

# Food webs in space: On the interplay of dynamic instability and spatial processes

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Ecologists increasingly recognize that a consideration of spatial dynamics is essential for resolving many classical problems in community ecology. In the present paper, I argue that understanding how trophic interactions influence population stability can have important implications for the expression of spatial processes. I use two examples to illustrate this point. The first example has to do with spatial determinants of food chain length. Prior theoretical and empirical work has suggested that colonization–extinction dynamics can influence food chain length, at least for specialist consumers. I briefly review evidence and prior theory that food chain length is sensitive to area. A metacommunity scenario, in which each of various patches can have a food chain varying in length (but in which a consumer is not present on a patch unless its required resource is also present), shows that alternative landscape states are possible. This possibility arises if top predators moderate unstable interactions between intermediate predators and basal resources. The second example has to do with the impact of recurrent immigration on the stability of persistent populations. Immigration can either stabilize or destabilize local population dynamics. Moreover, an increase in immigration can decrease average population size for unstable populations with direct density-dependence, or in predator–prey systems with saturating functional responses. These theoretical models suggest that the interplay of temporal variation and spatial fluxes can lead to novel qualitative phenomena.

**Key words:** food chain length; metacommunity; spatial flows; spatial food web ecology.

## INTRODUCTION

Since the time of Charles Elton (1927), food webs have been a basic organizing theme in ecology (Pimm 1982; Polis & Winemiller 1996). Analyses of the structure and dynamics of food webs are central to several of the core issues of community ecology, such as the relationship between species diversity and environmental heterogeneity (e.g. Schneider 1997), the implications of direct and indirect interspecific interactions for community structure (e.g. Yodzis 1988), and the recognition of multiple stable states and, more broadly, the role of historical contingencies in determining realized assemblages of species (Law & Morton 1993; see below). All food webs, of course, exist in space. Yet

until rather recently, ecologists have paid scant attention to how spatial patterns and processes influence food chain structure and dynamics (Schoener 1989). The tragic accident in the Sea of Cortez on March 27, 2000, which took the lives of Takuya Abe, Masahiko Higashi, Shigeru Nakano, Gary Polis, and Michael Rose, snatched from the world five fine scientists who were at the forefront of dealing with the spatial dimension of food web ecology. Towards the end of his life, Gary Polis was also beginning to focus on the interplay of temporal variation and spatial subsidies as a major determinant of food web dynamics (Sears *et al.* in press). The present paper is dedicated to their memory and will deal with issues I know to be of direct interest to them (as expressed in conversations I had with Dr Higashi, and collaborative research with Dr Polis).

What are the important spatial attributes of food webs? I suggest that it is useful to consider

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separately the following four distinct ways that space matters in food web ecology:

(1) The spatial context of community assembly. All local food webs are necessarily assembled by colonization, and depleted by extinction (MacArthur & Wilson 1967; Holt 1993; Lockwood *et al.* 1997; Morton & Law 1997; Belyea & Lancaster 1999). Both colonization and extinction are influenced by spatial processes, as well as by the web of interactions defined by a local food web. The rate of colonization into a focal community obviously depends upon factors such as the distance between that community and source pools of potential colonists, as well as the dispersal propensities of particular species (Whittaker & Jones 1994), but it is also influenced by the ability of an invader to withstand local predation and competitive pressures. Extinction rates scale with population size and variability which, in turn, are influenced by both area and the strength and pattern of interspecific interactions (Ritchie 1999). The structure of food webs thus emerges from the iterative process of colonization and extinction episodes defining a local trophic structure which, in turn, then influences future colonization and extinction events. How this feedback between trophic structure and community assembly plays out over time will be strongly influenced by spatial factors, such as area and distance to sources.

(2) Spatial strategies.

Local communities mix species with radically different 'spatial strategies', experiencing the world at different spatial scales (Holt 1993, 1996). For instance, the dynamics of a clonal plant population may be governed by finely reticulate processes at the scale of a few centimeters to meters, whereas the population dynamics of the ungulates that consume them are determined at a much coarser scale (up to hundreds of kilometers for migratory or nomadic species). Interspecific interactions within a given trophic level, and the responses of particular consumers to spatial variation, can be modulated by the disparate abilities of species differing in body size to respond to spatial heterogeneity in resources at differing spatial scales (Roland & Taylor 1997; Ritchie & Olff 1999).

(3) Dynamical implications of space, per se.

Even in homogeneous environments, the fact that interactions among individuals are localized and individual dispersal distances limited has profound

implications for population dynamics and species coexistence. For instance, this increase in the effective dimensionality of population dynamics permits transient spatial heterogeneities to arise in density, which then alter the impacts of density-dependent processes. Such transient heterogeneities can often be stabilizing, as in systems with strong predator-prey dynamics, where spatial separation can provide prey with temporary refuges from strong predation (Jansen 1995; Tilman & Kareiva 1997; Weisser *et al.* 1997; de Roos *et al.* 1998; Bonsall & Hassell 2000; Hassell 2000).

(4) Spatial fluxes.

In both natural and anthropogenic landscapes, spatial heterogeneity may not merely be a transient expression of population dynamics but instead reflect permanent sources of variation (e.g. in edaphic factors or environmental gradients). This will often imply that spatial fluxes (e.g. in resources, or individuals within populations) will be asymmetrical in nature. This leads to allochthonous inputs and spatial subsidies, which can have important consequences for population dynamics, community interactions, and ecosystem processes (Polis *et al.* 1997; Huxel & McCann 1998; Nakano & Murakami 2001; Ekerholm *et al.* in press; Power & Rainey in press).

A full consideration of each of the above issues would require an entire volume. In this paper, I explore some phenomena that emerge when one closely considers the interplay of spatial dynamics and local dynamical instability. I will first examine how community assembly can influence one aspect of food web structure – food chain length. I show how the influence of trophic interactions on local population stability can imply alternative landscape states, differing in food chain length. I then briefly examine the impacts of strongly asymmetrical spatial fluxes on local population and community dynamics and, in particular, argue that such fluxes can have surprising effects in systems with unstable dynamics.

### **Spatial determinants of food chain length: Local dynamics and alternative states**

A classic problem in community ecology is understanding the factors that limit the length of food chains. Ecological communities vary much more in

species richness than in their realized food chain lengths (Pimm & Lawton 1977; Pimm 1982; Rosenzweig 1995). But why? Traditional ecological (*vs* evolutionary) explanations have emphasized one of two factors: ecological energetics, and local dynamical stability. Consider the energetic explanation. Because of the inevitable loss of free energy that accompanies trophic interactions, there is a predictable diminution in energy along food chains. This suggests that food chains should typically be longer in more productive habitats. Moreover, theoretical studies based on Lotka–Volterra dynamics suggest that longer food chains can be dynamically unstable (Pimm 1982). This suggests that longer food chains should be found in more stable environments.

Evidence to date does not strongly support the productivity hypothesis, except possibly when productivity is extremely low or in some simple aquatic systems (Spencer & Warren 1996; Townsend *et al.* 1998; Post *in press*; see Rosenzweig 1995 for a contrary opinion). The theoretical basis for the dynamical constraints hypothesis has also recently been argued to be unconvincing by Sterner *et al.* (1997), who point out that even long chains can be dynamically stable if higher trophic levels experience direct density dependence (e.g. due to territoriality or aggressive interference competition). My own suspicion is that both energetics and local dynamic stability play a role in constraining food chain length, but they do not provide a full explanation.

By contrast to the traditional energetic explanation, there is growing evidence that food chain length can reflect the spatial attributes of ecosystems (Holt 1993; Post *et al.* 2000; Post *in press*; Holt and Post, unpubl. obs., 2001–2002). This is particularly clear for community modules (small sets of interacting species; Holt 1997a) in which the consumers are specialized to particular prey or host species. For instance, Komonen *et al.* (2000) studied a food chain based on a bracket fungus, *Fomitopsis rosea*, which is found solely in old-growth boreal forest. The numerically dominant food chain consisted of the fungus as the basal resource, the tineid moth *Agnathosia mendicella* as the primary consumer and, for the top consumer a tachinid fly, *Elfia cingulata*, which is a specialist parasitoid on the moth. These authors examined food chain length on suitable fallen spruce logs, as

a function of whether or not the forest was a large, spatially continuous area, or instead fragmented and, if fragmented, for how long. The median food chain length decreased from three in the control areas, to one (just the fungus) in those fragments that had been isolated for the longest period of time. Indeed, the top specialist consumer (the parasitoid fly) was completely missing from fragments isolated for 12–32 years. In this study, effects of habitat fragmentation were most sharply manifested at high positions in a food chain.

It is an open question how often such effects can be discerned at the level of entire food webs. Post *et al.* (2000) recently used a stable isotope technique to quantify the average food chain length in a set of north temperate lakes in North America varying in volume from roughly  $10^5$ – $10^{12}$  m<sup>3</sup>, and in phosphorus loading from 2 to 200 µg/L. They convincingly demonstrated that food chain length increases strongly with ecosystem size, but not with productivity. By contrast, in a literature review of community responses to habitat fragmentation, Mikkelsen (1993) concluded that trophic organization (the fraction of species found at different trophic levels) did not differ among habitat fragments varying in size. Cohen and Newman (1991) spliced the cascade model of trophic organization (Cohen & Newman 1985) with a species–area relationship and concluded that the maximal and average chain length of communities should increase extremely slowly with increasing area. However, Steffan-Dewenter and Tscharrntke (2000) showed that in a guild of herbivorous insects (butterflies of old meadows in central Europe), the strength of the species–area relationship decreased with the degree of trophic generalization. This suggests that the domain within which one should seek the strongest influence of space on food chain length may be at the level of modules or guilds, rather than entire communities, unless the food web is dominated by trophic specialists rather than generalists.

There are many mechanisms by which ecosystem area or volume could influence food chain length (Post *in press*; Holt and Post, unpubl. obs., 2001–2002). Spatial dynamics can constrain food chain length through at least two broad mechanisms: the mechanics of assembly (Holt 1993, 1996, 1997a,b; see also Schoener *et al.* 1995), and the effects of area upon dynamical stability

(Spencer & Warren 1996; Wilson *et al.* 1998). Here, I briefly review the basic ideas, and then present some novel results.

### Community assembly and food chain length

One of the core ideas of island biogeographic theory is that area can influence community structure via colonization and extinction. All else being equal, a species is more likely to be found on a large island, than a small island, because the large island provides a larger target for colonization and, following establishment, populations can grow larger there and so be less likely to become extinct (MacArthur & Wilson 1967). Now take this basic idea, and add trophic specialization. If dispersal is an infrequent event, a specialist consumer will persist on an island or habitat patch as a population only if its required resource also persists. So in the course of community assembly, one should observe sequential colonization, in effect with colonization proceeding up the food chain. If its resource is itself a living population, extinctions of the resource population should also drag along any specialized, dependent consumer population. These effects imply nested spatial distributions (Holt 1993). This logic is, of course, repeated if the consumer supports a higher-order consumer. Moreover, if the rates of colonization or extinction are sensitive to area (or distance to source pools) at a low trophic level this influences not just the incidence of species at that level, but of any species either directly or indirectly dependent upon them. There thus can be a compounding of spatial effects up a food chain. Van Nouhuys and Hanski (1999) describe a concrete example in which area can affect the total population size of a host herbivorous insect and, in turn, the colonization success of the parasitoid attacking it increases with host population size; area effects at one level translate into area effects on colonization and hence occupancy at a higher level. In turn, species at higher levels may have their own colonization and extinction rates influenced by area or distance. The process of interlinked colonizations and extinctions at different levels leads to a kind of compounding, so that species at higher trophic levels are expected to be more sensitive to island area or distance to source pools (for formal theory on this

see Holt 1993, 1996, 1997b; Schoener *et al.* 1995; Holt *et al.* 1999).

A comparable phenomenon arises in patchy environments, where no patch is a permanent source for the other patches. If a given habitat type is sparse on the landscape, then overall rates of colonization can be reduced, and extinction rates elevated (if there are rescue effects via recurrent immigration into occupied patches), compared to a more widespread habitat type. If consumers are specialized, one expects a compounding of spatial effects. Specialist food chains should tend to be shorter in sparser habitats, and also shorter if the basal resource species itself has high extinction or low colonization rates (Holt 1997a). Even in widespread habitats, given local extinctions and constraints on colonization rates, food chain length may be constrained by spatial dynamics.

These effects may arise even in 'donor-controlled' systems in which consumers have little impact upon resource populations. An additional area effect may occur if trophic interactions are strong enough to risk local extinction by over-exploitation. If individual interaction and dispersal distances are short, one can schematically view large islands or patches as a cluster of contiguous small areas, within which interactions occur, and among which dispersal occurs (Holt 1992). With localized extinctions driven by trophic interactions, an internal metapopulation dynamic may arise, in which persistence is permitted because of recurrent dispersal among these localized arenas of interactions. Wilson *et al.* (1998) illustrate this for a host-parasitoid-hyperparasitoid model, in which interactions within each cell of a lattice are violently unstable (because of the Nicholson-Bailey dynamics assumed in each trophic interaction, Hassell 2000). Despite this instability, the system can persist for very long simulation runs if the lattice is large enough. However, the lattice required to sustain the full three-species system is considerably greater than that needed for just the basal host and primary parasitoid (Wilson *et al.* 1998), so again food chains will be longer on larger areas. Experimental studies have demonstrated the potential for habitat subdivision to promote the persistence of strong, intrinsically unstable predator-prey interactions (e.g. Holyoak 2000), so the moderation of strong interactions by area could

be a powerful mechanism leading to area effects on food chain length.

In short, spatial dynamics can constrain food chain length. Moreover, the potential for local overexploitation of resources by consumers and unstable dynamics can lead to additional phenomena at the landscape level, such as alternative equilibria. I will illustrate this possibility using a metapopulation model for a food chain (Holt 1997a).

Consider a 'metacommunity' in which each patch in a landscape can be in one of these three states: unsuitable, suitable but empty, or occupied. A fraction  $b$  of all patches is suitable for the basal species. If a patch is occupied, it could be by the basal member of a food chain alone (state 1, a food chain of length 1), or by the basal species along with a primary consumer (state 2, a food chain of length 2), or by both those species with a top consumer (state 3, a food chain of length 3). For simplicity, we assume that we can ignore the exact spatial location of patches, and the abundance of each species in each patch, and instead just monitor the fraction of patches,  $p_i$ , that are in community state  $i$ . We use ' $c$ ' to denote colonization rates, and ' $e$ ' extinction rates. Subscripts will denote transitions (e.g.  $e_{10}$  describes the rate of extinctions in patches with just the basal prey – a transition from state 1 to state 0). Colonization is assumed to occur sequentially up the food chain, so that for the full chain to be present on an initially empty patch, that patch must have experienced the transitions 0–1, then 1–2 and then, finally, 2–3.

The following metacommunity model was presented, along with a few basic results, in Holt (1997a):

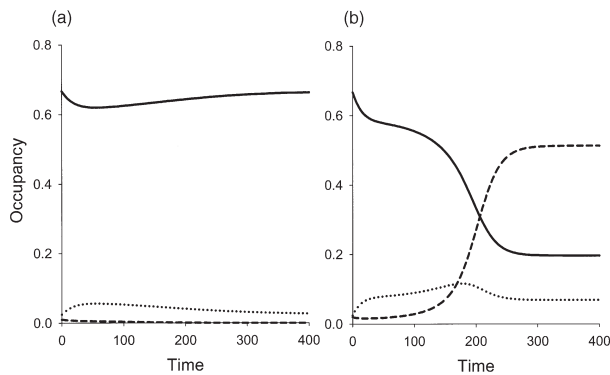
$$\begin{aligned} \frac{dp_1}{dt} &= (c_{01}p_1 + c'_{01}p_2 + c''_{01}p_3)(b - p_1 - p_2 - p_3) \\ &\quad - (c_{12}p_2 + c''_{12}p_3)p_1 + e_{31}p_3 + e_{21}p_2 - e_{10}p_1, \\ \frac{dp_2}{dt} &= (c_{12}p_2 + c''_{12}p_3)p_1 - (e_{20} + e_{21})p_2 \\ &\quad + e_{32}p_3 - c_{23}p_3p_2, \\ \frac{dp_3}{dt} &= c_{23}p_3p_2 - (e_{30} + e_{31} + e_{32})p_3. \end{aligned} \quad (1)$$

The model is complicated, because one must allow for colonists of low-ranked species emerging

from patches with higher-ranked species. In Holt (1997a), the model was used to examine conditions for food chain persistence. It was shown that if the habitat required by the basal species is scarce, metapopulation dynamics makes it unlikely that a long chain of specialists will persist. It was noted there without elaboration that the model can generate alternative, stable landscape states. One way this can happen is for the top predator to stabilize an inherently unstable interaction between the intermediate predator and the basal prey (May 1973; Rosenzweig 1973). For instance, in a standard Lotka–Volterra model of a food chain, if the top predator experiences mild direct density-dependence (e.g. due to territoriality), and the intermediate predator has no such direct density-dependence, and satiates readily, the two-link system may show large-amplitude limit cycles, whereas the full three-link system is locally stable. Large-amplitude oscillations in turn could imply elevated local extinction rates. Thus, in some systems, extinction rates may actually be reduced with longer food chains.

The effects of trophic interactions on colonization rates could also be complicated. If the number of individuals emanating from a patch (entering a pool of potential colonists) scales with local abundance, then one needs to know how trophic interactions affect local equilibrium abundance (for stable systems) or time-averaged abundances (for unstable systems). In general, one expects predators to depress the abundance of their prey, with indirect positive effects on the resources of those prey. If so, then a top predator should depress the colonization potential of its own prey, and indirectly increase the colonization potential of the basal resource.

However, there are a variety of circumstances in which predators increase prey abundance (Abrams 1992). This can occur if the prey's isocline, relative to its own resource population, is 'humped' (Abrams 1992); in effect, the predator can prevent the prey from over-exploiting its resource base. Moreover, counterintuitive effects of predators upon prey abundance may occur if systems are unstable and trophic interactions are strongly non-linear (Abrams & Roth 1994). If the intrinsically unstable interaction between the basal species and the intermediate predator is stabilized by a top predator, the time-averaged abundance of the



**Fig. 1.** Alternative landscape states for a simple food web. Numerical runs for the metacommunity food chain model described in the text are shown. The parameter values are:  $b = 0.95$ ,  $c_{01} = c_{01}' = c_{01}'' = 0.2$ ,  $c_{12} = c_{12}' = c_{12}'' = 0.3$ ,  $e_{20} = e_{21} = 0.1$ ,  $e_{10} = 0.05$ ,  $c_{23} = 0.6$ ,  $e_{30} = e_{31} = 0.02$ ,  $e_{32} = 0.001$ . (a) The initial conditions are such that the top predator dies out, leaving a landscape predominantly comprising patches with just the basal prey species; (b) there are initially more patches with the full food chain, and because the full food chain has a lower extinction rate (because the top predator prevents unstable oscillations between the intermediate predator and the basal species), the top predator persists. (—)  $p_1$ , Fraction of patches with just the basal species in the food chain; (...)  $p_2$ , fraction of patches with both the basal species and the intermediate species (i.e. a food chain of length 2); (---)  $p_3$ , fraction of patches with all 3 species (i.e. a food chain of length 3). Note that the total occupancy for the basal species is the sum of  $p_1 + p_2 + p_3$  (all those sites where it occurs alone, plus with the other members of the food chain), and in like manner the total occupancy for the intermediate species is  $p_2 + p_3$ .

intermediate predator in the unstable two-link system may be lower than its equilibrium abundance in the full system. Hence, in some situations it should be reasonable to assume that the main effect of the top predator will be on the stability of the other species (and hence likelihood of local extinction) rather than on their abundances (and hence colonization propensity). This is what I assume in the following examples.

Figure 1 shows a dynamical example, in which it is assumed that 95% of the patches are suitable for the basal species. Here, we assume that the main metapopulation effect of local trophic dynamics is through extinction rates, but not colonization rates. In particular, we assume that the intermediate predator has a much higher extinc-

tion rate than does the basal species alone, whereas systems with all three species present enjoy a considerably reduced extinction rate (a possibility suggested by the trophic exploitation models of May 1973 and Rosenzweig 1973). This implies that the intermediate predator on its own will have a low occupancy (assuming it can persist at all), in the absence of the top predator.

If we start with just the basal species and the intermediate predator, each at their respective equilibria, and introduce a very small propagule of the top predator, the top predator disappears (Fig. 1a). The reason is that the low occupancy exhibited by the intermediate predator means that the net colonization rate of the top predator is depressed to too low a level to balance extinctions. (Note that the overall occupancy of the basal prey is the sum of occupancy by just the prey, and by the prey with the predators.) However, if we introduce a larger propagule of the top predator, the system moves into an alternative landscape state, where the full food chain persists, and all species enjoy a higher total occupancy (Fig. 1b). The reason for this is that patches with the top predator have lower extinction rates. Because we have assumed that there is little or no impact of trophic interactions upon colonization rates, patches with the top predator continue to emit colonists of the intermediate predator and the basal prey species, which can colonize other suitable patches. This, in turn, feeds back to increase the fraction of patches that are suitable for colonization by the top predator; this positive feedback leads to a substantial increase in occupancy for the top predator (and indirectly for the lower-ranked species as well).

Figure 2 depicts these alternative landscape equilibria, as a function of the fraction of the landscape ( $b$ ) which is suitable for the basal species. The black symbols indicate equilibrium abundances for the basal species and intermediate predator, for these two species taken alone. At very low values of  $b$ , not even the basal species can persist. At higher  $b$ , the basal species persists, but because of our assumption of high extinction rates the intermediate species cannot persist unless  $b$  is very high, and even then its occupancy is low. One feasible landscape state is thus to have a very short food chain. The open symbols depict the alternative landscape equilibria, in which all three species

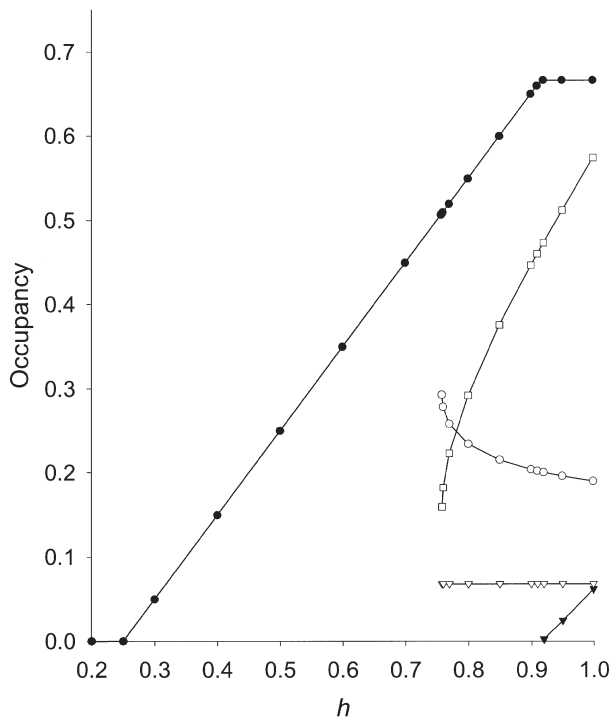


Fig. 2. Food chain occupancies as a function of habitat suitability. The parameters are the same as used in Fig. 1, except now the system equilibria are shown as a function of the fraction of the landscape which is suitable for occupancy by the basal species,  $h$ . At high values of  $h$ , the landscape can contain either the full food chain, or just the intermediate predator and prey, or (depending on the exact value of  $h$ ) just the basal prey species alone. At lower values for  $h$ , the landscape cannot sustain the food chain at all. Filled symbols, stable state with 0, 1 or 2 species; open symbols, alternative stable state, with 3 species. (●, ○), prey; (□), top predator; (▼, ▽), intermediate predator.

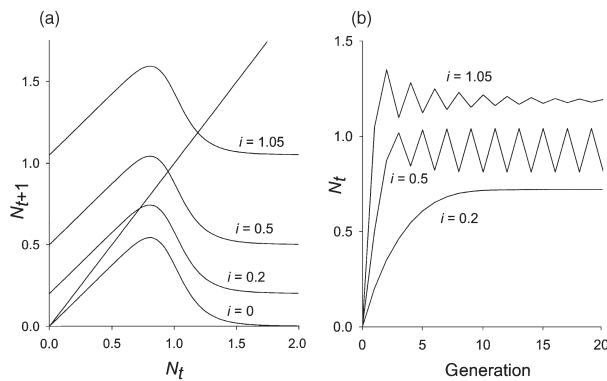
occur. (Numerical studies show that all the equilibria shown are stable to small perturbations.) At high  $h$ , the full food chain persists, and most patches in the landscape are occupied by chains of length varying from one to three. With lower  $h$ , however, the occupancy of the top predator declines precipitously (and, indeed, occupancies of all species are depressed). Below a value of  $h$  of about 0.92, the alternative landscape states are either the full chain (on a substantial fraction of patches, with the others having chains of length one or two), or just the basal species. If there is a large perturbation, there could be a system-wide collapse of the entire food chain.

### Impacts of asymmetric fluxes in heterogeneous environments

The above model in essence deals with qualitative impacts of spatial flows given local dynamical instability, in that it keeps track only of the presence or absence of species in each patch. More generally, one will be concerned with how spatial flows alter quantitative aspects of population and community dynamics, even in the absence of local extinctions or recurrent colonization. A useful limiting case is to imagine that one is concerned with a focal community, embedded in a much larger landscape, where the landscape influences the local community via immigration (e.g. allochthonous inputs or spatial subsidies at various trophic levels), but where the reciprocal effect of the local community on the surrounding landscape can be to a first approximation ignored. If such inputs are constant in time, the question then becomes how the properties of the local community (stability, equilibrium abundances etc.) are influenced by the magnitude of the input. Here we briefly examine two systems: single species with density-dependence, and predator-prey interactions.

#### *Single species models: Diverse effects of immigration on population stability and size*

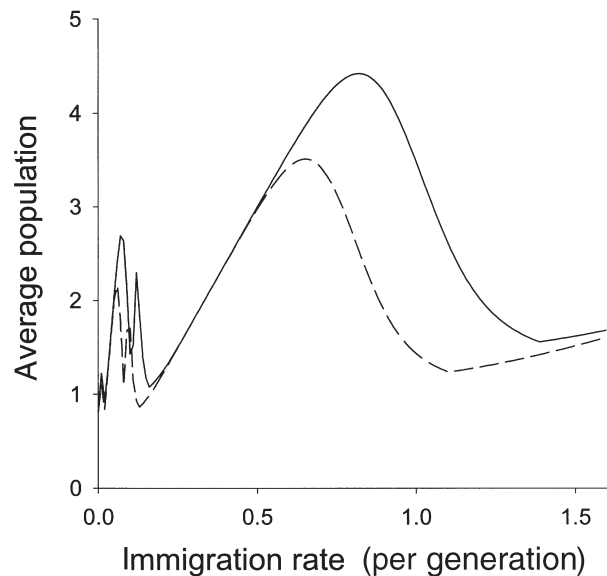
In recent years, there has been considerable interest in assaying impacts of immigration on population dynamics (Holt 1983a, 1983b; McCallum 1992; Stone 1993; Doebeli 1995; Ruxton & Rohani 1998; Stone & Hart 1999), with particular focus on species with discrete generations whose dynamics fits  $N_{t+1} = F[N_t] + i$ . Here,  $N_t$  is population size in generation  $t$ ,  $F$  describes local population growth, and  $i$  is immigration from an external source. In any reasonable model,  $F$  asymptotes or declines at high  $N$ . If a population is stable (at  $N = N^*$ ), increasing  $i$  simply increases  $N^*$  (Holt 1983b), to a value above the local carrying capacity. High rates of immigration will almost always lead to stable dynamics. However, low rates of immigration can either stabilize or destabilize local dynamics (although the former seems to occur more often in models that have been explored in the literature). Which occurs can be assayed graphically by constructing graphical maps of  $F$ , and examining the slope of  $F$



**Fig. 3.** Immigration can either stabilize, or destabilize, single-species population dynamics. The particular model shown is  $N_{t+1} = N_t R / (1 + aN_t^c) + i$ , where  $R$  is the finite rate of increase,  $c$  measures non-linearity in the action of direct density-dependence, and  $a$  determines the overall strength of such density-dependence. The parameter  $i$  is the rate of immigration. In the example shown,  $R = 0.75$  (the population is a sink population),  $c = 10$  (strongly non-linear density-dependence), and  $a = 1$ . (a) plots of  $N_{t+1}$  vs  $N_t$ , and (b) dynamical time-series. Increasing  $i$  in effect translates the map of  $N_{t+1}$  vs  $N_t$  upward. The local stability is determined by the slope of this map at the equilibrium. As can be seen, small amounts of immigration lead to a stable equilibrium; higher immigration, to a two-point cycle; and yet higher immigration, to an equilibrium with damped oscillations.  $N$ , population size;  $t$ , generation.

evaluated near the equilibrium. If the slope is negative at  $i = 0$ , and becomes less negative at higher  $N$  (corresponding to population equilibria with higher  $i$ ), immigration tends to be stabilizing (Holt 1983a; Stone & Hart 1999). If, instead, the slope is more negative at higher  $N$ , immigration can be destabilizing. (Given instability, whether or not the emerging dynamics are ‘complex’ (e.g. chaotic) or ‘simple’ (e.g. two-point cycles) is a more complicated and subtle question; Stone & Hart 1999). Figure 3 shows an example of this behavior, with unstable dynamics at intermediate levels of immigration (Holt 1983a, 1983b provide other examples of immigration both stabilizing and destabilizing dynamics).

Given that unstable dynamics occur, it is of interest to know how immigration influences average population size. Figure 4 depicts how the time-average abundance of population size ( $\langle N \rangle$ ) varies as a function of the immigration rate  $i$ . The non-monotonic relationship between  $\langle N \rangle$  and  $i$



**Fig. 4.** Effects of recurrent immigration upon average population size ( $\langle N \rangle$ ) in unstable populations. The parameters are  $R = 10$  and  $c = 10$ . These imply strongly unstable, chaotic dynamics when immigration rate ( $i = 0$ ) (not shown). The relationship between immigration rate and population size is non-monotonic; at intermediate values for  $i$ , increases in  $i$  lead to a decrease in population size. The parameter is strength of density dependence; the lines shown correspond to (—)  $a = 1$  and (--)  $a = 10$ .

emerges in a wide range of models (e.g. Holt 1983a). The reason this phenomenon occurs in models of chaotic population dynamics is that one typically observes population ‘outbreaks’, followed by crashes to low abundance, with varying lengths of time to the next outbreak. A small amount of immigration reduces the length of time between successive outbreaks, leading to increases in time-average abundance. Further increases in immigration, however, lead to population lows which are great enough to experience direct density-dependence, depressing the magnitude of population overshoots. Because this effect increases with increasing  $i$ , average population size can decline with increasing immigration in unstable populations over a range of intermediate values for  $i$ .

#### *Predator–prey interactions: The diverse effects of immigration*

Understanding these effects in simple one-species models helps interpret comparable effects of immigration in predator–prey systems. Consider the



canonical Rosenzweig-MacArthur model of predator-prey interactions with immigration added (Rosenzweig & MacArthur 1963):

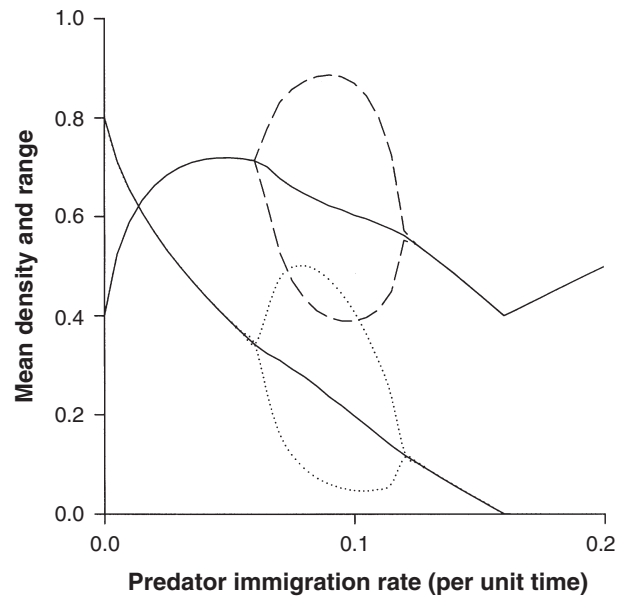
$$\begin{aligned}\frac{dN}{dt} &= N\left(\frac{abR}{1+abR} - c\right) + i_N, \\ \frac{dR}{dt} &= R\left(r\left[1 - \frac{R}{K}\right] - \frac{aN}{1+abR}\right) + i_R.\end{aligned}\quad (2)$$

The prey has logistic growth, and the predator has a saturating functional and numerical response. The rate of immigration for each species is independent of population size. The predator does not experience any direct density-dependence, and dies off exponentially in the absence of prey. As is well known, if the predator is effective at limiting the prey to abundances well below  $K$ , one observes limit cycle behavior (May 1973), in effect because of the time-lagged density-dependence experienced by the predator via its effect upon prey abundance.

We can illustrate the range of outcomes with some examples. As in the single species model, immigration in this model tends to be stabilizing, but one can find examples of instability forced by recurrent immigration (Fig. 5; in this and the following figures, the dashed and dotted lines indicate maximal and minimal population sizes for fluctuating populations). Moreover, given that the system is unstable, immigration frequently can reduce average population size (Figs 5–7 show three examples). There are two distinct effects at work here. First, when immigration reduces the magnitude of oscillations, it has a disproportionate impact on reducing population highs, than on increasing population lows. This is true for both predator and prey immigration. Hence, immigration can depress abundance. Second, predator immigration reduces the prey abundance at which the predator population has a zero growth rate. Because the prey's isocline is humped (due to the predator's saturating functional response), increasing predator immigration can depress the equilibrium abundances of both predator and prey.

## CONCLUSIONS

In the present paper, I have dealt with two broad themes. First, I have argued that many traditional



**Fig. 5.** Effects of predator immigration upon predator and prey population size. The solid lines (—) denote equilibrium abundances, or the time-average abundances for unstable populations. The range of fluctuations for unstable populations is denoted by (–) for the predator, and (···) for the prey. The model is described in the text; the parameter values are  $K = r = b = 1$ ,  $c = 0.4$ ,  $a = 2.5$ ,  $b = 2$ . The example shown has zero prey immigration; above a certain level of predator immigration, the prey is excluded. Predator immigration can be destabilizing (at intermediate levels), and also depress predator population size, as well as prey numbers. Note that the upper line refers to the predator population, whereas the lower line refers to the prey population.

issues in food web ecology can be illuminated by thinking of food webs in a spatial context. For instance, by fusing food web dynamics with island biogeography and metapopulation dynamics, we can arrive at a fresh perspective on the traditional problem of understanding the determinants of food chain length. Second, I have demonstrated that it is crucial to understand temporal variability in populations when considering the implications of both colonization-extinction dynamics and spatial fluxes. In the case of food chains of trophic specialists, the modulation of local dynamical instability by trophic interactions can lead to phenomena such as alternative states for landscapes. In the case of populations that are potentially unstable due to time-lagged density dependence (either in single species models, or in predator-prey systems), immigration can either

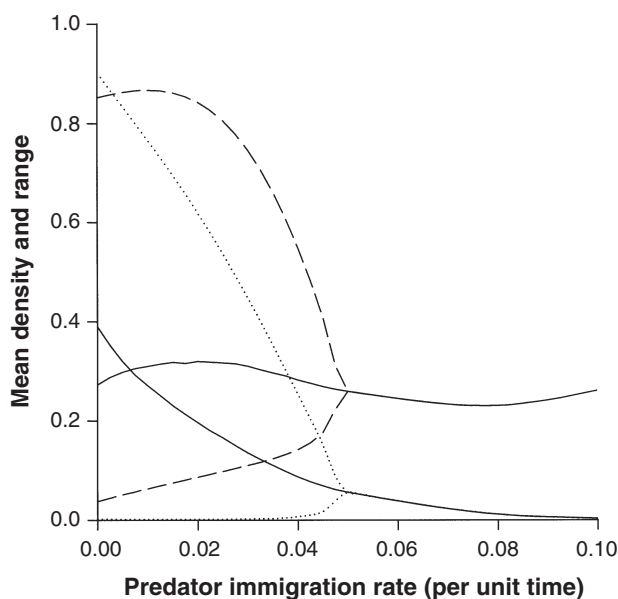


Fig. 6. Effects of predator immigration upon population size and magnitude of fluctuations (notation as in Figure 5). The parameter values are  $K = r = b = 1$ ,  $c = 0.4$ ,  $a = 4.994$ ,  $b = 1.244$ . We now add a small amount of prey immigration, so the prey does not become extinct. Overall, predator immigration is now broadly stabilizing. But predator immigration has only a weak effect on its own abundance. Notation as shown in Figure 5.

stabilize or destabilize local dynamics. Moreover, given that local population dynamics are unstable, immigration can have counterintuitive effects on local abundance (e.g. an increase in immigration of a focal species can depress its average population size.)

The results I have presented here of course barely scratch the surface of the topics of impacts of spatial openness and temporal variability on food webs and community structure. I, however, choose not to end this paper in the usual way, for instance with an attempt towards conceptual generalization or a distillation of caveats about the particular results I have presented. As I said in the Introduction, this paper is dedicated to the memory of Takuya Abe, Masahiko Higashi, Shigeru Nakano, Gary Polis, and Michael Rose. All were supposed to have been major participants at the Kyoto Food Web Symposium and, indeed, in my last conversation with Gary Polis on March 24, 2001, just before the accident, we spoke at length about plans for this meeting, and the centrality of the topic of the interplay of temporal

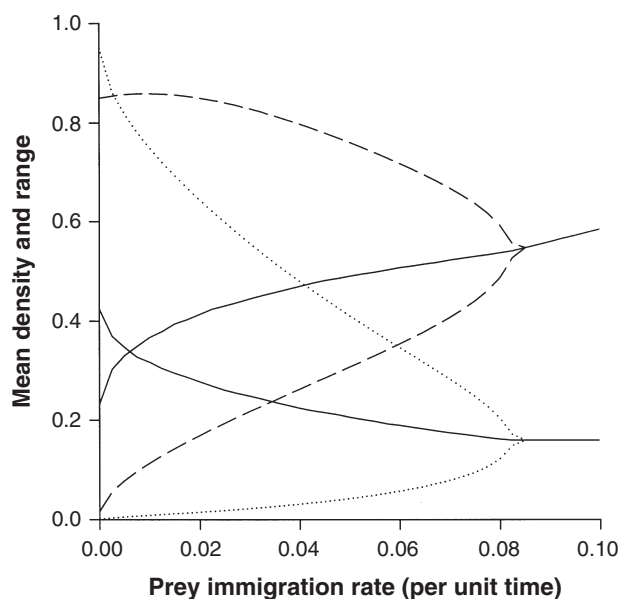


Fig. 7. Effects of prey immigration upon population size and magnitude of fluctuations (notation as in Figure 5). The parameter values are as in Fig. 6. Prey immigration boosts predator numbers, and reduces the magnitude of population fluctuations. However, prey immigration depresses the prey's own abundance, because it depresses highs in numbers (in fluctuating populations) more than it increases lows in numbers. Notation as shown in Figure 5.

variability and spatial subsidies in food web ecology.

As scientists, I believe we honor the deceased when we incorporate, in whatever fashion, their ideas, discoveries, philosophical perspectives, and sheer sense of wonder about the world into our own thinking. In honor of these great scientists and fine human beings, who will be missed so much by their families and friends, and who are such a loss to the community of scholars, I would like to close with a haiku by one of the masters of that noble Japanese art-form,

Buson (Japan 1715–1783):

*Regret at parting*

Yesterday – a flight;

Today – a flight;

The wild geese are not here tonight!

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