (loss of a specialized filter feeder), which would be reflected in lower NR and TA values. Alternatively, loss of the stocky cerith snail (*Cerithium litteratum*; $\delta^{13}C$ = −13.2‰, $\delta^{15}N$ = 2.5‰; solid triangle) would not affect NR, CR, or TA because the false cerith snail (*Batillaria minima*) has a very similar trophic niche in this system (−13.0‰, 2.3‰). The stocky and false ceriths are redundant species in this sense, and thus loss of the stocky cerith would represent a loss of trophic redundancy (reflected by an increase in NND), but would not affect overall trophic diversity. In this manner, the community-wide metrics provide a novel framework with which to quantify trophic diversity and trophic redundancy in food webs, as well as to link individual species to characteristics of the food web in which they are embedded.

Metric values based on a snapshot characterization of a single food web provide limited insights into food web structure or function. The most promising applications of the community-wide metrics will be to compare multiple, similarly defined, food webs across environmental gradients, or to examine the same food web from a temporal perspective. The metrics are useful in each of these contexts because they provide a more detailed set of response variables (i.e., continuous measures of

NR = 11.5   CR = 7.1   TA = 54.3
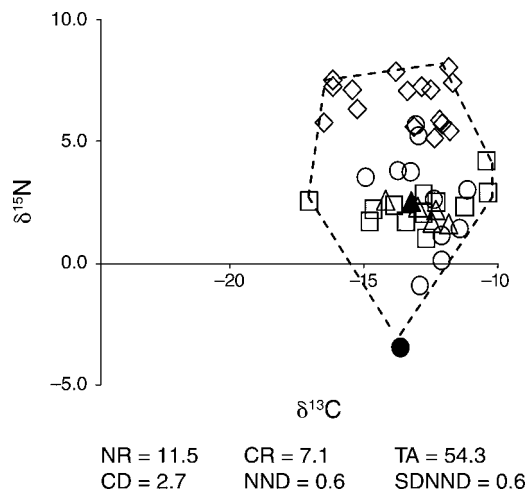CD = 2.7   NND = 0.6   SDNND = 0.6

FIG. 1. Stable isotope bi-plots based on species collected from a Bahamian tidal creek. Each point on the graph represents the mean value of 2–9 individuals of that particular species with error bars around the mean omitted for simplicity. Calculation of community-wide metrics was based on the distribution of species in niche space: diamonds, fish; squares, crustaceans; triangles, mollusks; and circles, other invertebrate taxa. Solid symbols are used to illustrate how individual species' niches, and dispersion of those niches, affect values of the community-wide metrics (see *Discussion*). The convex hull used to calculate the TA metric is represented by the dotted line.

trophic structure) and thus an alternative to the commonly employed "aggregate" variability measures (sensu Micheli et al. 1999) such as species richness, biomass, or number of individuals.

We provide an example in Fig. 2 of how the metrics can be applied as response variables to assess changes in a food web through time. The species in Fig. 2A comprise the food web of a fragmented tidal creek system in which the majority of tidal flow has been blocked by construction of a road (see Layman et al. 2004). The conceptual scenarios (Fig. 2B–D) provide examples of how food web structure may change through time, and how the community-wide metrics would reflect the changes, following restoration of hydrologic connectivity to the fragmented system (an example of such a restoration project can be found in Layman et al. 2005). In the first scenario (Fig. 2B), immigration of new top predator species would serve to increase trophic diversity in the post-restoration food web, and this change would be reflected by an increase in NR and TA. CR does not change because the new species couples energy flow pathways originating from existing basal resource pools in the system. NND and SDNND decrease because the three immigrant species have very similar trophic niches.

The scenario depicted in Fig. 2C represents a change in food web structure that may result following establishment of a new basal resource with a relatively enriched $\delta^{13}C$ signature (e.g., seagrass). Primary consumers may immigrate to utilize this resource, thereby
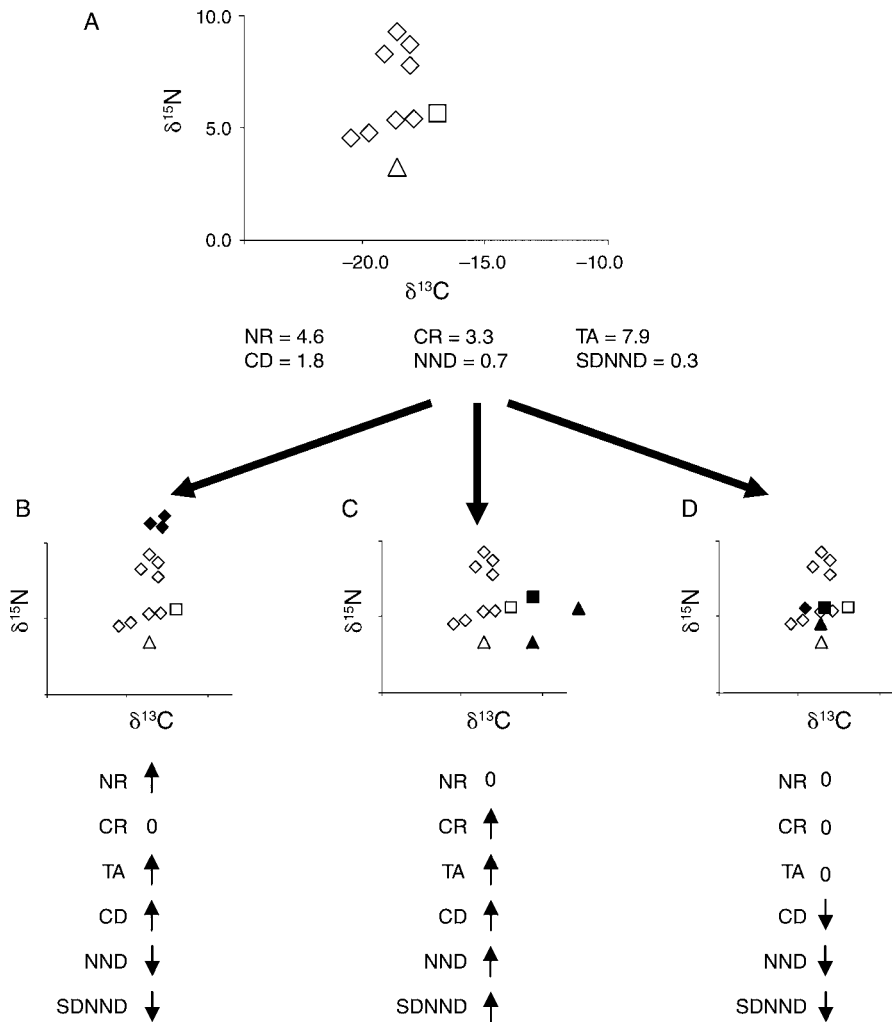
FIG. 2. Conceptual models (B–D) of different ways food web structure can be altered through the addition of three new species to an existing tidal creek food web (A). Symbols are consistent with Fig. 1, and solid symbols represent new species added in each scenario. The ways community-wide metrics will vary under each scenario are depicted below each graph.

increasing trophic diversity at the base of the food web, a change which would be reflected by an increase in CR and TA. In this scenario, NND and SDNND would increase because the new consumer species have more distinct trophic positions (greater distance among them in niche space). Scenario Fig. 2D represents immigration of redundant species that would not affect the overall degree of trophic diversity in the web (NR, CR, and TA would remain unchanged). This species addition would be reflected by decreased NND and SDNND. Obviously, these are simplified conceptual models, whereas actual changes in the food web structure could be far more complex (e.g., simultaneous immigration of species with diverse trophic niches, or existing species that undergo niche shifts). Yet these examples demonstrate how hypotheses regarding ecological phenomena can be tested based on specific aspects of underlying trophic structure using the community-wide metrics as primary response variables.

We emphasize that between- and among-system comparisons using community-wide metrics will be most meaningful when food webs are defined in the same fashion. Some of the most well-defined food webs (or food web "modules," sensu Holt 1997) are found in the context of experimental manipulations, and thus community-wide metrics could be applied as new response variables in many experimental contexts. For example, in a recent study of colonization dynamics of patch habitats in a tropical river, species density was employed as the primary response variable (Arrington et al. 2005). It was argued that patches eventually became saturated with species and that biological interactions limited community membership. Yet, by relying solely on an aggregate response variable (species density), there was little ability to distinguish among potential underlying mechanisms. Depictions of species' trophic niches using isotopes, and application of the community-wide metrics, may have provided significantly more insight into

the underlying factors that may drive dynamics of community membership. For example, increased trophic redundancy (inferred from decreasing NND) would have suggested a role of competitive interactions in limiting species density, whereas an increase in trophic diversity at the top of the web (higher NR) would have suggested predation may have influenced community membership. Such an approach could provide a new perspective to assess experimental results and to direct further scientific inquiry in experimental contexts.

Community-wide metrics based on species' positions in niche space also may provide for a novel way to link species richness and measures of ecosystem function. Recent studies suggest that although functional groupings are often informative as a construct in linking species and ecosystem-level characteristics (e.g., Stevens et al. 2003, Downing 2005, Micheli and Halpern 2005), they are at times arbitrary and may be limited in their predictive power (Petchey and Gaston 2002, Petchey et al. 2004, Wright et al. 2006). Such limitations may stem from an inability to provide adequate resolution with respect to the realized niches (and thus functional role) of constituent species (Petchey et al. 2004). The community-wide metrics provide a new perspective from which to link species-level traits to overall food web structure and ecosystem function because they provide a means to account for "subtle" differences in trophic ecology among species (see Duffy 2002), differences that may not be reflected through use of functional groupings.

Community-wide metrics based on stable isotopes provide a different type of information than traditional food web metrics (e.g., connectance or linkage density). The latter typically rely on detailed stomach content analyses documenting all feeding links among taxa (Winemiller 1990). Food web characteristics, such as connectance, then are generated from diet data to describe the general form of feeding linkages across an entire food web. Community-wide metrics derived from stable isotope data cannot be used to this end, because they provide a sum representation of all energy pathways leading to an organism. Yet isotopic depictions of species' niches reflect temporally (and spatially) integrated data, which is difficult to compile with stomach content data alone (Winemiller 1990, Post 2002b, Winemiller and Layman 2005). Stable isotopes also provide a quantitative means to infer the basal resource pools that support particular consumers, which often can be very difficult (especially for species positioned higher in a food web) when using diet data to construct feeding relationships in complex food webs (Winemiller 1990).

We acknowledge several caveats with this approach that will affect its scope of application. Limitations generally associated with stable isotope analyses also apply to community-wide metrics derived from stable isotope data. For example, temporal and spatial variation in isotopic signatures of food sources (espe-cially basal resources with rapid turnover rates) contribute to variation in isotopic signatures of consumers (Post 2002b, Matthews and Mazumder 2003), and thus will influence a consumer's position in niche space. Second, total isotopic variation of a consumer is not only a function of trophic ecology, but of all factors that affect assimilation of food items into tissue. Many factors (e.g., type of food item and environmental conditions) may contribute to variability in fractionation with trophic transfers, and isotopic routing may vary among tissue types or among species (DeNiro and Epstein 1981, Macko et al. 1982, Hobson and Clark 1992, Vanderklift and Ponsard 2003). It also is acknowledged that disparate feeding pathways may lead to the same position of two or more species in niche space, and thus the metrics will be most informative in systems when distinct feeding niches are reflected by different positions of species in $\delta^{13}C$–$\delta^{15}N$ space. Bias (at the species level) introduced by these factors, however, may have minimal impact on metrics as derived across all species in a web, especially when comparing across gradients that have significant effects on food web structure. In fact, this may be viewed as one of the promising aspects of the community-wide approach, i.e., by looking for overall patterns in food web structure, intricacies of determining every factor affecting a single species' isotope ratios are not essential to elucidate.

Additionally, community-wide metrics, as described in the present study, are based on mean positions of species in niche space. In reality, each species is composed of a cloud of points reflecting the degree of trophic generality among individuals of each species (Bolnick et al. 2003, Bearhop et al. 2004, Matthews and Mazumder 2004). We agree with Bearhop et al. (2004) that stable isotopes can be a powerful tool to investigate the degree of trophic specificity/generality among individuals in a population, and suggest the metrics proposed herein can also be useful at the population level. For example, TA could be used as a quantitative measure of a population's total niche width, whereas NND as a means to assess the overall similarity of trophic niches among individuals in a population.

Conclusions

Any single methodology, including stable isotope ratios, cannot provide a complete description of food web structure and function. Application of a variety of research methodologies, as well as a thorough understanding of natural history of organisms and of species interactions, will lead to the most thorough understanding of food webs. Use of community-wide metrics based on stable isotope representations of species' niches is one additional tool that deserves consideration. This approach may reveal important insights into food web structure by providing quantitative response variables that reflect specific characteristics of trophic structure. With extensive application of stable isotope ratios by

ecologists, and with many existing community-level isotope databases, we hope there will be numerous opportunities to use this approach to provide new insights into food web structure, particularly as a means to assess variation in trophic diversity and/or trophic redundancy in and among food webs.

Literature Cited

Arrington, D. A., K. O. Winemiller, and C. A. Layman. 2005. Community assembly at the patch scale in a species-rich tropical river. Oecologia 144:157–167.

Bearhop, S., C. E. Adams, S. Waldron, R. A. Fuller, and H. Macleod. 2004. Determining trophic niche width: a novel approach using stable isotope analysis. Journal of Animal Ecology 73:1007–1012.

Bolnick, D. I., R. Svanbäck, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey, and M. L. Forister. 2003. The ecology of individuals: incidence and implications of individual specialization. American Naturalist 161:1–28.

Connolly, R. M., M. A. Guest, A. J. Melville, and J. M. Oakes. 2004. Sulfur stable isotopes separate producers in marine food-web analysis. Oecologia 138:161–167.

Cornwell, W. K., D. W. Schwilk, and D. D. Ackerly. 2006. A trait-based test for habitat filtering: convex-hull volume. Ecology 87:1465–1471.

DeNiro, M. J., and S. Epstein. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. Geochimica et Cosmochimica Acta 45:341–351.

Downing, A. L. 2005. Relative effects of species composition and richness on ecosystem properties in ponds. Ecology 86:701–715.

Duffy, J. E. 2002. Biodiversity and ecosystem function: the consumer connection. Oikos 99:201–219.

Elton, C. S. 1927. Animal ecology. Sidgwick and Jackson, London, UK.

Findley, J. S. 1973. Phenetic packing as a measure of faunal diversity. American Naturalist 107:580–584.

Hobson, K. A., and R. G. Clark. 1992. Assessing avian diets using stable isotopes II: factors influencing diet-tissue fractionation. Condor 94:189–197.

Holt, R. D. 1997. Community modules. Pages 333–351 in A. C. Gange and V. K. Brown, editors. Multitrophic interactions in terrestrial systems. Blackwell Science, Oxford, UK.

Jacob, U., K. Mintenbeck, T. Brey, R. Knust, and K. Beyer. 2005. Stable isotope food web studies: a case for standardized sample treatment. Marine Ecology Progress Series 287:251–253.

Layman, C. A., D. A. Arrington, and M. A. Blackwell. 2005. Community-based collaboration restores tidal flow to an island estuary (Bahamas). Ecological Restoration 23:58–59.

Layman, C. A., D. A. Arrington, R. B. Langerhans, and B. R. Silliman. 2004. Degree of fragmentation affects fish assemblage structure in Andros Island (Bahamas) estuaries. Caribbean Journal of Science 40:232–244.

Layman, C. A., and B. R. Silliman. 2002. Preliminary survey and diet analysis of juvenile fishes of an estuarine creek on Andros Island, Bahamas. Bulletin of Marine Science 70:199–210.

Layman, C. A., K. O. Winemiller, D. A. Arrington, and D. B. Jepson. 2005. Body size and trophic position in a diverse food web. Ecology 86:2530–2535.

Leibold, M. A. 1995. The niche concept revisited: mechanistic models and community context. Ecology 76:1371–1382.

Macko, S. A., W. Y. Lee, and P. L. Parker. 1982. Nitrogen and carbon isotope fractionation by two species of marine amphipods: laboratory and field studies. Journal of Experimental Marine Biology and Ecology 63:145–149.

Matthews, B., and A. Mazumder. 2003. Compositional and interlake variability of zooplankton affect baseline stable isotope signatures. Limnology and Oceanography 48:1977–1987.

Matthews, B., and A. Mazumder. 2004. A critical evaluation of intrapopulation variation of delta C-13 and isotopic evidence of individual specialization. Oecologia 140:361–371.

Micheli, F., K. L. Cottingham, J. Bascompte, O. N. Bjørnstad, G. L. Eckert, J. M. Fischer, T. H. Keitt, B. E. Kendall, J. L. Klug, and J. A. Rusak. 1999. The dual nature of community variability. Oikos 85:161–169.

Micheli, F., and B. S. Halpern. 2005. Low functional redundancy in coastal marine assemblages. Ecology Letters 8:391–400.

Petchey, O. L., and K. J. Gaston. 2002. Functional diversity (FD), species richness and community composition. Ecology Letters 5:402–411.

Petchey, O. L., A. Hector, and K. J. Gaston. 2004. How do different measures of functional diversity perform? Ecology 85:847–857.

Peterson, B. J., and B. Fry. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics 18:293–320.

Post, D. M. 2002a. The long and short of food-chain length. Trends in Ecology and Evolution 17:269–277.

Post, D. M. 2002b. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703–718.

Post, D. M. 2003. Individual variation in the timing of ontogenetic niche shifts in largemouth bass. Ecology 84:1298–1310.

Post, D. M., M. W. Doyle, J. L. Sabo, and J. C. Finlay. In press. The problem of boundaries in defining ecosystems: a potential landmine for uniting geomorphology and ecology. Geomorphology.

Post, D. M., M. L. Pace, and N. G. Hairston, Jr. 2000. Ecosystem size determines food-chain length in lakes. Nature 405:1047–1049.

Ricklefs, R. E., and D. B. Miles. 1994. Ecological and evolutionary inferences from morphology: an ecological perspective. Pages 13–41 in P. C. Wainwright and S. M. Reilly, editors. Ecological morphology. University of Chicago Press, Chicago, Illinois, USA.

Ricklefs, R. E., and J. Travis. 1980. A morphological approach to the study of avian community organization. Auk 97:321–338.

Stevens, R. D., S. B. Cox, R. E. Strauss, and M. R. Willig. 2003. Patterns of functional diversity across an extensive environmental gradient: vertebrate consumers, hidden treatments and latitudinal trends. Ecology Letters 6:1099–1108.

Valentine, L., C. A. Layman, and D. A. Arrington. In press. Habitat fragmentation affects fish secondary production in Bahamian tidal creeks. Bulletin of Marine Science.

Vanderklift, M. A., and S. Ponsard. 2003. Sources of isotopic variation in consumer-diet d15N enrichment: a meta-analysis. Oecologia 136:169–182.

Vander Zanden, M. J., G. Cabana, and J. B. Rasmussen. 1997. Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios (delta N-15) and

literature dietary data. Canadian Journal of Fisheries and Aquatic Sciences 54:1142–1158.

Vander Zanden, M. J., and Y. Vadeboncoeur. 2002. Fishes as integrators of benthic and pelagic food webs in lakes. Ecology 83:2152–2161.

Winemiller, K. O. 1990. Spatial and temporal variation in tropical fish trophic networks. Ecological Monographs 60: 331–367.

Winemiller, K. O. 1991. Ecomorphological diversification in lowland freshwater fish assemblages from five biotic regions. Ecological Monographs 61:343–365.

Winemiller, K. O., and C. A. Layman. 2005. Pattern, process and scale in the food web paradigm: moving on the path from abstraction to prediction. Pages 10–23 *in* Dynamic food webs: multispecies assemblages, ecosystem development, and environmental change. Elsevier/Academic Press, Amsterdam, The Netherlands.

Wright, J. P., S. Naeem, A. Hector, C. Lehman, P. B. Reich, B. Schmid, and D. Tilman. 2006. Conventional functional classification schemes underestimate the relationship with ecosystem functioning. Ecology Letters 9:111–120.

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