Untangling Food Webs

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Just as the ecology of an organism is defined in large part by what it eats and what eats it, the properties of a community emerge largely from the network of trophic interactions among its members. Consequently, food webs are central to almost all ecological research, if not as the direct object of study then as the context in which species interactions and other processes are situated (Paine 1966, May 1983, Polis et al. 2004, McCann 2012).

But although food webs are fundamental to our understanding of ecology, we do not yet understand their most fundamental feature—the basic architecture of nodes and links that comprise the network. In vanishingly few cases and with inordinate effort, investigators have compiled something roughly approaching a complete map of trophic interactions for the set of macroscopic consumer and producer populations present at a site (Cohen et al. 2003, Brown and Gillooly 2003). But even the most finely resolved networks have missing pieces (and gaping holes if we include parasites and microbes (Lafferty et al. 2008)) and are merely static averages of what are inherently dynamic systems (Cohen et al. 2003).

Barriers to Knowing What Wild Consumers Actually Eat

Visitors to a zoo, standing in front of some big mammal from some exotic place, might field a basic question from a curious child: “What does it eat?” Although the informational placard provides only the vaguest of information (“plants”), the parents may assume that scientists know the answer. But with rare exceptions, they would be wrong. Zoo directors may appreciate the depths of our ignorance on this count better than anyone. As Mike Jordan of the Chester Zoo put it, “detailed information about the diet of the majority of free-ranging mammals and birds does not exist and often only the most generalized approximation of food items consumed is known” (Jordan 2005).

There are two major problems with the quality of empirical data used to construct food webs. First, they are poorly resolved taxonomically, with food items often lumped at the level of genus, family, or order, or else categorized into broad functional groups (large versus small, animal versus plant, grass versus shrub, foliage versus fruit) (Paine 1988, Solow and Beet 1998, Winemiller 2007). Such coarse data may be severely mismatched with the precision of consumers' foraging decisions: The distinctions among resource types that are most readily perceived and quantified by ecologists may or may not be those that are salient to the animals. Second, dietary data are poorly resolved in space and time, often being drawn either from a single population and averaged across time (as is common in field studies) or from individuals sampled at many points in space and time and averaged across both (as is common in studies of museum specimens). Consequently, we know little about individual dietary variation within populations, about dietary differences between populations across environmental and geographic gradients (i.e., dietary beta diversity), or about dietary shifts in response to changing seasonal or climatic conditions.

The simple reason for these problems is that it is extremely difficult to accurately and representatively characterize the diet of most free-ranging consumers. This statement is coincidentally illustrated by something happening nearby as I write this. About ten meters away from me, a habituated warthog (*Phacochoerus africanus*) is grazing the unusually homogeneous lawn of the Chitengo Camp in Gorongosa National Park, Mozambique. I know that warthogs in this park eat mostly grass (Pansu et al. 2019), and that the dominant grass in this particular lawn is *Urochloa mosambicensis* (Hack.) Dandy. But although the lawn is unusually homogeneous, it nonetheless has multiple species of grasses and forbs coexisting at small spatial scales, and I cannot see—even through binoculars—exactly which species are being eaten. And although this pig is unusually tame, it is not tame enough that I could reach into its mouth, remove the food, and sort the foliage by species. The best I could do instead is walk up to the place where the animal is grazing and try to identify which plants have been bitten or not (Kleynhans et al. 2011). But now the warthog has walked off—how long would I have to follow it before I had a complete list of the plant species in its diet? Would its foraging decisions be altered by my following it around? Probably. And before long, I would come across a plant species that I could not identify, perhaps one that only a few people in the world could identify, perhaps even one that has no name because it has never been scientifically described. The biota of Mozambique, like that of many African countries, is understudied and poorly understood.

I face all of these problems just for the tamest of warthogs; never mind trying to follow one of Gorongosa's shier or more lethal large herbivores at close range. And forget about shooting large numbers of them and sifting through their guts—a once-preferred method of diet analysis for large

African herbivores (Field 1972). In addition to being legally prohibited and ethically outrageous, stomach-contents analysis would not solve the problem. Buss (1961) shot dozens of Ugandan elephants in 1959, and although he was able to identify some forage items to the species level—71 elephant stomachs collectively contained 266 kg of *Combretum collinum* and 59 kg of *Vitex doniana*—the overwhelmingly dominant food types were identified only as "mature grass" and "young grass" (3793 and 479 kg respectively). Even some of the nongrass species in Buss' elephant stomachs could only be identified to the genus or family level, and others could not be identified at all ("unidentified woody materials" weighed in at 27 kg, making it the seventh-most-abundant food type). Microhistologic examination of feces to visually match undigested plant fragments with reference specimens is an ethically uncomplicated nonlethal alternative, but it is extremely laborious and tends to yield low-quality data (Newmaster et al. 2013). Stable-isotope analysis is a profoundly important tool for inferring many food-web properties (Layman et al. 2012), but it provides only coarse-grained insights into the taxonomic composition of a consumer's diet.

Similar limitations pertain to other traditional methods of diet assessment. Expert opinion (Stier et al. 2016) is unreliable. Cafeteria choice experiments (Ford 2014) are unwieldy. Gastric lavage and allied techniques (Holechek and Pieper 1982) require capture and can harm animals. Some study species are more tractable than others. Sea otters conveniently consume all their prey at the ocean's surface where people can see them, which facilitates the study of individual- and population-level dietary variation (Estes et al. 2003, Tinker et al. 2008). Sea stars (Paine 1966) and caterpillars (Hebert et al. 2004, Janzen et al. 2017) conveniently sit on their foods for a long time while consuming them. But for the vast diversity of animals that lack such agreeable traits, conventional approaches are insufficient to thoroughly and accurately identify food types to species, and our knowledge of diet composition and food-web structure remains spotty at best. These difficulties are compounded for species-rich food types that are not easily identified from a distance or as partially digested fragments. That category includes essentially all arthropods and herbaceous plants, especially in the tropics.

Cryptic Diversity and Taxonomic Imprecision Compound the Challenges of Food-Web Analysis

Identifying many organisms to species level is a serious challenge even for a taxonomic specialist with a high-quality specimen in hand. Many ecologists underestimate the difficulties associated with identifying and distinguishing species and overestimate their own ability to make determinations by consulting published field guides, keys, and reference collections. Many community-level studies proceed on the grounds that similar-looking species are probably ecologically "close enough," even if not quite the same thing. This is the implicit premise underpinning the reliance of many field studies upon supraspecific lumpings or morphospecies determinations by nonspecialists (Oliver and Beattie 1996). It is tempting to view taxonomic imprecision as functionally inconsequential—unlikely to bias our conceptual understanding of food-web organization, and perhaps even necessary to achieve theoretical clarity.

To what extent is that true? That is an unsolved question that needs answering. More precisely: When is what degree of taxonomic approximation sufficient to capture the mechanistic essence of trophic interactions and predict the outcomes of ecological processes? More simply: How good is good enough?

A growing body of evidence indicates that even fairly narrow approximations are not good enough to understand the structure and dynamics of food webs. Over the past 15 years, we have learned that cryptic species are commonplace, and that accounting for them can dramatically alter our understanding of consumers' dietary niches and hence food-web architecture (Hebert et al. 2004; Janzen et al. 2017; Smith et al. 2006, 2007, 2008). In a now-famous example, the neotropical skipper butterfly *Astraptes fulgerator,* thought since 1775 to be a single wide-ranging species, was discovered to be "a complex of ≥10 food plant specialists with differing ecological attributes" in northwestern Costa Rica alone (Hebert et al. 2004). Farther up the food chain, a braconid wasp parasitoid of Costa Rican skipper caterpillars, *Apanteles leucostigmus*, formerly considered a generalist consumer of 32 skipper species, was found to comprise at least 36 species, each of which eats only "one or a very few closely related species of caterpillars." Examination of the six microgastrine braconid genera of northwestern Costa Rica revealed more than 300 provisional species, 95% of which were undescribed and 90% of which "attack only 1 or 2 species of caterpillars" (Smith et al. 2008). Cryptic diversity and cryptic host specificity were likewise found within the tachinid fly parasitoids of this region: 16 presumed generalist species were found to represent 73 mitochondrial lineages, of which only 9 were true generalists (Smith et al. 2007).

In short, what appeared to be a fairly generalized plant–herbivore–parasitoid food web resolved, on more rigorous inspection, into a series of far more specialized food chains. One obvious general lesson is that fine-grained taxonomic distinctions are not ecologically trivial. Heaps of closely related butterfly species, identical enough to pass for one another in plain sight for hundreds of years, are ecologically and trophically disparate. Any theory of food webs that elided such distinctions in the search for "useful generalizations" (Lawton 1999) would be anti-progress, because the mischaracterization of network architecture, diet breadth, and niche overlap would preclude any reliable inferences about the eco-evolutionary processes that produced those attributes. The quest for a predictive conceptual framework of ecological specialization (Poisot et al. 2011, Vamosi et al. 2014) is doomed if we are routinely and unknowingly mistaking specialists for generalists in nature.

This kind of problem is not confined to megadiverse tropical-forest food webs of tiny wasps and flies and caterpillars. In a semiarid African savanna ecosystem in Kenya, we have found similar patterns of cryptic diversity and dietary specificity among large mammalian herbivores. Since 2008, Jake Goheen, Todd Palmer, and I have maintained the UHURU study—a network of 1-ha experimental plots where we simulate size-biased extinction by selectively excluding first the megaherbivores (elephants and giraffes), followed by successively smaller sets of species (mesoherbivores, then dwarf antelopes), until only hares and rodents remain (Pringle 2012, Goheen et al. 2013, Kartzinel et al. 2014, Goheen et al. 2018). To assess the ecological impacts of removing larger species, we regularly monitor plants, trap small mammals, and survey other animal populations and ecosystem processes (Coverdale et al. 2016, 2018, 2019; Ford et al. 2014, 2015; Long et al. 2017; Louthan et al. 2013, 2014, 2018; Ngatia et al. 2014; Pringle et al. 2011, 2014, 2016; Titcomb et al. 2017; Young et al. 2013, 2015, 2017). Among the few-dozen small-mammal species in this region, there are two genera, *Mus* and *Crocidura*, that each contain multiple species that we cannot distinguish in the field (Goheen et al. 2013, Young et al. 2015). A 'species' known to us for the first several years of the study as *Gerbilliscus robustus* was later revealed to be two species from different genera, *G. robustus* and *Taterillus harringtoni* (Goheen et al. 2013). Two species of hares (*Lepus* spp.) that occur in the plots can be distinguished based on mitochondrial DNA, but our attempt to identify these two haplotypes based on the reference DNA sequences available in GenBank produced hopelessly confusing results (Kartzinel et al. 2019); we are forced to refer to them as Hare A and Hare B. Notably, fecal DNA analysis reveals that Hare A and Hare B—whoever they are—have different diets (Kartzinel et al. 2019). For plants, our initial list of 105 morphotaxa in the experimental plots has been painstakingly refined and expanded over the past decade with the assistance of taxonomic experts and DNA barcoding, currently numbering 189 (Goheen et al. 2013; Kartzinel et al. 2014, 2015; Gill et al. 2019).

Just as in Costa Rica, these fine-grained taxonomic distinctions have implications for our understanding of ecological specialization and food-web architecture. African savanna herbivores are often classified as grazers, browsers, or mixed-feeders—a taxonomically coarse typology that refers to the proportion of monocots (primarily grasses, family Poaceae) versus all other plant lineages ("browse") in the diet (du Toit and Olff 2014). The most common large-herbivore species at our Kenyan site include three pairs of species that consume roughly equivalent proportions of grass and browse (as inferred from carbon stable-isotope analysis), yet strikingly partition different plant species within those categories (as inferred from fecal DNA metabarcoding): plains and Grevy's zebra (*Equus quagga* and *E. grevyi*, respectively), Cape buffalo and domestic cattle (*Syncerus caffer* and *Bos indicus*, respectively), and elephant and impala (*Loxodonta africana* and *Aepyceros melampus*, respectively) (Kartzinel et al. 2015). Thus, depending on the taxonomic resolution with which diet is assessed, one could conclude that diet composition is highly redundant within these pairs (comprising similar proportions of grass and browse), or that each species is relatively specialized and distinct (consuming different amounts of particular grass and browse species). The as-yet unanswered question is to what extent these subtler distinctions influence broader system-level processes and properties—competition, coexistence, productivity, stability—and thus to what extent we must account for all nodes and edges before we can have a functional understanding of a food-web network.

Old Wine in New Bottles

These perspectives throw modern light onto a longstanding problem. Concerns about the inadequacy of empirical data to resolve food-web structure and dynamics go way back. Ecologists' interest in "the structure of food webs" (May 1983, Pimm 1979) intensified in the late 1970s, with hopes that general rules of community organization could be distilled (Cohen 1977, Briand and Cohen 1984). May (1983) outlined the contours of an emerging field: "Although a good deal of scattered information about individual food webs has been available for some time, it is only in the last 10 years or so that people have begun a systematic attempt to understand what factors determine the structure of food webs."

However, the accuracy and resolution of the empirical food webs being used to guide theoretical development left much to be desired. This was especially true for the small and inconspicuous species at low trophic levels. Whereas large vertebrates were rarely overlooked and were often resolved to the species level, basal consumers and resources were often lumped into coarse taxonomic or functional groups (not always the correct ones) or else omitted entirely. Paine (1988) argued that existing empirical food webs provided only an approximate "road map" of interactions in a community:

> These qualitative descriptions were never intended to be data, to serve as grist for the theoretician's mill. I do not believe that clever theory can overcome this handicap and generate testable, interesting predictions about web structure and dynamics. Profitable theory can be done, and often is, for theory's sake. However, when theory is developed in concert with data, the partnership should be more or less equal. This has not been the case with food webs, where theory seems far ahead of the data, often to the theory's detriment. I know of no one who, having assembled a data set on feeding relationships, considers those data to constitute much more than an incomplete preliminary description. I believe a fresh start is called for.

Paine argued that food webs must at least be subjected to "common sense" scrutiny as to whether they represent "a biologically realistic representation," and that "whenever possible, species should be identified rather than aggregated so that individual roles can be identified and ties to mainstream ecological mathematics facilitated." He also suggested that it might be more profitable to shift focus away from patterns of connectance in complex whole-community food webs as a basis for theory, and towards the use of interaction strength as a currency to generate more easily testable predictions.

The latter recommendation foreshadowed many advances in community ecology throughout the 1990s. By focusing on simplified bi- and tritrophic modules of strongly interacting species, it was possible to demonstrate the importance of indirect effects in shaping communities and their responses to perturbations (Power 1990, Strauss 1991, Polis 1994, Wootton 1994, Menge 1995, Holt and Polis 1997, Schmitz et al. 2000). The ability to experimentally exclude or add individual species in natural communities or mesocosms facilitated the bridging of theory and empiricism that had been lacking in whole-community connectedness-web approaches. Dynamic models of interactions within these modules could be parameterized and tested in ways that complex food-web networks could not.

Via judicious simplification, these developments sidestepped the logistical challenges of fully characterizing food-web architecture. Yet these two approaches are not substitutable: The value of understanding food-web modules underscores the importance of resolving food-web architecture. Attempts to construct food-web theory piecewise by linking modules will struggle to reproduce the emergent properties that arise at successively higher levels of organization, which are difficult if not impossible to predict based on their modular subsystems. In other words, "food webs are more than the sum of their tri-trophic parts," just as a cell is more than a bag of molecules (Cohen et al. 2009). Although it may ultimately prove possible to build upwards towards predictive and dynamic food-web models (McCann 2012), doing so will minimally require a precise understanding of how the constituent pieces fit together and how each modifies the others—as any home-furniture assembler would attest.

Meanwhile, the development and testing of complex network models continues to be hindered by the scarcity of good data. New-and-improved theory, computers, and numerical techniques mean that we can now do for complex networks what could not be done in the 1970s. This has reinvigorated efforts to characterize ecological communities and their dynamics using information about network architecture (Strogatz 2001, Dunne et al. 2002, Jordano et al. 2003, Tylianakis et al. 2008, Allesina et al. 2008, Stouffer and Bascompte 2011). Yet the theoretical advances in this area have not been matched by improvements in the datasets necessary to parameterize and test predictive models. Brown and Gillooly's (2003) observation that "theoretical progress has been hampered by lack of adequate data" echoes the concerns previously voiced by May (1983) and Paine (1988) and subsequently voiced by others (Lafferty et al. 2008). Yet there has been little concerted effort over the past four decades to rectify this situation. In 1983, May had counted 62 empirical food webs. Thirty-two years later, Cirtwill et al. (2015) found 196 webs of sufficient quality to be usable; of these 196, only 31 were from terrestrial ecosystems, and those 31 were drawn from a mere 19 primary sources with a mean age of more than 50 years (as of 2016). Cohen et al. (2009) found a total of three webs (all aquatic, and two from the same lake in different years) that included information on both link structure and the average body mass and population density of each taxon in the network.

Ecological Forensics: Inroads Using Molecular Methods

One bright spot in the landscape painted above is that recently developed molecular and bioinformatics techniques such as DNA barcoding and metabarcoding can vastly facilitate both reliable taxonomic assignation and delineation (Hebert et al. 2004, Janzen et al. 2017) and dietary analysis (Taberlet et al. 2007; Pompanon et al. 2011; Wirta et al. 2014; Craine et al. 2015; Kartzinel et al. 2015, 2019; Kartzinel and Pringle 2015; Evans et al. 2016; Atkins et al. 2019; Pringle et al. 2019). Allied techniques are enabling us to approach the microbial component of food webs for the first time (Henderson et al. 2015, Reese et al. 2018, Kartzinel et al. 2019). Integration of DNA-based methods with complementary approaches such as stable-isotope and fatty-acid analyses can compensate for the limitations of each method in isolation (Traugott et al. 2013, Nielsen et al. 2018).

These approaches, if creatively harnessed to the conceptual frameworks that community ecologists have been honing for decades, have revolutionary potential. Lawton's (1999) lament that "community ecology is a mess" grew from the perception that system-specific contingencies thwart theoretical predictions and prevent ecologists from scaling up. This diagnosis resonated with many community ecologists, and the prescription—a retreat from mechanism, "reductionism, and experimental manipulation" in favor of the search for large-scale, "detail-free statistical patterns"—set an enduring tone for the field. But "contingency" simply means that our working model is incorrect, incomplete, or both. Contingency has mechanistic underpinnings, and they too can be untangled. Judicious simplification and abstraction will continue to be valuable tools for coping with ecological complexity. But it is increasingly unnecessary to reflexively shy away from complexity, as the reach and power of our tools grow more and more to scale with that complexity. And it is increasingly easy to envision a near future in which Lawton's (1999) "overwhelmingly complicated . . . intermediate scales" cease to seem quite so overwhelming.

References

Allesina, S., D. Alonso, and M. Pascual. 2008. A general model for food web structure. Science 320:658–661.

Atkins, J. L., R. A. Long, J. Pansu, J. H. Daskin, A. B. Potter, M. E. Stalmans, C. E. Tarnita, and R. M. Pringle. 2019. Cascading impacts of large-carnivore extirpation in an African ecosystem. Science 364:173–177.

Briand, F., and J. E. Cohen. 1984. Community food webs have scale-invariant structure. Nature 307:264–267.

Brown, J. H., and J. F. Gillooly. 2003. Ecological food webs: high-quality data facilitate theoretical unification. Proceedings of the National Academy of Sciences of the United States of America 100:1467–1468.

Buss, I. O. 1961. Some observations on food habits and behavior of the African elephant. Journal of Wildlife Management 25:131–148.

Cirtwill, A. R., D. B. Stouffer, and T. N. Romanuk. 2015. Latitudinal gradients in biotic niche breadth vary across ecosystem types. Proceedings of the Royal Society B: Biological Sciences 282:20151589.

Cohen, J. E. 1977. Ratio of prey to predators in community food webs. Nature 270:165–167.

Cohen, J. E., T. Jonsson, and S. R. Carpenter. 2003. Ecological community description using the food web, species abundance, and body size. Proceedings of the National Academy of Sciences of the United States of America 100:1781–1786.

Cohen, J. E., D. N. Schittler, D. G. Raffaelli, and D. C. Reuman. 2009. Food webs are more than the sum of their tritrophic parts. Proceedings of the National Academy of Sciences of the United States of America 106:22335–22340.

Coverdale, T. C., J. R. Goheen, T. M. Palmer, and R. M. Pringle. 2018. Good neighbors make good defenses: Associational refuges reduce defense investment in African savanna plants. Ecology 99:1724–1736.

Coverdale, T. C., T. R. Kartzinel, K. L. Grabowski, R. K. Shriver, A. A. Hassan, J. R. Goheen, T. M. Palmer, and R. M. Pringle. 2016. Elephants in the understory: Opposing direct and indirect effects of consumption and ecosystem engineering by megaherbivores. Ecology 97:3219–3230.

Coverdale, T. C., I. J. McGeary, R. D. O'Connell, T. M. Palmer, J. R. Goheen, M. Sankaran, D. J. Augustine, A. T. Ford, and R. M. Pringle. 2019. Strong but opposing effects of associational resistance and susceptibility on defense phenotype in an African savanna plant. Oikos 128:1772–1782.

Craine, J. M., E. G. Towne, M. Miller, and N. Fierer. 2015. Climatic warming and the future of bison as grazers. Scientific Reports 5:16738.

Dunne, J. A., R. J. Williams, and N. D. Martinez. 2002. Food-web structure and network theory: The role of connectance and size. Proceedings of the National Academy of Sciences of the United States of America 99:12917–12922.

Estes, J. A., M. L. Riedman, M. M. Staedler, M. T. Tinker, and B. E. Lyon. 2003. Individual variation in prey selection by sea otters: patterns, causes and implications. Journal of Animal Ecology 72:144–155.

Evans, D. M., J.J.N. Kitson, D. H. Lunt, N. A. Straw, and M.J.O. Pocock. 2016. Merging DNA metabarcoding and ecological network analysis to understand and build resilient terrestrial ecosystems. Functional Ecology 30:1904–1916.

Field, C. R. 1972. The food habits of wild ungulates in Uganda by analyses of stomach contents. African Journal of Ecology 10:17–42.

Ford A. T., J. R. Goheen, D. J. Augustine, M. F. Kinnaird, T. G. O'Brien, T. M. Palmer, R. M. Pringle, and R. Woodroffe. 2015. Recovery of African wild dogs suppresses prey but does not trigger a trophic cascade. Ecology 96:2705–2714.

Ford, A. T., J. R. Goheen, T. O. Otieno, L. Bidner, L. A. Isbell, T. M. Palmer, D. Ward, R. Woodroffe, and R. M. Pringle. 2014. Large carnivores make savanna tree communities less thorny. Science 346:346–349.

Gill, B. A., P. M. Musili, S. Kurukura, A. A. Hassan, J. R. Goheen, W. J. Kress, M. Kuzmina, R. M. Pringle, and T. R. Kartzinel. 2019. Plant DNA-barcode library and community phylogeny for a semi-arid East African savanna. Molecular Ecology Resources 19:838–846.

Goheen, J. R., D. J. Augustine, K. E. Veblen, D. M. Kimuyu, T. M. Palmer, L. M. Porensky, et al. 2018. Conservation lessons from large-mammal manipulations in East African savannas: The KLEE, UHURU, and GLADE experiments. Annals of the New York Academy of Sciences 1429:31–49.

Goheen, J. R., T. M. Palmer, G. K. Charles, K. M. Helgen, S. N. Kinyua, J. E. Maclean, B. L. Turner, H. S. Young, and R. M. Pringle. 2013. Piecewise disassembly of a large-herbivore community across a rainfall gradient: the UHURU experiment. PLOS One 8:e55192.

Hebert, P. D. N., E. H. Penton, J. M. Burns, D. H. Janzen, and W. Hallwachs. 2004. Ten species in one: DNA barcoding reveals cryptic species in the Neotropical skipper butterfly *Astraptes fulgerator*. Proceedings of the National Academy of Sciences of the United States of America 101:14812–14817.

Henderson, G., F. Cox, S. Ganesh, A. Jonker, W. Young, Global Rumen Census Collaborators, and P. H. Janssen. 2015. Rumen microbial community composition varies with diet and host, but a core microbiome is found across a wide geographical range. Scientific Reports 5:14567.

Holechek, J. L., M. Vavra, and R. D. Pieper. 1982. Botanical composition determination of range herbivore diets: A review. Journal of Range Management 35:309–315.

Holt, R. D., and G. A. Polis. 1997. A theoretical framework for intraguild predation. American Naturalist 149:745–764.

Janzen, D. H., J. M. Burns, Q. Cong, W. Hallwachs, T. Dapkey, R. Manjunath, M. Hajibabaei, P.D.N. Hebert, and N. V. Grishin. 2017. Nuclear genomes distinguish cryptic species suggested by their DNA barcodes and ecology. Proceedings of the National Academy of Sciences of the United States of America 114:8313–8318.

Jordan, M.J.R. 2005. Dietary analysis for mammals and birds: a review of field techniques and animal-management applications. International Zoo Yearbook 39:108–116.

Jordano, P., J. Bascompte, and J. M. Olesen. 2003. Invariant properties in coevolutionary networks of plant–animal interactions. Ecology Letters 6:69–81.

Kartzinel, T. R., P. A. Chen, T. C. Coverdale, D. L. Erickson, W. J. Kress, M. L. Kuzmina, D. I. Rubenstein, W. Wang, and R. M. Pringle. 2015. DNA metabarcoding illuminates dietary niche partitioning by African large herbivores. Proceedings of the National Academy of Sciences of the United States of America 112:8019–8024.

Kartzinel, T. R., J. R. Goheen, G. K. Charles, E. DeFranco, J. E. Maclean, T. O. Otieno, T. M. Palmer, and R. M. Pringle. 2014. Plant and small-mammal responses to large-herbivore exclusion in an African savanna: five years of the UHURU experiment. Ecology 95: 787–787.

Kartzinel, T. R., J. C. Hsing, P. M. Musili, B.R.P. Brown, and R. M. Pringle. 2019. Covariation of diet and gut microbiome in African megafauna. Proceedings of the National Academy of Sciences of the United States of America 116:23588–23593.

Kartzinel, T. R., and R. M. Pringle. 2015. Molecular detection of invertebrate prey in vertebrate diets: Trophic ecology of Caribbean island lizards. Molecular Ecology Resources 15:903–914.

Kleynhans, E. J., A. E. Jolles, M.R.E. Bos, and H. Olff. 2011. Resource partitioning along multiple niche dimensions in differently sized African savanna grazers. Oikos 120: 591–600.

Lafferty, K. D., S. Allesina, M. Arim, C. J. Briggs, G. De Leo, A. P. Dobson, et al. 2008. Parasites in food webs: The ultimate missing links. Ecology Letters 11:533–546.

Lawton, J. H. 1999. Are there general laws in ecology? Oikos 84:177–192.

Layman, C. A., M. S. Araujo, R. Boucek, C. M. Hammerschlag-Peyer, E. Harrison, Z. R. Jud, et al. 2012. Applying stable isotopes to examine food-web structure: an overview of analytical tools. Biological Reviews 87:545–562.

Long, R. A., A. Wambua, J. R. Goheen, T. M. Palmer, and R. M. Pringle. 2017. Climatic variation modulates the indirect effects of large herbivores on small-mammal habitat use. Journal of Animal Ecology 86:739–748.

Louthan, A. M., D. F. Doak, J. R. Goheen, T. M. Palmer, and R. M. Pringle. 2013. Climatic stress mediates the impacts of herbivory on plant population structure and components of individual fitness. Journal of Ecology 101:1074–1083.

Louthan, A. M., D. F. Doak, J. R. Goheen, T. M. Palmer, and R. M. Pringle. 2014. Mechanisms of plant–plant interactions: concealment from herbivores is more important than abiotic-stress mediation in an African savannah. Proceedings of the Royal Society B: Biological Sciences 281:20132647.

Louthan, A. M., R. M. Pringle, J. R. Goheen, T. M. Palmer, W. F. Morris, and D. F. Doak. 2018. Aridity weakens population-level effects of multiple species interactions on *Hibiscus meyeri*. Proceedings of the National Academy of Sciences of the United States of America 115:543–548.

May, R. M. 1983. The structure of food webs. Nature 301:566–568.

McCann, K. S. 2012. Food webs. Princeton, N.J.: Princeton University Press.

Menge, B. A. 1995. Indirect effects in marine rocky intertidal interaction webs: Patterns and importance. Ecological Monographs 65:21–74.

Newmaster, S. G., I. D. Thompson, R. A. D. Steeves, A. R. Rodgers, A. J. Fazekas, J. R. Maloles, R. T. McMullin, and J. M. Fryxell. 2013. Examination of two new technologies to assess the diet of woodland caribou: video recorders attached to collars and DNA barcoding. Canadian Journal of Forest Research 43:897–900.

Ngatia, L. W., K. Ramesh Reddy, P. K. Ramachandran Nair, R. M. Pringle, T. M. Palmer, and B. L. Turner. 2014. Seasonal patterns in decomposition and nutrient release from East African savanna grasses grown under contrasting nutrient conditions. Agriculture, Ecosystems and Environment 188:12–19.

Nielsen, J. M., E. L. Clare, B. Hayden, M. T. Brett, and P. Kratina. 2018. Diet tracing in ecology: Method comparison and selection. Methods in Ecology and Evolution 9:278–291.

Oliver, I., and A. J. Beattie. 1996. Invertebrate morphospecies as surrogates for species: A case study. Conservation Biology 19:99–109.

Paine, R. T. 1988. Food webs: Road maps of interactions or grist for theoretical development? Ecology 69:1648–1654.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist 100:65–75.

Pansu, J., J. A. Guyton, A. B. Potter, J. L. Atkins, J. H. Daskin, B. Wursten, T. R. Kartzinel, and R. M. Pringle. 2019. Trophic ecology of large herbivores in a reassembling African ecosystem. Journal of Ecology 107:1355–1376

Pimm, S. L. 1979. The structure of food webs. Theoretical Population Biology 16:144–158.

Poisot, T., J. D. Bever, A. Nemri, P. H. Thrall, and M. E. Hochberg. 2011. A conceptual framework for the evolution of ecological specialisation. Ecology Letters 14:841–851.

Polis, G. A. 1994. Food webs, trophic cascades, and community structure. Australian Journal of Ecology 19:121–136.

Polis, G. A., M. E. Power, and G. R. Huxel. 2004. Food webs at the landscape level. Chicago: University of Chicago Press.

Pompanon, F., B. E. Deagle, W.O.C. Symondson, D. S. Brown, S. N. Jarman, and P. Taberlet. 2011. Who is eating what: Diet assessment using next generation sequencing. Molecular Ecology 21:1931–1950.

Power, M. E. 1990. Effects of fish in river food webs. Science 250:811-814.

Pringle, R. M. 2012. How to be manipulative: Intelligent tinkering is key to understanding ecology and rehabilitating ecosystems. American Scientist 100:30–37.

Pringle, R. M., J. R. Goheen, T. M. Palmer, G. K. Charles, E. DeFranco, R. Hohbein, A. T. Ford, and C. E. Tarnita. 2014. Low functional redundancy among mammalian browsers in regulating an encroaching shrub (*Solanum campylacanthum*) in African savannah. Proceedings of the Royal Society B: Biological Sciences 281:20140390.

Pringle, R. M., T. R. Kartzinel, T. M. Palmer, T. J. Thurman, K. Fox-Dobbs, C. C. Y. Xu, et al. 2019. Predator-induced collapse of niche structure and species coexistence. Nature 570:58–64.

Pringle, R. M., T. M. Palmer, J. R. Goheen, D. J. McCauley, and F. Keesing. 2011. Ecological importance of large herbivores in the Ewaso ecosystem. In: N. Georgiadis, ed. Smithsonian Contributions to Zoology (Conserving Wildlife in African Landscapes: Kenya's Ewaso Ecosystem), no. 632. Washington, D.C.: Smithsonian Institution Scholarly Press. 43–54.

Pringle, R. M., K. M. Prior, T. M. Palmer, T. P. Young, and J. R. Goheen. 2016. Large herbivores promote habitat specialization and beta diversity of African savanna trees. Ecology 97:2640–2657.

Reese, A. T., F. C. Pereira, A. Schintlmeister, D. Berry, M. Wagner, L. P. Hale, et al. 2018. Microbial nitrogen limitation in the mammalian large intestine. Nature Microbiology 3:1441–1450.

Schmitz, O. J., P. A. Hambäck, and A. P. Beckerman. 2000. Trophic cascades in terrestrial systems: A review of the effects of carnivore removals on plants. American Naturalist 155:141–153.

Smith, M. A., J. J. Rodriguez, J. B. Whitfield, A. R. Deans, D. H. Janzen, W. Hallwachs, and P.D.N. Hebert. 2008. Extreme diversity of tropical parasitoid wasps exposed by iterative integration of natural history, DNA barcoding, morphology, and collections.

Proceedings of the National Academy of Sciences of the United States of America 105:12359–12364.

Smith, M. A., D. M. Wood, D. H. Janzen, W. Hallwachs, and P.D.N. Hebert. 2007. DNA barcodes affirm that 16 species of apparently generalist tropical parasitoid flies (Diptera, Tachinidae) are not all generalists. Proceedings of the National Academy of Sciences of the United States of America 104:4967–4972.

Smith, M. A., N. E. Woodley, D. H. Janzen, W. Hallwachs, and P.D.N. Hebert. 2006. DNA barcodes reveal cryptic host-specificity within the presumed polyphagous members of a genus of parasitoid flies (Diptera: Tachinidae). Proceedings of the National Academy of Sciences of the United States of America 103:3657–3662.

Solow, A. R., and A. R. Beet. 1998. On lumping species in food webs. Ecology.

Stier, A. C., J. F. Samhouri, S. Gray, R. G. Martone, M. E. Mach, B. S. Halpern, C. V. Kappel, C. Scarborough, and P. S. Levin. 2017. Integrating expert perceptions into food web conservation and management. Conservation Letters 10:67–76.

Stouffer, D. B., J. Bascompte. 2011. Compartmentalization increases food-web persistence. Proceedings of the National Academy of Sciences of the United States of America 108:3648–3652.

Strauss, S. Y. 1991. Indirect effects in community ecology: Their definition, study and importance. Trends in Ecology & Evolution 6:206–210.

Strogatz, S. H. 2001. Exploring complex networks. Nature 410:268–276.

Taberlet, P., E. Coissac, F. Pompanon, L. Gielly, C. Miquel, A. Valentini, et al. 2007. Power and limitations of the chloroplast *trn*L (UAA) intron for plant DNA barcoding. Nucleic Acids Research 35:e14.

Tinker, M. T., and G. Bentall, J. A. Estes. 2008. Food limitation leads to behavioral diversification and dietary specialization in sea otters. Proceedings of the National Academy of Sciences of the United States of America 105:560–565.

Titcomb, G., B. F. Allan, T. Ainsworth, L. Henson, T. Hedlund, R. M. Pringle, et al. 2017. Interacting effects of wildlife loss and climate on ticks and tick-borne disease. Proceedings of the Royal Society B: Biological Sciences 284:20170475.

du Toit, J. T., and H. Olff. 2014. Generalities in grazing and browsing ecology: using across-guild comparisons to control contingencies. Oecologia 174:1075–1083.

Traugott, M., S. Kamenova, L. Ruess, J. Seeber, and M. Plantegenest. 2013. Empirically characterising trophic networks: what emerging DNA-based methods, stable isotope and fatty acid analyses can offer. Advances in Ecological Research 49:177–224.

Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. Ecology Letters 11:1351–1363.

Vamosi, J. C., W. S. Armbruster, and S. S. Renner. 2014. Evolutionary ecology of specialization: insights from phylogenetic analysis. Proceedings of the Royal Society B: Biological Sciences 281:20142004.

Winemiller, K. O. 2007. Interplay between scale, resolution, life history and food web properties. In: N. Rooney, K. S. McCann, and D.L.G. Noakes, eds. From energetics to ecosystems: The dynamics and structure of ecological systems. Dordrecht, Netherlands: Springer, 101–126.

Wirta, H. K., P.D.N. Hebert, R. Kaartinen, S. W. Prosser, G. Várkonyi, and T. Roslin. 2014. Complementary molecular information changes our perception of food web structure. Proceedings of the National Academy of Sciences of the United States of America 111:1885–1890.

Wootton, J. T. 1994. Putting the pieces together: Testing the independence of interactions among organisms. Ecology 75:1544–1551.

Young, H. S., D. J. McCauley, R. Dirzo, J. R. Goheen, B. Agwanda, C. Brook, et al. 2015. Context-dependent effects of large-wildlife declines on small-mammal communities in central Kenya. Ecological Applications 25:348–360.

Young, H. S., D. J. McCauley, R. Dirzo, C. L. Nunn, M. G. Campana, B. Agwanda, et al. 2017. Interacting effects of land-use and climate on rodent-borne disease in central Kenya. Philosophical Transactions of the Royal Society B: Biological Sciences 372:20160116.

Young, H. S., D. J. McCauley, K. M. Helgen, J. R. Goheen, E. Otárola-Castillo, T. M. Palmer, et al. 2013. Effects of mammalian herbivore declines on plant communities: Observations and experiments in an African savanna. Journal of Ecology 101:1030–1041.