Food Webs 1 (2014) 10–17

Contents lists available at ScienceDirect

Food Webs

journal homepage: www.journals.elsevier.com/food-webs

Why there are so few trophic levels: Selection against instability explains the pattern☆

Jonathan J. Borrelli *, Lev R. Ginzburg

Department of Ecology and Evolution, Stony Brook University, Stony Brook, NY 11794, United States

ARTICLE INFO

Article history:
Received 13 June 2014
Received in revised form 10 November 2014
Accepted 11 November 2014
Available online 20 November 2014

Keywords:
Food chain
Food web
Stability
Trophic level

ABSTRACT

Food chains are short, rarely more than five trophic levels long. The cause of this pattern remains unresolved, and no current hypothesis fully explains this phenomenon. We offer an explanation based on the stability of food chains that have been shifted away from linearity to be more web-like. We start with a simple example of food webs of two to six species arranged so that species consume all those with a trophic level less than their own. The probability of stability, for such "universal omnivory" chains declined strongly with chain length, and was as low as 1% with six level chains but highest for two and three level chains. We further explored the influence of chain length on food web stability by testing food webs with varying levels of connectance that were constructed either randomly or with the niche model. By additionally altering the relative impacts of predators on prey, and vice-versa, we test the role of our assumptions on the relationship between chain length and stability. Food webs characterized by low to moderate degrees of connectance, asymmetrical interactions, and relatively weak density dependence showed a pattern of reduced stability with longer trophic chains. The simple view that food webs characterized by long trophic chains are less stable seems to resolve the long-standing question of why there are so few trophic levels in nature.

1. Introduction

Food chains are typically short, often having as few as two steps (Elton, 1927; Pimm and Lawton, 1977) and rarely more than four (Pimm, 1982; Yodzis, 1981). Food chain length is directly related to the number of trophic levels in a food web. A food chain with two steps has three trophic levels: a producer, intermediate consumer, and a top predator. By defining trophic level this way, however, it becomes difficult to determine the trophic levels of species embedded in complex food webs. To better define the trophic level of a given species in a food web, we will use two related, but distinct, definitions: trophic position and longest chain.

The distribution of trophic position, measured as one plus the average trophic position of a species' prey, for 50 published food webs shows that 98.8% of consumer nodes have a trophic position less than or equal to four (Fig. 1a). Very few species have a trophic position higher than five in these food webs (see Appendix A for details on the webs used). Alternatively, the maximum number of steps between a given consumer and a basal species, the longest chain, in 39 of the 50 published webs (78%) is less than or equal to five levels (Fig. 1b).

A recent study by Ulanowicz et al. (2013) demonstrated that by accounting for the amount of biomass flowing along the links (links with more biomass flow are weighted more heavily) the number of effective trophic levels is approximately three for a set of 16 networks. Ulanowicz et al. (2013) speculated that this pattern may result from the elimination of configurations of interacting species that are less likely to persist than others.

The most commonly tested hypotheses for variation in food chain length are associated with relatively conflicting support. The earliest explanation for food chain shortness is that the efficiency of energy transfer between trophic levels is low. Available energy at a trophic level should therefore decrease rapidly going up the chain (Elton, 1927; Hutchinson, 1959; Lindeman, 1942). Areas with higher energy availability (often measured as productivity) should then support longer chains, a prediction not supported by empirical observations. Up to five trophic levels are observed in both the highly productive tropics and the low productivity polar regions (Pimm, 1982). An alternative explanation is that larger ecosystems allow for longer food chains (Post et al., 2000). Ecosystem size has been found to be related to food chain length in lakes and some islands (Post, 2002; Takimoto et al., 2008) but not on other islands (Young et al., 2013). The combination of productivity and ecosystem size, the productive-space hypothesis, has also been proposed to explain variation in food chain length (Post et al., 2000; Schoener, 1989; Spencer and Warren, 1996; Vander Zanden et al.,

☆ Statement of authorship: JB and LG designed the research; JB performed simulations; JB wrote the article.

* Corresponding author at: Department of Ecology & Evolution, Stony Brook University, 650 Life Sciences Building, Stony Brook, NY 11794-5245, United States. Tel.: +1 607 372 0644; fax: +1 631 632 7626.

E-mail addresses: jonathan.borrelli@stonybrook.edu (J.J. Borrelli), lev.ginzburg@stonybrook.edu (L.R. Ginzburg).

http://dx.doi.org/10.1016/j.fooweb.2014.11.002

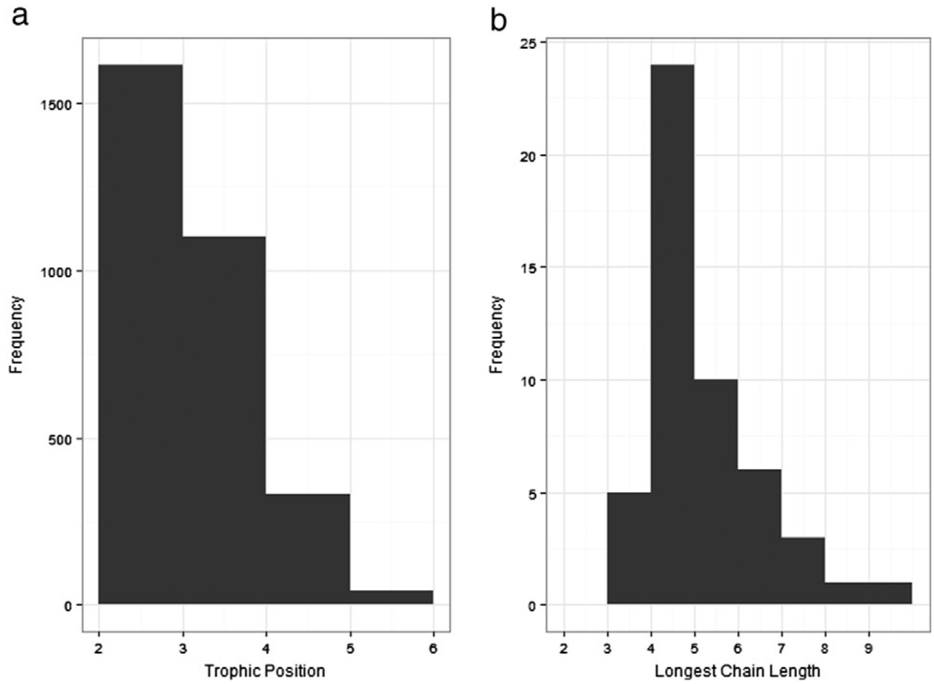

Fig. 1. The trophic position of each species in 50 published food webs (a) and the length of the single longest chain in each web (b). The data sources and code for generating this figure can be found in Appendix A.

1999). Evidence for the productive-space hypothesis, however, is contradictory with an equal number of studies finding support as those failing to find support (Post, 2002, 2007; Young et al., 2013).

Longer food chains are also expected to be dynamically fragile. Pimm and Lawton (1977) explored the role of dynamic constraints in limiting the length of food chains. Dynamic constraints would occur if the number of trophic levels in a community was limited by population dynamics of the constituent species. Using analyses of community matrices of four species food webs, they found that as the number of trophic levels increased, so too did the time it took to return to equilibrium following a small perturbation. A decrease in stability with increasing chain length is also supported by evidence from protist microcosm studies (Holyoak and Sachdev, 1998; Morin and Lawler, 1996).

Sterner et al. (1997), however, found that the theoretical result of Pimm and Lawton (1977) was primarily a methodological artifact resulting from differences in the number of negative (density-dependence) terms along the diagonal of the community matrix. Following the results of Sterner et al. (1997) studies exploring limits to food chain length have generally not explored the role of dynamic constraints. Most argue that dynamic constraints are less important to regulating the number of trophic levels compared to other mechanisms such as ecosystem size (Post, 2002). Dynamic constraints due to colonization and extinction in a spatial context, however, have also been suggested as an alternative (Holt, 2002) that seems to fit in with ecosystem size based hypotheses.

Nonetheless through systemic selection against dynamically unstable structures as suggested by Ulanowicz et al. (2013), dynamic constraints can provide a foundation for determining why the number of trophic levels is typically low. Systemic selection occurs when unstable food web structures (here referring to patterns of interactions) lead to the loss of some or all of the species in a web, thus altering web topology by eliminating nodes (species) and links (interactions). Food webs that are unstable are less likely to persist over time and more likely to undergo a change in species composition (e.g., through extinction) or interactions (such as by prey-switching). If systemic selection against unstable food web configurations leads to shorter food chains, then food webs made of longer chains (meaning more trophic levels) should be less stable.

Webs of interactions that have a higher degree of stability, measured as quasi sign-stability (QSS; Allesina and Pascual, 2008), should provide a buffer against changes in the magnitudes of interaction strengths resulting from stochastic environments, demography, and evolutionary change. Food webs that have greater QSS should be more persistent over time because the region of potentially stable parameter space will be larger, leading to a higher probability that the true values may remain within it. We hypothesize that webs with more trophic levels have lower QSS compared to webs with fewer trophic levels.

Omnivory, feeding on a range of trophic positions, was found by Pimm and Lawton (1977, 1978) to reduce the probability that a food web would be stable. This result, however, was given less weight compared to return time to equilibrium. They suggested that omnivory should be uncommon because chains that included omnivory were frequently unstable. Thompson et al. (2007), however, found that omnivory is common among species that occupy a trophic position higher than that of herbivores, with relatively few species occupying an integer trophic position (but see Thompson and Hemberg, 2009). Likewise, other studies have found that anywhere between 46% (Williams and Martinez, 2004) and 87% (Arim and Marquet, 2004) of taxa in a given community feed on more than one trophic level. Furthermore, omnivory does not become less common when only looking at the strongest interactions in the web (Fig. A1).

Below we examine how increasing food chain length (more trophic levels) impacts the degree to which the web is stable. We use food webs constructed at three levels of ecological realism; oversimplified chains with omnivory, random webs, and niche model food webs. The simplest example of chains with omnivory is used to demonstrate the expected relationship, while the random and niche model constructed webs allow us to further explore the impact of our assumptions, and determine under what conditions there is a relationship between food chain length and stability.

2. Methods

The stability of food chains and food webs is typically determined by calculating the eigenvalues of the Jacobian matrix, whose elements a_{ij} represent the impact of the population of species j on the ith species'