



Proximate structural mechanisms for variation in food-chain length

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Food-chain length is a central characteristic of ecological communities because of its strong influence on community structure and ecosystem function. While recent studies have started to better clarify the relationship between food-chain length and environmental gradients such as resource availability and ecosystem size, much less progress has been made in isolating the ultimate and proximate mechanisms that determine food-chain length. Progress has been slow, in part, because research has paid little attention to the proximate changes in food web structure that must link variation in food-chain length to the ultimate dynamic mechanism. Here we outline the structural mechanisms that determine variation in food-chain length. We explore the implications of these mechanisms for understanding how changes in food-web structure influence food-chain length using both an intraguild predation community model and data from natural ecosystems. The resulting framework provides the mechanisms for linking ultimate dynamic mechanisms to variation in food-chain length. It also suggests that simple linear food-chain models may make misleading predictions about patterns of variation in food-chain length because they are unable to incorporate important structural mechanisms that alter food-web dynamics and cause non-linear shifts in food-web structure. Intraguild predation models provide a more appropriate theoretical framework for understanding food-chain length in most natural ecosystems because they accommodate all of the proximate structural mechanisms identified here.

Food-chain length has captured the imagination of ecologists for nearly a century (Elton 1927, Hutchinson 1959, Pimm 1982, Persson et al. 1992, Post 2002a) both because it is a tractable characteristic of food-web complexity and because it is an important regulator of community structure and ecosystem function (Pimm 1982, Carpenter et al. 1987, Elser et al. 1988, DeAngelis 1992, Hairston and Hairston 1993, Cole et al. 2000, Schmitz et al. 2000). Food-chain length has been measured in a variety of ways, but is generally a measure of the height of the food web (Post 2002a). There are a number of widely cited hypotheses for explaining variation in food-chain length. For example, energetic hypotheses invoke the second law of thermodynamics as the ultimate determinant of food-chain length (Hutchinson 1959, Pimm 1982, Yodzis 1984, Schoener 1989, Post 2002a), while dynamic stability hypotheses argue that the stability of local dynamics, and by extension the strength of external disturbances,

are the ultimate determinant of food-chain length (Pimm and Lawton 1977, Pimm 1982, Pimm and Kitching 1987, Jenkins et al. 1992). Other studies have pointed towards a role of ecosystem size as a determinant of food-chain length (Schoener 1989, Spencer and Warren 1996, Vander Zanden et al. 1999, Post et al. 2000, Post 2002a).

While recent studies have clarified the relationship between natural variation in food-chain length and environmental variables such as resource availability and ecosystem size (Schoener 1989, Spencer and Warren 1996, Vander Zanden et al. 1999, Post et al. 2000, Post 2002a), they have not provided a strong mechanistic link between food-chain length and the potential causes of variation (Post 2002a). This is, in part, because the response of food-chain length to environmental variables such as ecosystem size and resource availability emerges as an aggregate property of complex changes in food-web structure. The causal chain of interactions

that link the ultimate causal mechanisms to observed variation in food-chain length includes, at a minimum, two steps: 1) the effects of environmental variables such as resource availability on food-web structure, and 2) the effects of changes in food-web structure on food-chain length. Despite the central importance, there has been little discussion of the type of changes in food-web structure (proximate structural mechanisms) that must underlie variation in food-chain length (Post 2002a).

Here we outline the two classes of change in food-web structure and the three proximate structural mechanisms that must underlie variation in food-chain length. We describe, as a general example, the role of the three structural mechanism in determining food-chain length in an intraguild predation community model across a gradient in resource availability, and we provide support for the relevance of these mechanisms in natural ecosystems using studies from north temperate lakes and islands in the Bahamas (Schoener 1989, Post et al. 2000, Takimoto et al., unpubl.). We also discuss whether these mechanisms are necessary or sufficient conditions to cause changes in food-chain length. Finally, we place these mechanisms back into the context of the ultimate mechanisms (energetic constraints, dynamic stability, etc.) that motivate most contemporary research on food-chain length.

Definition

We start with definitions of trophic position, food-chain length, top predators and the apical predator because they are essential to understanding and applying the three mechanisms. Trophic position is the vertical position of an organism within a food web (Post et al. 2000, Post 2002b). It can refer to individuals, populations, species or a group of species, but here we talk mostly about the trophic position of species. Formally, trophic position of species i is:

$$\tau_i = \sum_{j \in L} w_{ij} \tau_j + 1 \quad (1)$$

where w_{ij} is the proportion of species j in the diet of species i ($0 \leq w_{ij} \leq 1$ and $\sum_{j \in L} w_{ij} = 1$ for all i), τ_j is the trophic position of species j , and L is a set of species in the local community. This definition of trophic position is identical to the “flow-based trophic level” used by Williams and Martinez (2004) and trophic height used by Cohen et al. (2003). Top predators (T) are species within the local community (L) with a trophic position that places them at or near the top of the food web (i.e. species that are preyed upon by few if any other predators).

Food-chain length is a measure of the height of the food web (Post 2002a). Here we use the commonly used maximum trophic position based definition of

food-chain length (Vander Zanden et al. 1999, Post et al. 2000, Diehl and Feissel 2001, Post 2002a), which is based on patterns of energy or material flow and can be estimated from theoretical food webs (Diehl and Feissel 2001) or in natural food webs using stable isotope techniques (Post et al. 2000, Post 2002b). Formally, food-chain length (maximum trophic position) is defined as:

$$\max\{\tau_i | i \in T\} \quad (2)$$

where τ_i is the trophic position of species i from T , the set of top predators. The apical predator is the top predator that holds the maximum trophic position (Eq. 2), and therefore resides at the apex of the food web. Within any one food web there can be many top predators but, given the definition of food-chain length used here, there can be only one apical predator.

Proximate mechanisms for variation in food-chain length

Food-web structure can change in a myriad of ways; however, given the definition of food-chain length provided by Eq. 2, variation in food-chain length is caused by either:

- A. the addition or removal of top predators (T) which changes the identity of the apical predator or,
- B. changes in the trophic position (τ_i) of top predators.

The addition or removal of top predators, when it changes the identity of the apical predator, is a relatively straightforward change in food-web structure that we call the additive mechanism (Fig. 1). This addition of a new trophic link to the top of a food web is the most widely discussed (Pimm 1982, Lawton 1989, Post 2002a) and most easily observed of the structural mechanisms that underlie variation in food-chain length (Schoener 1989, Post et al. 2000), although this might derive in part from the reliance on simple food chain models to portray food-web structure.

Changes in the trophic position of top predators (τ_i) affect food-chain length a) when the top predator is the apical predator and changes in trophic position translate directly into changes in food-chain length, or b) when changes in trophic position cause a change in the identity of the apical predator. Based on Eq. 1, changes in the trophic position of a top predator (τ_i) must be caused by:

1. the addition or removal of intermediate predators (or basal species; L), which we call the insertion mechanism;

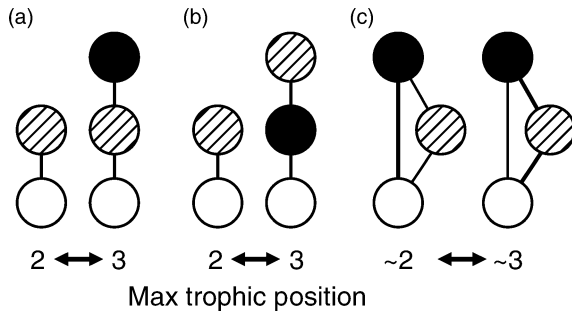


Fig. 1. The three structural mechanisms that underlie changes in food-chain length. The circles represent different species or life stages, the thickness of the lines represents differences in energy flow. Food-chain length changes when a) the addition or removal of a new top predator or life history stage adds or removes a link at the top of the food web (black circle), b) the addition or removal of an intermediate consumer or life history stage changes intermediate links in the food web (black circle), or c) a change in the degree of trophic omnivory.

2. changes in the degree of trophic omnivory by the top predator (w_{ij}), which we call the omnivory mechanisms; or
3. changes in the trophic position of intermediate predators (τ_i) that are prey for the top predator (τ_i).

Changes in the trophic position of intermediate predators (τ_i) are, in turn, caused by the insertion and omnivory mechanisms at the next lower trophic level. The insertion and omnivory mechanisms are closely related mathematically, because the insertion mechanism could be considered a binary (0/1) representation of changes in omnivory. Furthermore, new intermediate species (insertion) may change patterns of energy flow by providing new opportunities for omnivory. Here we separate the mechanisms because the insertion mechanism represents changes in species richness and food-web topology, while the omnivory mechanism represents changes in the pattern of energy flow through a food web with the same species richness and food-web topology (Fig. 1). The insertion and omnivory mechanisms have received less attention than the additive mechanism, but they can have considerable impact upon food-chain length in food webs where multi-trophic level or multi-pathway omnivory (preying upon multiple trophic levels) is widespread and community membership is variable. The insertion and omnivory mechanisms are also commonly overlooked in systems where top predator identity is invariant. Where these two mechanisms operate, it is not appropriate to assume that food-chain length is invariant just because apical predator identity is constant (Post et al. 2000), as is

often done when constructing or interpreting connectance food webs.

Changes in food-chain length are, therefore, caused by changes in the identity of the apical predator or changes in the trophic position of top predators both of which can be influenced by the additive, insertion and omnivory mechanisms. These mechanisms are the three proximate structural mechanisms that must underlie all variation in food chain length. Below, we provide theoretical and empirical examples of their role in regulating variation in food-chain length.

Caveats

We note that the additive, insertion and omnivory mechanisms are tailored to the maximum trophic position definition of realized food-chain length provided in Eq. 2 (sensu Post 2002a) because they are mechanisms that determine the set of potential apical predators or an organism's trophic position. These three mechanisms may not explain variation in food-chain length when the definition of food-chain length is not directly based on the trophic position of organisms'. For example, the omnivory mechanism, which depends upon differences in energy or material flow, is not easily related to Cohen's mean food-chain length (Cohen et al. 1986, Briand and Cohen 1987), which is calculated as the mean length of all individual food chains in a connectance food web that typically contains no representation of variation in energy or material flow.

Intraguild predation model as an example

Intraguild predation (IGP) is common in food webs (Polis et al. 1989), and the intraguild community module illustrates much of the complexity found in natural food webs (Holt and Polis 1997). The IGP module is also the simplest community module to incorporate all three of the proximate structural mechanisms for variation in food-chain length. For example, the linear food chain modules that are often used to discuss food-chain length cannot incorporate changes in the degree of trophic omnivory. Here we use the IGP model developed by Holt and Polis (Holt and Polis 1997) and expanded upon by Diehl and Feissel (Diehl and Feissel 2000, 2001) to highlight the general causal relationships among local dynamics, changes in food-web structure (specifically the three proximate structural mechanism outlined above) and variation in food-chain length. Following Diehl and Feissel (2001), we explore dynamics across a range of resource enrichment where the intraguild predator (IGpredator)

and intraguild prey (IGprey) coexist at intermediate resource availability. For full model details and parameters see Diehl and Feissel (2001).

In general, this model demonstrates the highest food-chain length at intermediate levels of resources (Fig. 2; Diehl and Feissel 2001). At low resource availability, food-chain length is short because the IGprey and IGpredator are excluded by low resource availability. As resource availability increases, first the IGprey, and then the IGpredator, are able to invade the local system (the order of invasion depends upon model assumptions; this order represents the necessary condition for coexistence between the IGprey and IGpredator), increasing maximum trophic level through the additive mechanism (Fig. 2). Once the IGprey and IGpredator coexist, food-chain length decreases with increasing resource availability. Through this region,

the IGprey abundance declines as the IGpredator biomass increases (a special case of apparent competition; Holt 1977, Holt and Polis 1997). The combination of declining IGprey abundance and increasing abundance of the shared resource causes the IGpredator to prey more upon the shared resource than the IGprey which, in turn, causes the trophic position of the IGpredator to decline. In the region of coexistence, the omnivory mechanism causes all of the changes in food-chain length (Fig. 2). Finally, at high resource availability, the IGpredator reaches sufficiently high densities to extirpate the IGprey, therefore reducing maximum trophic position to two (Fig. 2a; Holt and Polis 1997, Diehl and Feissel 2001). Where the IGprey is extirpated, the reduction in food-chain length is caused by the loss of an intermediate link resulting from a change in the degree of trophic omnivory by the IGpredator. This demonstrates the strong link between the insertion and omnivory mechanisms in dynamic systems.

The dynamics of this simple IGP community model illustrate the importance of all three of the proximate structural mechanisms in determining food-chain length. In this example, differences in food-web structure and the resulting changes in food-chain length all emerged from the local dynamics of the IGP system. The IGP model should be the theoretical framework of choice for exploring food-chain length because it incorporates all three of the structural mechanisms that underlie variation in food-chain length and, therefore, makes clear the causal links among dynamic mechanisms, changes in food-web structure, and food-chain length.

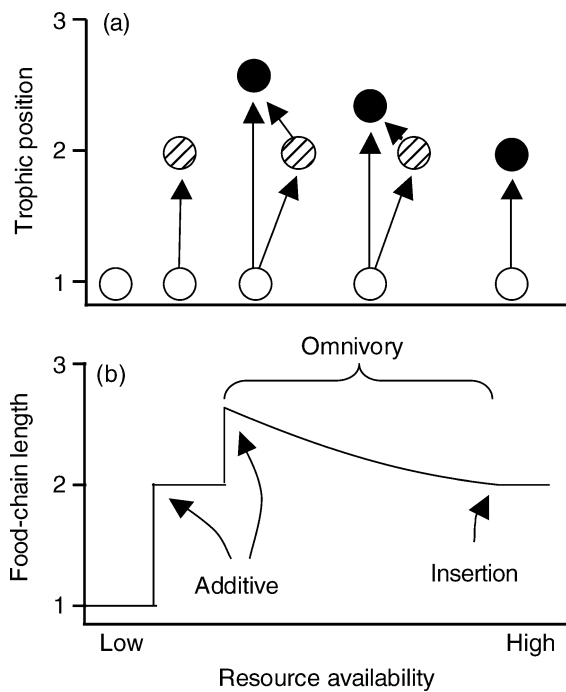


Fig. 2. The influence of resource availability (enrichment) on food web structure (a) and food-chain length (b) in a Lotka-Volterra based intraguild predation community model. Resource availability affects food-chain length of the intraguild predation community model by altering the trophic position and presence/absence of the intraguild predator (closed circle) and intraguild prey (cross hatched circle). All three structural mechanisms operate as food-chain length increases through the additive mechanism when the intraguild prey and predator invade the system. Food-chain length then decreases through the omnivory mechanisms as the degree of trophic omnivory by the intraguild predator changes, and then through the insertion mechanism as the intraguild predator drives the intraguild prey extinct.

Empirical evidence for the three structural mechanisms

The three structural mechanisms provide a powerful tool for understanding how complex changes in food-web structure influence food-chain length in complex natural food webs. As examples, we provide evidence for the influence of each of the three structural mechanisms on food-chain length in north temperate lakes (Vander Zanden et al. 1999, Post et al. 2000) and islands in the Bahamas (Schoener 1989, Spiller and Schoener 1994, Schoener et al. 2002, Takimoto et al., unpubl.).

Evidence for the additive mechanism is provided by changes in the incidence or identity of the apical predator because any addition or removal of a trophic link at the top of the food web will cause changes in food-chain length. As we note below, however, the insertion and omnivory mechanisms may also cause changes in the identity of the apical predator as they

cause shifts in the relative trophic position of existing top predators. In the lakes studied by Post et al. (2000), the identity of the apical predator in each lake changed systematically as food-chain length increased with increasing lake size. Largemouth bass (*Micropterus salmoides*) or northern pike (*Esox lucius*) held the maximum trophic position in smaller lakes, while walleye (*Stizostedion vitreum*) or lake trout (*Salvelinus namaycush*), which are not found in the smallest lakes, held the maximum trophic position in larger lakes. More generally, changes in apical predator identity are commonly observed along gradients of ecosystem size in aquatic ecosystems because fish are often absent from the smallest aquatic ecosystems (Tonn and Magnuson 1982, Schneider 1997, McPeck 1998).

Schoener (1989) and Takimoto et al. (unpubl.) note similar changes in the identity of the apical predator with increasing island size in the Bahamas. Spiders are apical predators on the smallest islands (<0.1 ha), *Anolis* lizards are apical predators on moderate sized islands (0.1 to 1000 ha), and larger lizard-eating lizards and birds are apical predators on the largest islands (Schoener 1989, Takimoto et al., unpubl.).

Evidence for the insertion and omnivory mechanisms as causes of variation in food-chain length is best demonstrated by changes in the trophic position of top predators. The insertion and omnivory mechanisms can operate throughout the food web, but not all of these changes in food-web structure affect food-chain length in reticulate food webs. The changes that do affect food-chain length will be evidenced by changes in the trophic position of top predators in general and, in particular, the trophic position of the apical predator. Because both mechanisms lead to changes in the trophic position of top predators, they can be detected easily using stable isotope techniques (Post 2002b). Changes in the trophic position of top predators that are commensurate with a change in food-chain length implicate either or both the insertion and omnivory mechanisms as proximate causes of variation in food-chain length, but further evidence (like diet data) is required to separate the importance of the two mechanisms. In the north temperate lakes studied by Post et al. (2000), trophic position of all species of top predators increased with increasing food-chain length, indicating that some of the increase in food-chain length with increasing lake size was caused by some combination of the additive and omnivory mechanisms. Vander Zanden et al. (1999) observed a similar increase in trophic position of lake trout in the lakes they studied. In north temperate lakes, changes in the trophic position of top predators likely resulted from the addition of new intermediate predators such as mysid shrimp (*Mysis relicta*) and large predatory copepods (e.g. *Epischura lacustris*; Sprules and Bowerman 1988, Vander Zanden and Rasmussen

1996) or an increase in energy flow through these links (e.g. Fig. 3 in Hairston and Hairston 1993). Mysids are found in many of the largest lakes studied by Post et al. (2000; e.g. lakes Erie, Ontario, Champlain, Cayuga), and likely form an important extra link in the food webs of larger lakes.

Data on food-web structure from islands in the Bahamas suggests that similar changes in intermediate trophic links and the degree of trophic omnivory may be important for explaining variation in food-chain length (Schoener 1989, Spiller and Schoener 1994, Schoener et al. 2002, Takimoto et al., unpubl.). For example, the trophic position of anolis lizards increases with island size both because of the addition of intermediate trophic links, in this case spiders (spiders and lizards do not coexist on island <1 ha) and because of shifts in the degree of trophic omnivory by lizards (Schoener 1989, Schoener and Spiller 2006, Takimoto et al., unpubl.).

In reticulate natural food webs, the three proximate structural mechanisms likely interact in complex ways to determine food-chain length. For example, in the lakes studied by Post et al. (2000), much of the increase in food-chain length with increasing ecosystem size can be explained by the addition of lake trout and changes in the trophic position of lake trout and other top predators such as largemouth bass (Fig. 3). In the smallest lakes where lake trout are found, largemouth bass have a higher trophic position than lake trout; however, the trophic position of lake trout increases more quickly than that of largemouth bass. Thus, the addition of lake trout alone did not cause the increase in food-chain length, rather it was the addition of lake trout (additive mechanism) interacting with the rapid increase in their trophic position (insertion or omnivory mechanisms) that caused the increase in food-chain length. This example demonstrates the complex

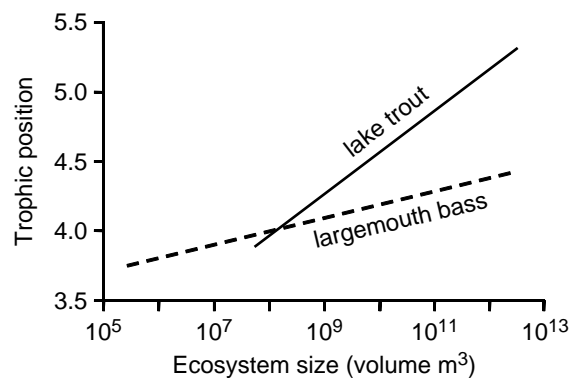


Fig. 3. Relationship between ecosystem size and trophic position of Lake trout and Largemouth bass in lakes studied by Post et al. (2000).

interplay between the three structural mechanisms and highlights a case where changes in food-chain length emerged from an interaction among the mechanisms. We suspect this is a common phenomenon.

Necessary and sufficient conditions for changes in food-chain length

The above empirical and theoretical examples provided evidence that the three proximate structural mechanisms are each sufficient conditions for changes in food-chain length. The additive, insertion, and omnivory mechanisms can all, on their own, cause changes in food-chain length; however, in most food webs two or more of the mechanisms are typically necessary conditions to explain the observed variation in food-chain length (often the additive mechanism and either one or both of the insertion or omnivory mechanisms; e.g. Fig. 3). Taken together, these three mechanisms provide the necessary and sufficient conditions for changes in food-chain length. Many factors may conspire to initiate changes in food-web structure but only these three types of change in food-web structure influence food-chain length.

Ultimate mechanisms

The myriad of ways in which food-web structure can change makes it difficult to isolate the role of potential ultimate mechanism in determining food-chain length. By ultimate mechanisms we mean mechanisms or environmental gradients that influence food-chain length through their effects on food-web structure. They include changes in resource availability, ecosystem size (which can represent components of species richness, habitat heterogeneity and resource availability), disturbance and dynamic stability, and the history of community assembly (including evolution and human activities), all of which can strongly influence food-web structure (Post 2002a). The three proximate structural mechanisms we identify here reduce the food-web complexity to a manageable level and provide the structural framework required to link natural variation in food-chain length to ultimate mechanisms. Here we briefly link these three mechanisms to the commonly discussed ultimate mechanism of resource availability, disturbance, and ecosystem size. Because these mechanisms may interact to affect food-chain length, a full and formal treatment of this topic awaits the analysis of an IGP model that can simultaneously incorporate variation in resource availability, disturbance and ecosystem size (Takimoto et al., unpubl.).

Resource availability

As outlined above, the IGP model described by Diehl and Feissel (2001) predicts a complex relationship between food-chain length and resource availability. This predicted relationship runs contrary to many of the energetic hypotheses that predict increasing food-chain length with increasing resource availability (Oksanen et al. 1981, Pimm 1982, Schoener 1989). The humped shaped relationship between resource availability and food-chain length predicted by the IGP model results from the dynamic interplay between the omnivory and insertion mechanisms; two mechanisms that are not included in simple food-chain models. At low resource availability, the IGP model behaves like a simple food-chain model (Oksanen et al. 1981) and the additive mechanism is the only mechanisms needed to explain variation in food-chain length. At moderate to high resource availability, when both the IGprey and IGpredator are present in the system, the IGP and food-chain models diverge. In this region of resource availability, omnivory becomes the primary determinant of dynamics in the IGP model and food-chain length declines as the IGpredator drives the IGprey extinct and receives more of its energy from the shared resource. In contrast, because the insertion and omnivory mechanisms are not possible in simple food-chain models, there are no mechanisms that allow for a reduction in food-chain length once the top predator is present. As a consequence, the IGP and food-chain models make very different predictions about how resource availability should affect food-chain length. Simple food-chain models predict that food-chain length will increase with increasing resource availability while IGP models predict the highest food-chain length at intermediate levels of resources (Fig. 2; Diehl and Feissel 2001).

The comparison of IGP and simple food chain model suggests that the relationship between food-chain length and resource availability depends upon the incidence of omnivory in food webs and role of the omnivory and insertion mechanisms in determining food-chain length (Diehl and Feissel 2001). Where omnivory is present, the dynamic interplay between the omnivory and insertion mechanisms may override the direct energetic constraints that cause food-chain length to increase in simple food-chain models. This observation may help reconcile results from many natural food webs where omnivory is commonplace and there is no relationship between food-chain length and resource availability (Pimm 1982, Briand and Cohen 1987, Spencer and Warren 1996, Post et al. 2000, Post 2002a) with the positive relationship between food-chain length and resource availability found in simple food-chain models and empirical

studies where omnivory was absent (Oksanen et al. 1981, Kaunzinger and Morin 1998).

Disturbance

Disturbance is most commonly thought to affect food-chain length through the removal of species via the additive and insertion mechanisms, although there is some evidence from streams that it can effect the degree of omnivory (Power 1995, Persson et al. 1996, Power et al. 1996, Marks et al. 2000, Post 2002a). On small islands in the Bahamas, hurricanes and winter storms appears to more strongly affect the incidence of top predators, anolis lizards, than their trophic position (Takimoto et al., unpubl.), suggesting that disturbance is affecting food-chain length through the additive mechanism. Indeed, the additive and insertion mechanisms are likely most important where the effects of disturbance on food-chain length depend upon the colonization ability of food-web members (Persson et al. 1996, Power et al. 1996, Post 2002a). In contrast, there is some evidence from streams that floods can favor disturbance-resistant species that are less resistant to predation, and thus can channel more energy to higher trophic levels which increases food-chain length (Power et al. 1996). This suggests a role of the omnivory mechanism, which could change food-chain length rapidly even when all species remain present in an ecosystem.

Ecosystem size

Ecosystem size may have two primary effects on food-chain length through the three proximate mechanisms. First, an increase in the number of species with increasing ecosystem size may lead to an increase in food-chain length through the additive and insertion mechanisms (Cohen and Newman 1992). On the other hand, the greater number of species could increase the degree of trophic omnivory and shorten food-chain length (or slow the rate of increase in food-chain length) with increasing ecosystem size. Second, greater ecosystem size often provides greater habitat heterogeneity and more prey refugia, and can reduce predator foraging efficiency (Persson et al. 1992, Post et al. 2000, Post 2002a) all of which reduces the strength of local interactions and reduces the likelihood that local interactions would truncate food-chain length through the omnivory mechanism (as was seen at high resource levels in the IGP model). Under these circumstances, ecosystem size may relax the dynamic constraints (Pimm and Lawton 1977) that would otherwise prevent longer food chains in larger ecosystem with greater species richness (Takimoto et al., unpubl.).

Conclusions

The additive, insertion and omnivory mechanisms described here summarize the changes in food-web structure that must underlie all variation in food-chain length (given the definition of food-chain length used here). These three structural mechanisms provide a way to link natural variation in food-chain length to macroecological gradients such as resource availability, ecosystem size, and disturbance, and, ultimately, the dynamic mechanisms that determine food-chain length. Identification of these proximate mechanisms also provides insight into the likely effects of different processes on food-chain length. For example, where omnivory is widespread, the dynamic interplay between the omnivory and insertion mechanisms predicts a hump shaped relationship between food-chain length and resource availability; a very different predictions than that made by simple linear food chain models. As a consequence, it is clear that simple food chain models, because they cannot accommodate all three structural mechanisms, are not appropriate for exploring variation in food-chain length in systems with complex trophic interactions. The challenge ahead is to evaluate the relative importance of these mechanisms in driving variation in food-chain length in different ecosystem types. For example, is the additive mechanisms the only important mechanisms regulating food-chain length when it increases with increasing resource availability (Oksanen et al. 1981, Kaunzinger and Morin 1998)? Likewise, what is the relative importance of the three mechanisms in explaining the strong relationship between food-chain length and ecosystem size? Answering these and related questions would provide the mechanistic understanding required to make more rapid progress in addressing the long standing debate about what determines food-chain length (Sturner et al. 1997, Post 2002a).

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