APPENDIX 3. A BRIEF HISTORY OF FOOD WEB THEORY

The development of ecological theory concerning the patterns exhibited by food webs and the underlying processes they reflect can be divided into three temporal stanzas. Prior to 1970, "food web theory" was largely encapsulated in Elton's (1958) conceptual model that complexity engendered stability in ecological communities. Small webs evinced cyclic population fluctuations in both natural (high-latitude predator-prey populations) and model (two-species Lotka-Volterra models) systems. Furthermore, species-poor systems (e.g., agricultural plots) appeared to be more vulnerable to devastating pest outbreaks than highly speciose systems. Finally, increased food web complexity (i.e., links) led to rapid increases in the pathways available for energy to flow from basal to top species. The complexity-engenders-stability hypothesis enjoyed considerable support and approached the status of a mathematical theorem prior to theoretical attacks by May (1972, 1973) and others. Suffice it to say, we do not suspect that this stability-complexity debate is going to dampen any time soon, particularly regarding the determinants thereof (Paine 1988, Pimm et al. 1991, Haydon 1994, de Ruiter et al. 1995, McCann et al. 1998, Closs et al. 1999, Martinez 1992, 1994, Polis and Strong 1996, Dunne et al. 2002a, 2002b, 2004, Loreau et al. 2002, Berlow et al. 2004, 2009).

Subsequent to this initial stanza, May (1972, 1973), following up on computer simulation results by Gardner and Ashby (1970), developed a criterion for community stability related to connectance ($b(SC)^{1/2}<1$, where b is mean interaction strength) based on analysis of randomly-constructed webs. Under the assumption that mean interaction strength is independent of food web size, May's formula predicts that connectance should decline hyperbolically as the number of species increases. This prediction ushered in the second stanza of food web theory and led to numerous comparisons of catalogs of empirical food webs in attempts to test it (Briand and Cohen 1984; Cohen and Briand 1984; Sugihara et al. 1989; Cohen et al. 1990; Pimm et al. 1991; Havens 1992;). Other topological web metrics (see above) were introduced in these and associated studies to identify other potential patterns associated with food webs. By the end of the 1980s, food web theorists had developed a set of empirical relations based on these food web catalogs, some of which included 100+ webs (e.g.,). Cohen (1989) summarized several of these empirical relations as five "laws": (1) excluding cannibalism, cycles are rare, (2) food chains are short, (3) the proportions of top, intermediate and basal species (%T, %I, %B) are independent of web scale (the "species scaling law"), (4) the proportions of link types (%T-I, %T-B, %I-I, %I-B) are independent of web scale (the "link scaling law"), and (5) linkage density ($L_D = L/S$) is independent of web scale (the "link-species scaling law"). The last of these laws also encapsulates support for May's stability criterion as a constraint on trophic structure as it implies that connectance declines hyperbolically with increased species richness. In addition, Cohen (1978) found that the "niche overlap graph" of most webs was an "interval graph," that is, the overlaps of species' resource niches as revealed in food web diagrams could be collapsed onto a single dimension. Cohen (1989) also presented a model of community organization, the "cascade" model, that gave "remarkable quantitative agreement" between his empirical laws and the model's predictions based on a single parameter—the expected linkage density.

However, the edifice of empirical evidence supporting these relations has been seriously challenged on a number of grounds concerning the cataloged food webs. These include concerns that real species diversity was inadequately represented, species were poorly resolved and over-aggregated, actual links between species were under-represented, criteria for aggregation were inconsistent, ontological changes in diet were absent, cannibalism was ignored, and inconsistencies in sampling effort, spatiotemporal resolution and spatiotemporal aggregation

giving rise to sampling artifacts could not be assessed (Paine 1988, Winemiller 1990, Hall and Raffaelli 1991, Kenny and Loehle 1991, Martinez 1991, Polis 1991, Goldwasser and Roughgarden 1997, Martinez et al. 1999). To some extent, these criticisms reflected the fact that few, if any, of the collected food webs had originally been developed with the intent of testing food web theory (Warren 1994).

The beginning of the third (and current) stanza in the development of food web theory around 1990 is marked by the crescendo in these criticisms and the development of the first webs designed to address them (e.g., Winemiller 1990, Hall and Raffaelli 1991, Martinez 1991, Polis 1991). In contrast to earlier webs, of which the structure of many resulted more from artistic convenience than from objective ecological criteria (Paine 1988), the procedures used to construct these new webs were objectively defined and well-documented. The new webs exhibited higher species diversity and topological complexity than typical older webs (Winemiller 1990: 4 tropical aquatic habitats, 58-104 species, 208-1243 links; Hall and Raffaelli 1991: temperate estuary, 92 species, 409 links; Martinez 1991: temperate lake, 93 trophic species [182 original taxa], ~1000 links; Polis 1991, desert community, ~3000 species). Topological properties associated with the new webs differed substantially from older webs: the average number of links per species was much higher in the new webs and food chains were much longer. Omnivory, cannibalism and looping were also more common than previously thought. In addition, it was shown that many food web properties were sensitive to the criteria used to aggregate species, as well as the level of aggregation, thus casting previous scale invariance laws (species, link, and link-species scaling laws) into question (Winemiller 1990, Martinez, 1991). Subsequently, using an analysis of the new webs, Martinez (1992) challenged the previously-observed hyperbolic scaling relation for connectance (Pimm 1982, Cohen and Newman 1988) and advanced the hypothesis of "constant connectance": that directed connectance is scale invariant. More recently, Williams and Martinez (2000) advanced an alternative to Cohen and Newman's (1988) cascade model, the model, thus completing the challenges to the empirical and theoretical edifice Cohen (1989) had outlined.

However, although the earlier results have been called into question by more recent analyses with new webs developed specifically to test hypotheses of food web theory, no clear consensus has emerged yet to replace the older (admittedly contentious even then) one. Simply put, food webs and their topological properties appear, at best, to be more complex than was previously hoped. However, this also means that the potential for significant additions to food web theory appears to be quite high.