

Food Web Stability: The Influence of Trophic Flows across Habitats

Gary R. Huxel* and Kevin McCann†

Institute of Theoretical Dynamics and Department of Environmental Science and Policy, University of California, Davis, California 95616

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ABSTRACT: In nature, fluxes across habitats often bring both nutrient and energetic resources into areas of low productivity from areas of higher productivity. These inputs can alter consumption rates of consumer and predator species in the recipient food webs, thereby influencing food web stability. Starting from a well-studied tritrophic food chain model, we investigated the impact of allochthonous inputs on the stability of a simple food web model. We considered the effects of allochthonous inputs on stability of the model using four sets of biologically plausible parameters that represent different dynamical outcomes. We found that low levels of allochthonous inputs stabilize food web dynamics when species preferentially feed on the autochthonous sources, while either increasing the input level or changing the feeding preference to favor allochthonous inputs, or both, led to a decoupling of the food chain that could result in the loss of one or all species. We argue that allochthonous inputs are important sources of productivity in many food webs and their influence needs to be studied further. This is especially important in the various systems, such as caves, headwater streams, and some small marine islands, in which more energy enters the food web from allochthonous inputs than from autochthonous inputs.

Keywords: allochthonous inputs, stability, food webs, energetic tritrophic model, trophic cascades.

Food web structure is greatly influenced by a number of factors that impinge on population densities. Polis and Strong (1996) developed a conceptual model that suggested that there are a number of donor-controlled (*sensu* DeAngelis 1980) resources and alternative pathways other than the traditional food chain resources. Do-

* E-mail: huxel@nine.ucdavis.edu.

† E-mail: kevin@three.ucdavis.edu.

nor control implies that food web dynamics are mainly controlled by resource availability (bottom-up control); this differs from many current food web hypotheses that theorize that predation controls food webs from top down (Hairston et al. 1960; Oksanen 1991). Polis and Strong (1996) reasoned that the alternative resources and pathways, such as detrital and other allochthonous inputs, result in donor-controlled “multichannel” omnivory, which plays a central role in consumer-resource interactions and food web dynamics. They further suggested that multichannel omnivory can dampen or facilitate trophic cascades. McCann and Hastings (1997) recently found that food web dynamics were stabilized by weak to moderate amounts of trophic omnivory, one component of multichannel omnivory. They did not, however, examine the influence of other types of multichannel omnivory on food web dynamics. In this article, we address this problem by extending a simple food chain to include a different component of multichannel omnivory: allochthonous inputs (inputs entering from another habitat). We demonstrate that allochthonous sources can also stabilize food web dynamics, further suggesting that donor control may be an important factor in community dynamics and that trophic cascades may be weakened in systems that have relatively large allochthonous inputs.

The movement of resources across habitat boundaries can increase productivity in low productive areas, thereby influencing food web structure and stability (Polis et al. 1996). Allochthonous inputs include the movement of leaf litter into headwater streams or soil systems, marine detritus into mainland habitats, dry deposition into terrestrial systems, the movement of herbivores across boundaries, and the movement of prey species into a habitat occupied by a predator (or vice versa). Here we focus on allochthonous inputs of energetic resources (as opposed to nutrients) entering food webs that could arise from movement of detrital inputs or due to large-scale predator/prey movements.

Polis and Hurd (1996) demonstrated that, in coastal

and marine island systems, allochthonous inputs can greatly subsidize terrestrial food webs in areas of low productivity. In general, the movement of resources is in the direction of high-productivity to low-productivity systems (Polis et al. 1996). The question of whether energetic allochthonous inputs would stabilize food webs and its influence on biological diversity in the receptor systems is largely unknown. Polis et al. (1996) suggested that the impact of the inputs would be largely determined by which trophic level was the recipient of the energy. Regarding this, Polis and Hurd's (1996) study illustrated that the majority of the energetic allochthonous inputs into their system were at the detritivore level. Polis et al. (1996) hypothesized that bottom-up effects would dominate if the basal level received the input, whereas top-down effects would dominate if the top consumer level was the recipient. Similarly, DeAngelis (1992) showed that a constant input of nutrients into the basal level of a food web displayed bottom-up effects. In general, increased nutrients lead to higher carrying capacities and increased growth rates. At low input values, this can allow the system to maintain longer food chains, but as the input increases, the system can become unstable through the paradox of enrichment (Rosenzweig 1971). As the effects of nutrient inputs to the basal trophic level are fairly clear, we will concentrate on energetics inputs at consumer levels, which is important in food web dynamics (DeAngelis 1992) but not well studied (Polis 1991, 1994).

Tritrophic Model

To examine the impact of allochthonous inputs on food web stability, we used the Yodzis and Innes (1992) parameterization of the Hastings and Powell (1991) tritrophic food chain model. This model parameterization allows us to focus on consumer-resource systems that are biologically plausible. We examine four different dynamics that result from four parameter sets found by McCann and Yodzis (1995). These cases are chaotic dynamics, limit cycles, a stable system with all three trophic levels present, and a stable system with just the basal and consumer trophic levels present. These different dynamics represent potential outcomes that are found in model systems due to differences in body size relations taken from real food webs (McCann and Yodzis 1994b). The consumer and top predator trophic levels in our model are generalists in that they can feed on both allochthonous inputs (when available to that trophic level) and on the trophic level below them. Thus, we can think of this in two ways, first, that individuals (species) feed on both sources or, second, that different species feed on separate

sources (one set of individuals/species feeds on the allochthonous input and one set feeds on the trophic level below it).

The allochthonous inputs and the food chain resources are different and may be separated in space. The movement of consumers and predators across habitat boundaries to feed can contribute significant levels of productivity to a food web (Carpenter and Kitchell 1993; Polis and Hurd 1995, 1996; Persson et al. 1996; Polis et al. 1996, 1997). Hence, the implications of spatial subdivision of resources can be an important aspect of food webs that have significant allochthonous inputs (Holt 1985; Oksanen 1991). However, we assume that the spatial extent of our model system is such that consumers and predators can easily utilize all resources.

To the simple food chain model, we add allochthonous inputs with the consumer, the top predator, or both trophic levels as the recipient(s), thus creating a simple food web model. The model without allochthonous inputs is given by

$$\begin{aligned}\frac{dR}{dt} &= R \left(1 - \frac{R}{K} \right) - x_c y_c \frac{CR}{R + R_0}; \\ \frac{dC}{dt} &= -x_c C \left(1 - y_c \frac{R}{R + R_0} \right) - x_p y_p \frac{PC}{C + C_0};\end{aligned}\quad (1)$$

and

$$\frac{dP}{dt} = -x_p P + x_p y_p \frac{CP}{C + C_0},$$

where consumer-resource interactions use Type II functional responses; R is the basal species; C is the consumer trophic level; P is the top predator trophic level; R_0 is the half saturation point for the functional response between the consumer and predator levels; x_i is the mass-specific metabolic rate of trophic level i , measured relative to the production-to-biomass ratio of the resource density; y_c is a measure of the ingestion rate per unit metabolic rate of the basal trophic level by C ; and y_p is a measure of the ingestion rate per unit metabolic rate of P . The reason for parameterizing the equations in this manner is that the x_i parameters scale allometrically with individual body size, while the metabolic types of animals constrain the plausible ranges of parameter y_i (Yodzis and Innes 1992). Specifically, y_i lies within the interval $(1, y_{i\max})$, where the value of $y_{i\max}$ depends on the metabolic type of species i (see Yodzis and Innes 1992). The values given by Yodzis and Innes (1992) for x_i are derived from the ratio of predator to prey biomass, dependent on a coefficient for metabolic rate appropriate to the metabolic type of the species i . Hence, the parameters can be

deemed biologically plausible as they represent realistic predator/prey ratios in body size found in data surveys (Peters 1983; Cohen et al. 1993).

Allochthonous Inputs

Since Lindeman's (1942) study of food web dynamics, the debate over whether food webs are controlled top down or bottom up has continued. Hairston et al. (1960) argued that control of food webs is top down. This results in trophic cascades that are typified by increases in biomass of an odd number of trophic levels in odd-numbered food chains or increases in biomass of an even number of trophic levels in even-numbered food chains (Fretwell 1977, 1987; Oksanen et al. 1981; Carpenter and Kitchell 1993). However, others have argued that systems may exhibit bottom-up control (donor control), in which food web dynamics are controlled by resource input levels (White 1978; McQueen et al. 1986; DeAngelis 1992). Tritrophic food chain models that use a Type II functional response (Hastings and Powell 1991) produce trophic cascades when inputs to the bottom trophospecies are minimal. However, Abrams and Roth (1994) demonstrated that increasing the carrying capacity of the basal species can destabilize the system leading to extinction of the top species through the paradox of enrichment (Rosenzweig 1971). We extend this by asking whether allochthonous inputs to higher recipient trophic levels (above the basal level) alters food web stability.

Polis and Hurd (1996) suggest that for their island systems most of the allochthonous inputs are available to detritivores (included in our consumer level). Other systems that are driven by allochthonous inputs into the consumer level include marine filter-feeding communities in unidirectional currents or advective areas (Menge et al. 1996), soil communities (Moore and Hunt 1988; Strong et al. 1996), and headwater streams that receive leaf litter inputs (Vannote et al. 1980; Rosemond et al. 1993). The movement of herbivores across habitat boundaries to feed can also result in large energetic flows across habitats (Polis et al. 1996). In headwater streams, primary productivity is generally reduced by canopy cover of the riparian vegetation, which reduces light and temperature levels, so that litter inputs are the major source of productivity but consumers of litter also eat algae that is produced in situ. A measure of the importance of allochthonous inputs in food webs is the photosynthetic rate-to-respiration rate ratios in stream systems. Low photosynthetic rate to respiration ratios (<1.0) indicate that the streams are dominated by allochthonous inputs; typical headwater streams have photosynthetic rate-to-respiration values of no more than 0.1 (due to

total heterotrophic inputs and not just herbivory; Vannote et al. 1980). With allochthonous inputs into the consumer trophic level only, the system can now be written as

$$\begin{aligned}\frac{dR}{dt} &= R\left(1 - \frac{R}{K}\right) - x_c y_c \frac{(1 - \omega_1) CR}{(1 - \omega_1) R + R_0 + \omega_1 A_C}; \\ \frac{dC}{dt} &= -x_c C \left(1 - y_c \frac{(1 - \omega_1) R + \omega_1 A_C}{(1 - \omega_1) R + R_0 + \omega_1 A_C}\right) \\ &\quad - x_p y_p \frac{PC}{C + C_0};\end{aligned}\quad (2)$$

and

$$\frac{dP}{dt} = -x_p P + x_p y_p \frac{CP}{C + C_0},$$

where ω_1 is the parameter describing the preference for the allochthonous input by the consumer, and A_C is the allochthonous input into the consumer level. Thus, the allochthonous input is a constant, and feeding on that resource only depends on the amount of input and the preference parameter. Thus, the numerical response to allochthonous inputs should be dramatic at high input levels and preference levels.

Allochthonous inputs into the top level include carrion or carcasses, the movement of prey species into the habitat, and movement of predators across habitats (Holt 1985; Thornton et al. 1990; Polis and Hurd 1995, 1996; Polis et al. 1996). For example, the Allen paradox (Allen 1951) suggests that secondary production within streams can be insufficient to support levels of fish production found in them (Berg and Hellenthal 1992). Predators moving along the interface between ecosystems (i.e., shorelines, river banks, and benthic and pelagic systems) can utilize resources across habitats (Carpenter and Kitchell 1993; Polis and Hurd 1995, 1996). With allochthonous inputs into the predator trophic level only, the system can now be written as

$$\begin{aligned}\frac{dR}{dt} &= R\left(1 - \frac{R}{K}\right) - x_c y_c \frac{CR}{R + R_0}; \\ \frac{dC}{dt} &= -x_c C \left(1 - y_c \frac{R}{R + R_0}\right) \\ &\quad - x_p y_p \frac{(1 - \omega_2) PC}{(1 - \omega_2) C + C_0 + \omega_2 A_P};\end{aligned}\quad (3)$$

and

$$\frac{dP}{dt} = -x_p P + x_p y_p \frac{(1 - \omega_2) CP + \omega_2 A_P P}{(1 - \omega_2) C + C_0 + \omega_2 A_P},$$

where ω_2 is the parameter describing the preference for the allochthonous input by the predator, and A_p is the allochthonous input into the predator trophic level.

In addition, allochthonous inputs may enter at multiple trophic levels. The River Continuum Concept (Vannote et al. 1980) reasons that headwaters provide allochthonous inputs for systems downstream. These inputs include prey, dissolved and particulate organic matter, and litter fall. This type of pattern is also seen in estuarine systems in which rivers carry allochthonous inputs into estuaries. Similarly, runoff from terrestrial systems into aquatic systems (and vice versa in the case of marine to terrestrial) provides litter, dissolved and particular organic matter, and prey. The system with allochthonous inputs entering into both the consumer and top predator level can be written as

$$\begin{aligned} \frac{dR}{dt} &= R \left(1 - \frac{R}{K} \right) - x_c y_c \frac{(1 - \omega_1) CR}{(1 - \omega_1) R + R_0 + \omega_1 A_c}; \\ \frac{dC}{dt} &= -x_c C \left(1 - y_c \frac{(1 - \omega_1) R + \omega_1 A_c}{(1 - \omega_1) R + R_0 + \omega_1 A_c} \right) \\ &\quad - x_p y_p \frac{(1 - \omega_2) PC}{(1 - \omega_2) C + C_0 + \omega_2 A_p}; \end{aligned} \quad (4)$$

and

$$\frac{dP}{dt} = -x_p P + x_p y_p \frac{(1 - \omega_2) CP + \omega_2 A_p P}{(1 - \omega_2) C + C_0 + \omega_2 A_p}.$$

Numerical Analyses

We performed numerical analyses for systems (2)–(4) over a range of values in allochthonous inputs and values of the preference parameter, ω_i , for four different parameter sets (see McCann and Yodzis 1995 for details). Each parameter set produced different dynamical outcomes and implies different predator-prey body size ratios and metabolic types (i.e., endotherm, vertebrate ectotherm, or invertebrate ectotherm) of the animals involved (Yodzis and Innes 1992; McCann and Yodzis 1994a, 1995). The chaos set of parameters is inconsistent with an invertebrate predator-invertebrate consumer-resource food chain exhibiting chaotic dynamics ($x_c = 0.4$, $y_c = 2.009$, $R_0 = 0.16129$, $x_p = 0.08$, $y_p = 5$, $C_0 = 0.5$; McCann and Yodzis 1994b; McCann and Hastings 1997). The limit cycle set of parameters can represent a number of food chain types: an invertebrate predator-invertebrate consumer-resource chain; a vertebrate ectotherm predator-vertebrate ectotherm consumer-resource chain; or a vertebrate ectotherm predator-invertebrate consumer-resource chain ($x_c = 0.4$, $y_c = 2.009$, $R_0 = 0.3333$, $x_p = 0.5$, $y_p = 5$, $C_0 = 0.5$; McCann and Yodzis

1995; McCann and Hastings 1997). The point attractor parameter set is consistent with several food chain types: an invertebrate predator-invertebrate consumer-resource chain; a vertebrate ectotherm predator-vertebrate ectotherm consumer-resource chain; or a vertebrate ectotherm predator-invertebrate consumer-resource chain ($x_c = 0.4$, $y_c = 2.009$, $R_0 = 0.5$, $x_p = 0.01$, $y_p = 5$, $C_0 = 1.5$; McCann and Yodzis 1995; McCann and Hastings 1997). The two-trophic level set of parameters could represent any of the consumer-resource food chain types ($x_c = 0.4$, $y_c = 2.009$, $R_0 = 0.5$, $x_p = 0.01$, $y_p = 1.9$, $C_0 = 0.5$). Note that the four cases result from different parameter sets, but all initially started with all trophic levels present (McCann and Yodzis 1995).

In our model, the dynamics of the system are dependent on the interaction between the top two species because the mass-specific metabolic rates, x_c and y_c , are constant across the four scenarios. We make this assumption because we are attempting to simulate allochthonous inputs into consumer (C) and predator levels (P), thus requiring the basal species (R) to be a primary producer. This is motivated by Polis and Hurd's (1996) study showing that the majority of the energetic allochthonous inputs into their system were at the herbivore level (which is included in our consumers).

Numerical analyses were performed for each of the four parameter sets, each with the inputs utilized by the consumers, predators, or both. We held the amount of input constant across the analyses, so that when both the consumer and predator were recipients, each received half of the total allochthonous input but from different sources so those available to one are not available to the other. We selected these three scenarios as they represent extreme cases between which all others should fall ($A_p = 0$, $A_c = 1$; $A_p = 1$, $A_c = 0$; $A_p = A_c = 0.5$). Therefore, we have a total of 12 model cases: 4 parameter sets \times 3 allochthonous input scenarios. The analyses for each case were run for 10,000 integration steps and then the local maxima, local minima, equilibria points, and densities were collected over the next 1,000 integration steps. The analyses were performed only on the last 1,000 time steps because the model systems produce long-term transients (i.e., the system takes a long time before it begins to approach equilibrium). Similar transients have been found in a number of other coupled models (Engbert and Drepper 1994; Hastings and Higgins 1994; McCann and Yodzis 1994b; Hastings 1995; McCann and Hastings 1997). For each parameter set and allochthonous input scenario combinations, analyses were performed over a range of feeding preference from 0 (feeding only on autochthonous/classical food web sources) to 1 (feeding only on the allochthonous sources). We also varied the amount of allochthonous input from 0.01 to 1.00, corre-

sponding to approximately 0.1 to 10 times the biomass of the consumer or predator's autochthonous resource. While allochthonous inputs may vary temporally in natural systems, we model a continuous input scenario.

How do these values compare to inputs into natural systems? Polis and Hurd (1996) compared allochthonous inputs from the marine environment into the terrestrial systems versus terrestrial productivity. They found that the marine inputs can be nearly three orders of magnitude greater than the terrestrial productivity. Additionally, in a number of systems all productivity is due to allochthonous inputs in the form of nutrients, detritus, or prey (Howart 1983; Thornton et al. 1990; Seely 1991; Polis and Hurd 1996; Polis et al. 1996).

Model Dynamics

Chaos Parameter Set

Figure 1 shows that dynamics of these systems can be highly complex. Increasing the feeding preference parameter, ω_i , leads to period-doubling reversals that move the system from n -cycle regions toward two-cycle and limit cycle regions. At very low levels of allochthonous inputs, however, increasing the preference parameter can lead to the loss of the recipient trophic level because it becomes decoupled from the food chain and relies heavily on an inadequate source. At high levels of allochthonous inputs, the food chain can become decoupled, but the resource is adequate to support the recipient trophic level. The recipient level determines at what level of input and feeding preference the different dynamics occur and to what extent the system becomes decoupled. If the predator trophic level (P) is the only recipient, the system becomes decoupled at low values of A_p and ω_2 (fig. 1A). The input allows P densities to increase dramatically, causing the consumer trophic level (C) to go to 0 and the basal trophic level (R) to go to its carrying capacity. If C is the recipient, the decoupling occurs at higher levels of A_c and ω_1 compared to when P is the recipient (fig. 1). In this case, the high density of the consumer leads to large oscillations, which can drive all species extinct. At very high values of input and ω_2 , the system can support both C and P but the basal species is lost as the food web becomes driven by the allochthonous input (e.g., detrital food web). When the allochthonous inputs are split between the predator and the consumer trophic levels ($A_p = A_c$), the same period-doubling reversals occur at low to moderate levels of input and ω_i (fig. 1C). Above a threshold, however, these top two-trophic levels are lost and only R persists. Further increasing the input leads to the persistence of R and P only with a loss of C . At very high levels of input and ω , only P persists.

Notice in figure 1A–C that the boundaries between the

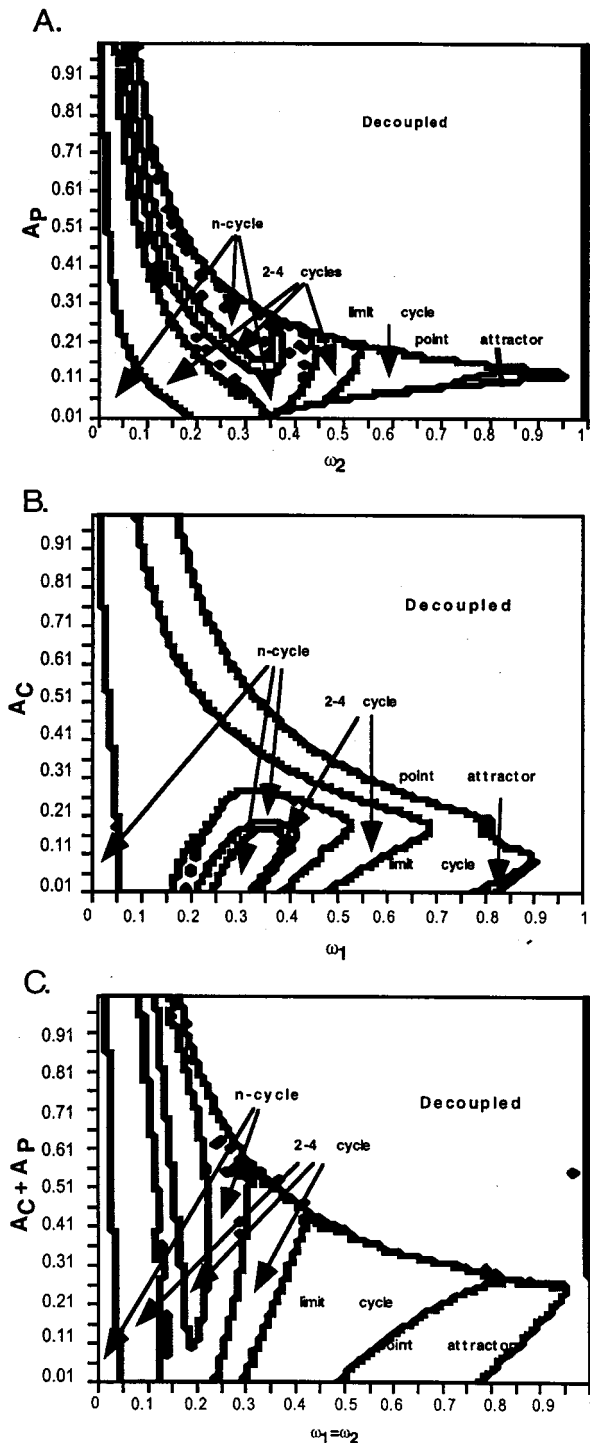


Figure 1: Dynamical results, using the chaotic parameter set, as a function of the feeding preference parameter (ω_i) and the value of allochthonous input (A_p and/or A_c). A, The input enters as a resource for the predator trophic level; B, the herbivore is the recipient; and C, both predator and herbivore are recipients.

different dynamical regions are not perfectly distinct. For example, in figure 1A in the middle n -cycle region there are small areas of two to four cycles. By n cycle we mean greater than four cycles, which may be, but is not necessarily, chaotic (depending on the Lyapunov exponent). This occurs because period-doubling cascades can cause the system to go from eight cycles back to four cycles before returning back to eight cycles again (fig. 2). This suggests there is some degree of sensitivity to small changes in parameter values resulting in sharp transitions between different dynamical outcomes.

Figure 2 shows bifurcation diagrams for the chaos parameter set in each of the three scenarios at a fixed value of allochthonous input (selected for demonstration purposes only—0.10). All show the same general pattern: increasing ω_2 results in period-doubling reversals with the system moving through regions of decreased cycles, eventually reaching limit cycles before P is lost from the system at relatively high values of ω_2 . Figure 2 shows another important influence of inputs and the differences between recipient trophic levels: when either P or C and P are the recipients, the minimum biomass values increase with low to moderate level ω_1 . However, when C is the only recipient, the minima actually decrease with ω_1 . The biological importance of this is that the cycling densities become less prone to extinction as their minimum density increases with the feeding preference.

Limit Cycle Parameter Set

For the limit cycle parameter set case when P is the only recipient trophic level, the region that contains limit cycles and point attractors is much more reduced than in the cases in which the allochthonous inputs enter only C or both C and P . As with the chaos parameter set and P as the recipient, above the point attractor region there is a narrow region of only R persisting, and at greater values of input and ω , both R and P persist, but C goes extinct as the food chain becomes decoupled at the C - P interaction and P becomes solely dependent on the input (e.g., a scavenger). At high values of ω_i and low values of input, P becomes dependent on an inadequate source and goes extinct.

When C is the recipient for this parameter set, the region of limit cycles is much greater. As the system moves away from the region of limit cycles, several outcomes may occur: a point attractor, R only, C only, or R and C . In this scenario, the majority of the state space is dominated by only R persisting.

If both C and P are recipients of input, the dynamics are intermediate between the first two scenarios. As with P as the recipient at high levels of input and ω , both R

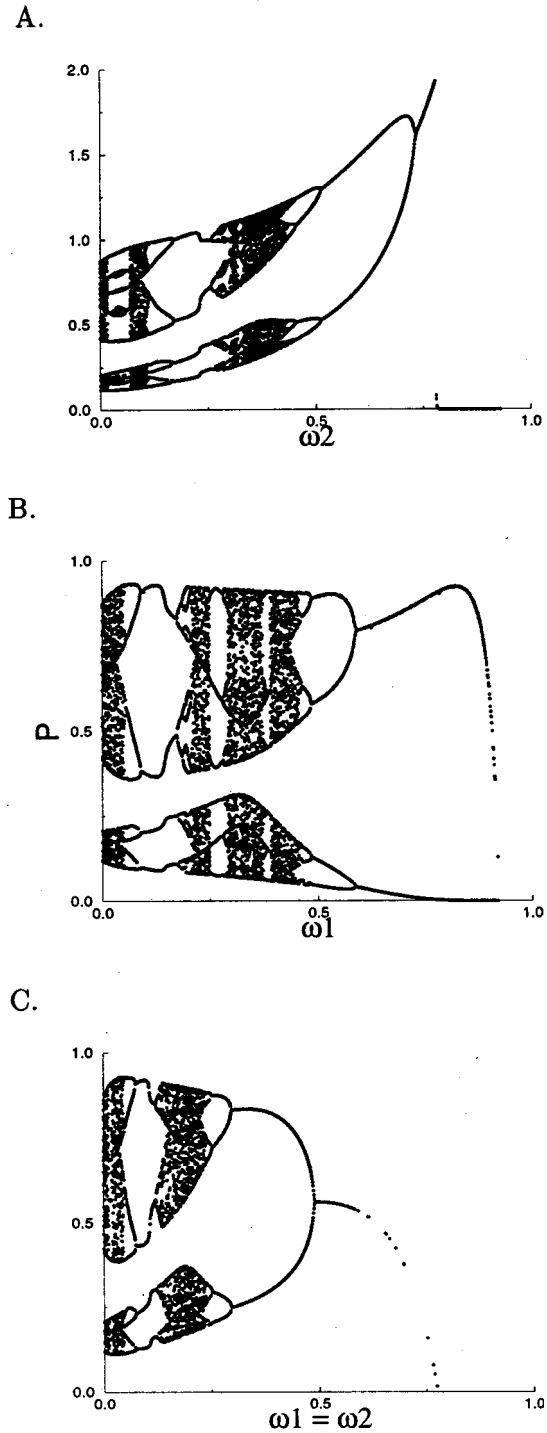


Figure 2: A slice through figure 1 setting and $\omega_i = 0.00$ – 1.00 . A, The input enters as a resource (ω_2) for the predator trophic level $A_p = 0.10$; B, the herbivore (ω_1) is the recipient— $A_c = 0.10$; and C, both predator and herbivore ($\omega_2 = \omega_1$) are recipients— $A_p = A_c = 0.05$.

and P persist. However, at high ω_i and low input, only R persists, which is similar to the C recipient case.

Point Attractor Parameter Set

In the P recipient scenario, only at high values of ω_2 is the system moved away from a point attractor. Relatively low levels of A_p result in the loss of P as it becomes too dependent on A_p , and at high levels of A_p , C is driven to extinction by large densities of P . For the C recipient scenario, at $A_c < 0.5$ there is a small band in which P goes extinct, but above and below this, a point attractor exists. At high levels of input and ω_1 , R goes extinct and the food chain becomes dependent on input (e.g., a detrital chain). Whereas when both C and P are recipients, only at moderate to high levels of ω is the system moved away from the point attractor. At moderate ω_i 's and low input, P goes extinct and increasing ω_i 's results in only R persisting. High values of both input and ω_i 's results in R and P persistence as the C - P link becomes decoupled.

Two Species Point Attractor Parameter Set

If P is the recipient trophic level, then the system never moves from this point attractor as P cannot persist. When P and C are both recipients, then at high levels of ω_i 's, only R persists as both C and P go extinct due to overreliance on the allochthonous inputs. However, if C is the recipient, at low to moderate values of input and high values of ω_1 , all three trophic levels can persist. Increasing input results in persistence of the system at lower values of ω_1 , but when ω_1 is increased, only P and C persist as the chain again becomes overly dependent on allochthonous resources.

Discussion

Our results suggest that allochthonous inputs at low levels can stabilize food webs, but at higher levels they can lead to a decoupling of the resource-consumer-predator chain and result in a system dependent on the allochthonous inputs such as in a detrital-consumer-predator chain. Similarly, increasing the preference for the resource can first stabilize then destabilize the original food chain. One can think of the preference parameter in terms of the composition of the species comprising a trophic level. For example, if we consider the consumer trophic level, an increase in ω_1 and/or ω_2 would mean that the trophic level is changing from being dominated by herbivores to being dominated by detritivores. However, if we assume that species are more generalists, then the preference parameter would be considered the average preference for species to feed on the allochthonous re-

source versus the autochthonous resource. Data from Polis and Hurd (1996) illustrate that, for their system, the species tend to specialize either as herbivores or as detritivores resulting in more reticulate food webs, which may be more representative of natural systems than nonreticulate food webs (Polis and Strong 1996).

The influence of reticulation of food web stability is largely unknown, and only a few studies have indicated what types of interactions or resources might increase reticulation (but see May 1973; Pimm and Lawton 1978; Pimm 1982; Moore and Hunt 1988; Raffaelli and Hall 1992; McCann and Hastings 1997). Polis and Strong (1996) suggest that there are numerous types of resources from across the trophic spectrum that comprise "multi-channel" omnivory, which leads to reticulated food webs. Among the components of multichannel omnivory that increase reticulation in food webs are classical omnivory and allochthonous inputs. Our results demonstrate that low to moderate amounts of allochthonous inputs utilized by either consumers or predators can have a stabilizing effect on food webs. Similarly, DeAngelis (1992) demonstrates that low to moderate levels of nutrient inputs to the basal trophospecies can stabilize food webs, and McCann and Hastings (1997) found that low to moderate levels of omnivory also can stabilize food web dynamics.

Consumer densities are often donor controlled in reticulate food webs; thus, both the amount of resource input and the degree of preferential feeding on this resource influence stability. In our model systems, the amount of allochthonous biomass can increase the minimum density required for the recipients to persist from autochthonous (i.e., classical food web) resources alone. However, this is also influenced by which trophic level is the recipient. In our model, if C is the only recipient, the minimum densities actually decrease with the degree of feeding preference on the allochthonous input (fig. 2B). Further, there are trade-offs between feeding preference and input level. For example, at low input level, increasing preference can precipitate decreased densities (and eventually extinction) of the recipient. Increasing both feeding preference and allochthonous inputs appears to have a synergistic effect that results in decoupling of trophic levels, leading to extinction of one or more trophic levels; notice the concave line above which the system becomes decoupled in figure 1.

Allochthonous inputs can result in parallel food chains and lead to increased interconnections between chains within a web. For their island systems, Polis and Hurd (1995, 1996) found that >90% of prey for terrestrial predators such as scorpions, spiders, and lizards are detritivores that feed on marine detrital inputs. The abundant spiders then can suppress population densities of

plant herbivores, decreasing plant damage (Polis and Hurd 1996). Our results also show this effect; when P is the recipient trophic level, the minimum and maximum densities of P increase (fig. 2A), resulting in the loss of C (fig. 1A). Thus, the marine detrital food web becomes inexorably linked with the terrestrial food web through common predators on these islands.

In our model, the same values of allochthonous input and the degree of feeding preference on this resource that increase stability and enhance persistence also appear to promote longer transients (the time required to reach an equilibrium) and multiple stable states. This is consistent with the suggestion that long transients may play a much larger role in real food webs (Hastings and Higgins 1994; McCann and Hastings 1997). The inclusion of allochthonous inputs (or any other multichannel omnivory source) may bound dynamic behavior in food webs but may do so at the cost of promoting longer transient dynamics. These transient dynamics may occur on timescales much greater than those experienced in ecological interactions and cannot be ignored.

May (1973) found, using Lotka-Volterra models, that increased numbers of species and links (i.e., higher complexity) resulted in lower stability. Pimm and Lawton (1978) found that omnivory also decreased stability. Our results suggest that allochthonous inputs increase stability up to some maximum level, agreeing with the finding of McCann and Hastings (1997), who found that omnivory also increased stability. Why the discrepancies? The results of Pimm and Lawton (1978) are due to the strength of the links that they drew from a uniform distribution, such that a large proportion of the links could be considered to be relatively strong. In essence, their results suggest that strong links are destabilizing. Our results and those of McCann and Hastings (1997) agree with the notion that strong links are destabilizing but that weak to moderate strength links should stabilize food web dynamics.

Increased stability in our system refers to two non-equilibrium tendencies: a decreased number of cycles resulting from period-doubling reversals; and the bounding of local minima on attractors away from zero (fig. 2). Stone (1993) found a similar result in a metapopulation model in which immigration bounds the minimum population size away from zero while simultaneously invoking period-doubling reversals. This is of particular concern in ecological systems, where increased biological complexity (i.e., allochthonous inputs, omnivory, immigration) may actually move systems away from chaotic dynamics (Stone 1993; McCann and Hastings 1997). Therefore, our results, which suggest that allochthonous inputs (up to some maximum level) can increase stability, are consistent with Stone's findings (1993).

Conclusion

Our results suggest that low to moderate levels of allochthonous inputs tend to increase food web stability. The amount of allochthonous inputs and the trophic level(s) that can utilize the resource also affect the dynamics of the system. In addition, the feeding preference parameters (ω_i 's) in our model are constant. This is a simplistic view of natural systems. Real food webs are dynamical systems in which feeding preference and community structure can either vary across allochthonous: autochthonous gradients or have patchy distributions (Moore and de Ruiter 1991; Polis and Hurd 1995, 1996; Persson et al. 1996; Polis et al. 1996, 1997). Given the existence of these gradients or patchiness in resource type and quantities, spatial dynamics should play important roles in structuring communities on both ecological and evolutionary timescales (Holt 1985; Oksanen 1991). Thus, future work should examine the dynamics of different forms of the feeding preference term, including those dependent on allochthonous: autochthonous ratios and spatial heterogeneity in resource availability.

Our simple model supports the conceptual donor-controlled, multichannel omnivory concept of Polis and Strong (1996), which suggests that real food webs are replete with direct and indirect connections that are important forces in food web dynamics and stability. The results from our model systems imply that food webs that experience low to moderate inputs of allochthonous resources can exhibit increased stability and result in food chains becoming decoupled—weakening of trophic cascades to trophic trickles (McCann et al. 1998). These model systems also demonstrate donor-controlled dynamics, suggesting that donor control may be common in natural systems where allochthonous inputs are important sources of productivity. These results are also dependent on which trophic level(s) can utilize the allochthonous resources. As research extends beyond the simple tritrophic food chain model to include various components of multichannel omnivory such as classical omnivory (McCann and Hastings 1997) and allochthonous inputs, it is becoming clear that the dynamics of food webs are both complex and highly dependent on the diversity of trophic connections. Thus we must continue to reexamine the structure, complexity, and dynamics of real food webs.

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