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Adaptive movement and food-chain dynamics: towards food-web theory without birth–death processes

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Abstract Population density can be affected by its prey [resource] and predator [consumer] abundances through two different mechanisms: the alternation of birth [or somatic growth] or death rate and inter-habitat movement. While the food-web theory has traditionally been built on the former mechanism, the latter mechanism has formed the basis of a successful theory explaining the spatial distribution of organisms in the context of behavioral and evolutionary ecology. Yet, few studies have compared these two mechanisms, leaving the question of how similar (or different) predictions derived from birth–death-based and movement-based food-web theories unanswered. Here, theoretical models of the tritrophic (resource–consumer-top predator) food chain were used to compare food-web patterns arising from these two mechanisms. Specifically, we evaluated the response of the food-chain structure to inter-patch differences in productivity for movement-based models and birth–death-based models. Model analysis reveals that adaptive movements give rise to positively correlated responses of all trophic levels to increased productivity; however, this pattern was not observed in the corresponding birth–death-based model. The movement-based model predicts that the food chain response to productivity is determined by the sensitivity of animal movement to the environmental conditions. More specifically, increasing sensitivity of a consumer or top predator leads to smaller inter-patch variance of the resource or consumer density, while increasing inter-patch variance in the consumer or resource density. In conclusion, adaptive movement provides an alternative mechanism correlating the food-web structure to environmental conditions.

Keywords Food-web theory · Mathematical model · Ideal free distribution · Game theory · Productivity · Two-patch model

Introduction

A central issue in community ecology is what determines species abundance, community structure, and their spatio-temporal variation. Ecological theory suggests that interspecific interaction is an important determinant of population dynamics and the pattern of species abundance. The key assumption in community ecology is that interspecific interactions drive population dynamics through the alternation of birth (or somatic growth rate in physiologically parameterized models; Yodzis and Innes 1992) and death rates. This assumption extends from the classical theory of Lotka (1925) and Volterra (1926) to the recent theory on mutualistic communities (e.g., Bastolla et al. 2009; Thébault and Fontaine 2010) and communities with multiple interaction types (Allesina and Tang 2012; Mougi and Kondoh 2012, 2014). For example, food-web theory (Polis and Winemiller 1995; deRuiter et al. 2005) has utilized the basic assumption that population growth rate increases with increasing food

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resource consumption, while the mortality rate increases with increasing attack by natural enemies.

When trophic interactions influence population levels via the alternation of birth, growth, or death rates, the rate at which new biomass is synthesized at the basal trophic level (termed primary productivity) represents a major determinant of local community structure (Rosenzweig 1971; Oksanen et al. 1981; Yodzis 1984; Abrams 1995). Theory on linear food chain predicts that changing productivity may not affect all trophic levels in the same way; instead, the equilibrium biomass at a given trophic level may be determined by either top-down or bottom-up force. Consequently, increased productivity only affects certain trophic levels (Oksanen et al. 1981; Mittelbach et al. 1988; DeAngelis et al. 1995; Power 1992). For example, in a tri-trophic food chain, the equilibrium biomass at the second level may be exclusively determined by top-down forces, and not affected by changing productivity (Hairstone et al. 1960, Oksanen et al. 1981; DeAngelis et al. 1995). This prediction holds as long as the population growth rate of the third level (top predator) is exclusively determined by its resource density ($\Delta N_{top}/N_{top}=f(N_{top-1})-m_{top}$). However, empirical studies suggest that, in some ecological communities, the biomass of all trophic levels increases with increasing productivity (Kagata and Ohgushi 2006), conflicting with the theoretical prediction.

Movement is another major driver of population dynamics (Johnson et al. 1992; Morales et al. 2010), which potentially modifies community dynamics that arises from direct interspecific interactions (Holt 1984; Briggs and Hoopes 2004; Abrams 2007; McCann et al. 2005; McCann and Rooney 2009). Inter-habitat movements (including both immigration and emigration) may be more important than birth and death when the time scale is too short for the birth–death process to influence population dynamics or when the spatial scale is so small that organisms easily depart or arrive at the focal habitat area. Furthermore, organisms often change the habitats they use to avoid high predation risk (Lima and Dill 1990) or to seek certain resources (Cowie and Krebs 1979; Lima 2002). Such adaptive movement generates a mechanism where population dynamics is influenced by its resources or consumers, even in the absence of direct contact. Thus, this phenomenon represents another potential mechanism relating food-web structure to population dynamics.

The ideal free distribution (IFD) theory (e.g., Fretwell and Lucas 1969; Fretwell 1972; Kacelnik et al. 1992; Křivan et al. 2008) correlates consumer population levels with resource distribution, without considering the birth–death process. This theory assumes that each consumer in a population adaptively chooses a resource patch from multiple resource patches characterized by a specific amount of available resource. According to the IFD theory, individuals with perfect information about within- and between-patch status should move from more competitive, resource-poor patches (fewer resource or more individuals) to less competitive, resource-rich patches (more resource or less individuals) to reach Nash equilibrium, where the animals distribute themselves among resource patches in a way that all the resource patches have the same intrinsic value (Holt 1984). Thus, a habitat with higher resource production is predicted to contain more consumer individuals. Originally, this theory did not take the top-down effect into account. Yet, it is straightforward to extend this theory to include the natural enemy effect; whereby, individuals move from a patch with higher predation risk to a patch with lower predation risk (Lima and Dill 1990). Under natural conditions, both resource availability and predation risk are expected to affect animal movement to drive community dynamics (Sih 1984; Lima and Dill 1990; Abrams 2007; Bolker et al. 2003; Křivan et al. 2008).

If adaptive movement, rather than the birth–death process, is the major driver of local population dynamics, how should trophic communities respond to productivity? How is the resulting community-level pattern different to that which arises when trophic interactions directly affect birth and death rates? A number of theoretical models have taken prey–predator habitat choice into account as a major driving force of prey–predator population dynamics (Iwasa 1982; Hugie and Dill 1994; Křivan 1997; van Baalen and Sabelis 1999; Alonzo 2002; Bolker et al. 2003; Jackson et al. 2004; Abrams 2007; Cressman et al. 2008; Křivan et al. 2008; Cressman and Garay 2009; Křivan and Cressman 2009; Wang and Takeuchi 2009). However, most studies, including IFD theory, have been carried out in the context of behavioral or evolutionary game theory, making its relevance to food-web ecology less clear. Moreover, previous studies that include animal movement often consider the confounding effect of trophic interactions on birth–death processes, which mask the pure movement-mediated effect (Hugie and Dill 1994; Křivan 1997; van Baalen and Sabelis 1999; Alonzo 2002; Abrams 2007; Wang and Takeuchi 2009), place more focus on evolutionary dynamics (Iwasa 1982; Alonzo 2002; Křivan and Cressman 2009; Cressman and Garay 2009), or do not address, or successfully isolate, the productivity effect on community structure (Iwasa 1982; Křivan 1997; van Baalen and Sabelis 1999; Abrams 2007; Cressman et al. 2008; Cressman and Garay 2009). As a result, the pure effect of productivity on trophic communities mediated by the alternation of animal adaptive movements remains unclear. Jackson et al. (2004) constructed an exceptional individual-based prey–predator model, where inter-habitat movements by prey and predators exclusively drive population dynamics. The authors used this model to show that the information organisms have about patch status influences how patch productivity is related to prey and predator distributions. However, the individual-based nature of their model and simulation-

dependent analysis prevent one from gaining a general, analytical solution. Furthermore, no comparison was made with what arises when prey–predator interactions directly affect birth–death processes.

Here, we present two mathematical models of a tri-trophic linear food chain. Prey–predator interaction affects population dynamics via the alternation of birth and death rates in the birth–death-based model, whereas population dynamics is solely driven by adaptive and non-adaptive (random) movements of consumers and top predators in the movement-based model. Adaptive movement in the latter model is based on the fitness function that is derived from the former model, allowing the two models to be directly compared. We focused on comparing the responses of the two models to inter-patch differences in productivity. We show that the birth–death-based and movement-based models leads to qualitatively different responses to increased productivity and discuss its mechanism and ecological implications.

Model

We present two models of tri-trophic food chain dynamics: (1) one driven by birth–death processes and (2) one driven by adaptive or non-adaptive movement. To evaluate how inter-patch variation in productivity is reflected in community structure, the equilibrium densities of three species and their responses to productivity were evaluated.

Food-chain dynamics driven by the birth–death process

Consider a tri-trophic food chain containing a resource, consumer, and top predator. The resource is added to the system at a constant rate, r, which represents ecosystem productivity. The population dynamics of the consumer and top predator are driven by the birth–death process linked to trophic interactions; that is, the birth rate increases when individuals in a population are eating more, while the death rate increases when more individuals in a population are being eaten.

The population dynamics of the three species are described as:

$$\frac{dR}{dt} = r - \alpha RC, \tag{1a}$$

$$\frac{dC}{dt} = e_C \alpha RC - \beta CT - d_C C, \tag{1b}$$

$$\frac{dT}{dt} = e_T \beta CT - d_T T, \tag{1c}$$

where R, C, and T are the population sizes of the resource, consumer, and top predator, respectively; r is the resource production rate (system productivity); α is the interaction strength between the consumer and the resource; β is the

interaction strength between the top predator and consumer; e_C and e_T are the energy conversion rates of consumer and top predator, respectively; d_C and d_T are the mortality rates of the consumer and top predator, respectively.

Food-chain dynamics driven by inter-patch movement

Consider a two-patch meta-community of a tri-trophic food chain, where the local dynamics of the consumer and top-predator populations are driven solely by inter-habitat movement. It is assumed that the resource level in habitat i ($i=1$ or 2) increases at the habitat-specific constant rate, r_i. To evaluate the effect of productivity on community structure, we assume that habitat 1 is richer in productivity than habitat 2 ($r_1 \geq r_2$), without loss of generality. The resource at habitat i is lost at rate, $\alpha R_i C_i$, due to exploitation by the consumer in the same habitat, while the density of the other species (i.e., the consumer and top predator) are not directly affected by other species. This setting allows us to isolate the dynamics that arise from just behavioral movement.

The population dynamics of the three species in habitat i are described by the following differential equations:

$$\frac{dR_i}{dt} = r_i - \alpha R_i C_i, \tag{2a}$$

$$\frac{dC_i}{dt} = m_C \{ -f_C C_i + (1-f_C) C_j \}, \tag{2b}$$

$$\frac{dT_i}{dt} = m_T \{ -f_T T_i + (1-f_T) T_j \}, \tag{2c}$$

where R_i, C_i, and T_i are the population sizes of the resource, consumer, and top predator in habitat i, respectively. r_i is the resource production rate of habitat i; m_C and m_T are the maximum movement rates of the consumer and top predator, respectively; f_C and f_T represent the effect of other species to the rate of movement of the consumer and top predator from habitat i to j, respectively. Assume that a consumer moves between habitat patches according to differences in both the resource (R_i) and top predator (T_i) densities of the two habitats, while a top predator moves according to difference in consumer density (C_i) between the two habitat patches. We set f_C and f_T as:

$$f_C = \frac{1}{1 + e^{\theta_C \left\{ \alpha(R_j - R_i) - \beta(T_i - T_j) \right\}}} \tag{3a}$$

and

$$f_T = \frac{1}{1 + e^{\theta_T \beta(C_i - C_j)}} \tag{3b}$$

respectively, where α is the interaction strength between the consumer and resource; β is the interaction strength between the top predator and consumer; θ_C and θ_T represent the

"sensitivity" of the consumer and top predator to the differences in habitat quality, respectively, and may be interpreted as the certainty of information about habitat status (larger θ_i represents higher certainty of information; $\theta_i=0$ if no information available as to habitat status). θ_i ($i=C$ or T) is set to 0 for random movement; whereby, as θ_i increases, the function becomes closer to a step function of the difference in habitat quality (Fig. 1).

Note that, with this model, it always holds that $(dC_1/dt)+(dC_2/dt)=0$ and that $(dT_1/dt)+(dT_2/dt)=0$; thus, the total population size of consumers, C_1+C_2, and top predators, T_1+T_2, are kept constant over time, confirming that the confounding effect via the alternation of birth–death processes is excluded.

Results

Food-chain dynamics driven by the birth–death process

The effect of system productivity, r, on the equilibrium density of each species depends on species composition (see Appendix, Fig. 2). When the community consists of a resource and consumer (no top predator), an increase in productivity, r, has no effect on resource level, $(R^*(=d_C/e_C\alpha))$, but does increase consumer population level at equilibrium, $C^*(=r/\alpha R^*)$. When the three species coexist, an increase in productivity, r, has no influence on the equilibrium population level of the consumer, $C^*(=d_T/e_T\beta)$, but does increase the equilibrium population levels of the resource level, $R^*(=re_T\beta/\alpha d_T)$ and predator, $T^*(=(re_Ce_T/d_T)-(d_C/\beta))$.

To compare these results with the results of following the two-patch, movement-driven model analysis easily, let us see what is expected if there are two isolated birth–death-driven communities with the same species composition (resource–consumer or resource–consumer-top predator), but different productivity (r). The population densities (R_i, C_i, T_i) in more and less productive habitats are denoted by subscripts, $i=H$ and L, respectively. When the community consists of a resource and consumer, the habitat with higher productivity is occupied by a consumer with a higher population level ($C_H^*>C_L^*$), but the resource level remains unchanged ($R_H^*=R_L^*$).
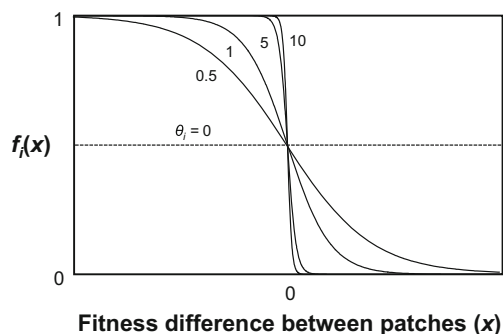
**Fig. 1** Shape of the movement function, $f_i(x)$, where i is C or T

When the community consists of a resource, consumer, and top predator, the habitat with higher productivity contains higher resource and top predator levels ($R_H^*>R_L^*$, $T_H^*>T_L^*$), but the population level of the consumer remains the same in both habitats ($C_H^*=C_L^*$).

Food-chain dynamics driven by adaptive inter-patch movement

Consider a resource–consumer system ($T_1^*=T_2^*=0$). The equilibrium densities (R_i^*, C_i^*) depend on the adaptive capability of the consumer, θ_C (Appendix, Figs. 2 and 3). When a consumer randomly moves between the two patches (i.e., the absence of consumer adaptation; $\theta_C=0$ and, thus, $f_C=0.5$), the population levels of the consumer, C_i, in the two habitats are the same ($C_1^*=C_2^*=C^*$); consequently, the plant population level, R_i, is higher in habitat 1 than in habitat 2 ($R_1^*=r_1/\alpha C^*>R_2^*=r_2/\alpha C^*$). When consumer movement is adaptive ($\theta_C>0$), the resource and consumer levels at equilibrium are higher at the more productive habitat 1 compared to the less productive habitat 2 ($R_1^*>R_2^*$, $C_1^*>C_2^*$). Note, here, the moving rate from habitat 2 to 1 is larger than the opposite direction ($f_C<(1-f_C)$); thus, the number of consumers moving from habitat 1 to 2 equals that from habitat 2 to 1 ($f_CC_1^*=(1-f_C)C_2^*$; balanced dispersal rate, sensu Holt 1985). Numerical calculations confirmed that the system is locally stable for the parameter space examined in this study (Fig. 2).

Next, consider a three-species system, where the resource, consumer, and top predator coexist (Appendix, Figs. 2 and 3). When the consumer randomly moves ($\theta_C=0$), inter-patch differences in the population levels of the consumer and top predator vanish ($C_1^*=C_2^*=C^*$, $T_1^*=T_2^*=T^*$), while the resource is more abundant in habitat 1 ($R_1^*>R_2^*$). The sensitivity of the top predator (θ_T) has no effect on the pattern; however, when the consumer adaptively moves ($\theta_C>0$), the sensitivity of the top predator (θ_T) matters. If the top predator randomly moves ($\theta_T=0$), its population levels are the same in both habitats ($T_1^*=T_2^*$), whereas the resource and consumer levels at equilibrium are higher in the more productive habitat ($R_1^*>R_2^*$, $C_1^*>C_2^*$). In contrast, if the top predator adaptively moves $\theta_T>0$, inter-patch differences in the population levels of all three species occur; that is, $R_1^*>R_2^*$, $C_1^*>C_2^*$, $T_1^*>T_2^*$. Numerical calculations confirmed that the system is stable within the parameter space examined in this study (Fig. 2).

Given two three-species local communities with different productivity, inter-patch variation in population levels is related to the sensitivity of the consumer (θ_C) and top predator (θ_T), as shown by the numerical calculation (Fig. 3). The spatial heterogeneity of the resource is larger when θ_T is larger or θ_C is smaller. The spatial distribution of the consumer is skewed to the habitat with higher productivity, because the consumer is more sensitive (larger θ_C) or the top predator is
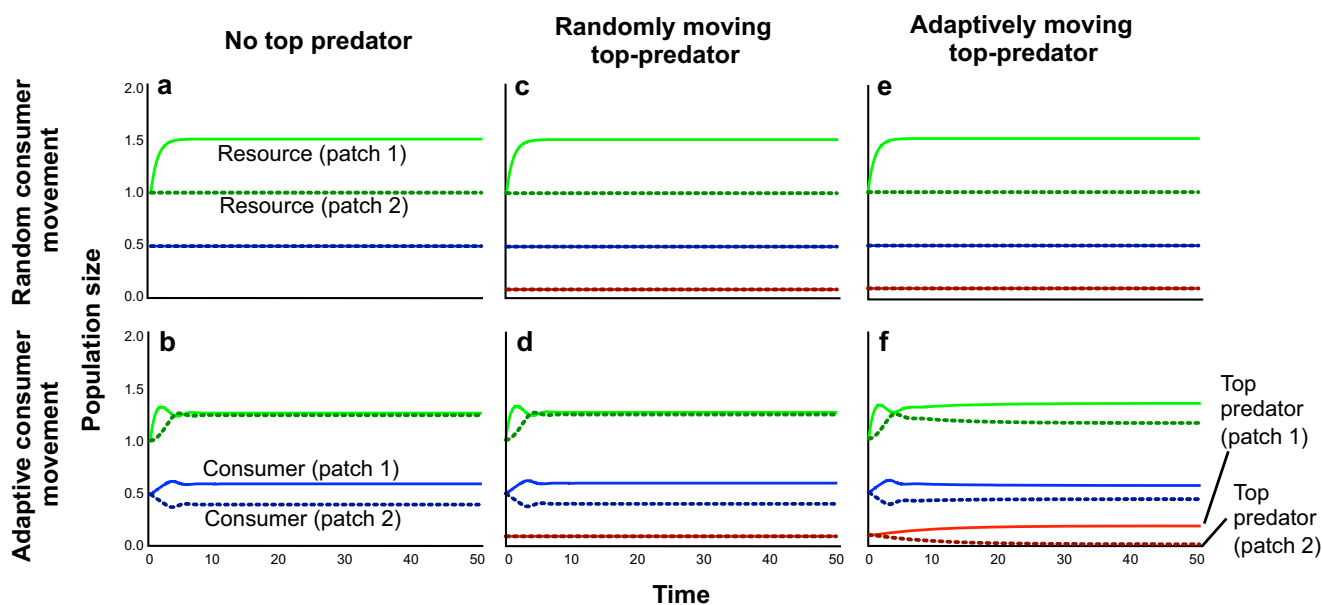
Fig. 2 Typical population dynamics driven by adaptive or random (non-adaptive) movement. Food chains are of two-species (resource and consumer; **a**, **b**) or three-species (resource, consumer, and top predator; **c**–**f**). Consumer movements are random (**a**, **c**, **e**) or adaptive (**b**, **d**, **f**). Movement of the top predator is random (**c**, **d**) or adaptive (**e**, **f**). *Solid* and *dashed lines* are for Habitat 1 (higher production) and habitat 2 (lower production), respectively. *Green*, *blue*, and *red* indicate plant, consumer, and top predator, respectively. Parameters are $r_1=1.5$, $r_2=1$, $m_C=m_T=0.1$, $\alpha=\beta=2$, and $\theta_C=\theta_T=10$. The initial population sizes of R_i, C_i, and T_i were set to 1.0, 0.5, and 0.1, respectively

less sensitive (smaller θ_T). In contrast, the spatial distribution of the top predator is skewed to the more productive habitat when the both animals are more sensitive (larger θ_C or θ_T; Fig. 3). The relative importance of the top-predator for the movement of the consumer, β/α, does not qualitatively alter these results (Fig. 3).

Discussion

Food-web theory may be built on the basis of the classic IFD theory. Our theoretical model demonstrated that adaptive movement in response to changing densities of interacting species drives population dynamics and shapes food-chain responses to habitat productivity. This finding implies that productivity-dependent patterns in the community-level structure may emerge, even in the absence of direct birth–death process-mediated effects between species, which are assumed to be necessary in the traditional community theory (Polis and Winemiller 1995; deRuiter et al. 2005). The comparison of two different models, one based on the traditional birth–death process and one based on just movement, allowed us to identify the similarities and differences between the patterns that emerge from these two models.

In movement-driven population dynamics, sensitivity (or certainty of information on resource patch status) is the main determinant of community structure (see Figs. 2 and 3), because an organism with stronger sensitivity is able to respond to smaller inter-habitat variances in resource availability or predation risk, generating a stronger interspecific effect. This phenomenon contrasts with the community dynamics arising from direct trophic interactions, where the strength of inter-specific effects on birth and death rates (per-capita predation rate in food-web dynamics, for example) are central for shaping communities. When adaptive movement drives population dynamics, the responses of trophic levels to inter-habitat difference in productivity are dependent on the sensitivity of both consumers and top predators. More specifically, an increase in the sensitivity of consumers leads to smaller inter-patch variance in resource density, but an increase in inter-patch variance in consumer and top-predator density. Similarly, an increase in the sensitivity of top predators lowers the inter-patch variance of consumer density, but increases the inter-patch variance in top-predator and resource densities (Fig. 3).

According to the IFD theory, organisms that adaptively choose habitat patches should eventually distribute themselves among patches, until all patches have the same their quality in terms of resource availability or predation risk, and to realize the fitness equivalence among individuals in different patches. This process provides a potential mechanism where adaptive consumers cause resource density to be independent of habitat productivity. Indeed, in our model, the consumer (i.e., the prey of the top predator) becomes equally distributed in the two habitats as the sensitivity of the top predator increases. Similarly, the resource levels of the two habitats become more similar as the sensitivity of the consumer increases (Fig. 3). However, population dynamics that do not only take movement into account also
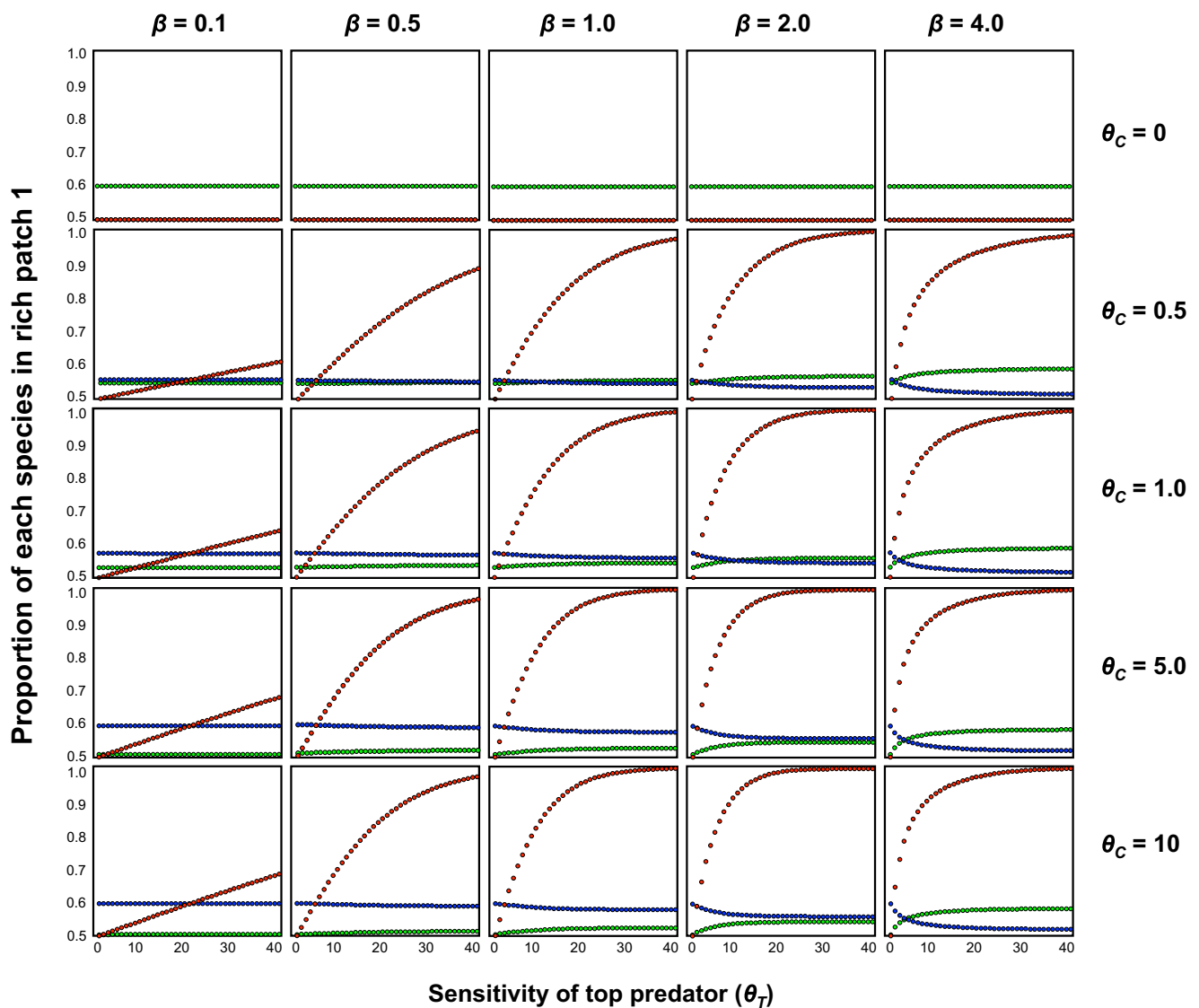
Fig. 3 Equilibrium proportion of each species in the rich patch in relation to the adaptive abilities of animals, θ_C and θ_T, and the interaction strength of the top predator and consumer, β. The other parameter values are the same as those presented in Fig. 2

give rise to "fitness equivalence" between habitats (Křivan et al. 2008). In fact, in the model with birth–death-driven dynamics, it should hold that $e_C\alpha R^*=d_C$ at the equilibrium in which only resources and consumers coexist (transformed from Eq. A1b in Appendix for $C^*>0$). This equation suggests that the amount of benefit a consumer receives, $e_C\alpha R^*$, is constant, d_c, and independent of system productivity, r. Similarly, in the three-species equilibrium, it holds that $e_C\alpha R^*-\beta T^*=d_C$ and $e_T\beta C^*=d_T$ (transformed from Eq. A3b and A3c in Appendix for C^*, $T^*>0$). This equation suggests that the benefit the consumer or top predator receives from the community, $e_C\alpha R^*-\beta T^*$ or $e_T\beta C^*$, is again constant, d_c or d_T, and independent of system productivity, r. It is clear that fitness equivalence alone is not enough to discriminate between birth–death-driven and movement-driven community dynamics.

There is a striking difference between birth–death-driven and movement-driven models in their response to productivity. When population dynamics is driven by adaptive movement, the population density at all the trophic levels is predicted to be higher in a habitat with higher productivity (Figs. 2 and 3; also see "(f) Three-species model with adaptive consumer and adaptive top predator" in Appendix). In contrast, the tri-trophic food chain model based on birth–death process predicts that the second level shows no response to changing productivity (e.g., the resource in the two-species system or the consumer in the three-species systems). The prediction derived from birth–death-based model is well known in food-chain theory (Oksanen et al. 1981), but the empirical support for it is ambiguous (e.g., the references in Persson et al. 1996). For example, in a review of bottom-up cascades in terrestrial plant-herbivore-parasitoid systems by Kagata and

Ohgushi (2006), it was found that positive effects to herbivores tended to be accompanied with positive effects to parasitoids. Ecological theory suggests that the positive responses of adjacent trophic levels can be explained by making additional assumptions to the birth–death-based model such as environmental heterogeneity (Oksanen 1990b), seasonality (Oksanen 1990a), ratio-dependent functional response (Arditi and Ginzburg 1989), transient dynamics (Abrams and Roth 1994), and species heterogeneity within a trophic level (Abrams 1993). Present model added adaptive movement as an alternative explanation for the pattern found in real trophic communities.

Trophic cascade is a well-known phenomenon in community ecology, where a change in species density is transmitted to non-adjacent trophic levels along the food chain via trophic interactions (Strong 1992; Schmitz et al. 2000, Kagata and Ohgushi 2006). Our model suggests that even in the absence of direct trophic interactions, an analogous phenomenon may occur when organisms adaptively move. In other words, adaptive movement of sensitive species sets a condition that drives the movement of adjacent adaptive species, potentially leading to the transmission of a behavior-mediated effect along the food chain. This phenomenon explains why inter-habitat heterogeneity in productivity leads to heterogeneity in all of the trophic levels in our model (Fig. 2f; see "(f) Three-species model with adaptive consumer and adaptive top predator" in Appendix). In fact, when the consumer is non-adaptive, the top-predator, whether it is adaptive or non-adaptive, shows no response to inter-habitat variance in productivity (Fig. 2e; see "(d) Three-species model with non-adaptive consumer and adaptive top predator" in Appendix). It is hypothesized that the insertion of non-adaptive species to a linear food chain would prevent the interspecific effect cascading along the food chain.

Movement-based and birth–death-based models of the food chain showed different responses to productivity change. The differences in their predictions might imply that the food-chain response depends on both spatial and temporal scales, in addition to the combination of species involved. In natural ecosystems, the relative importance of adaptive movement and birth–death processes is expected to vary with spatial and temporal scales. In the long-term scale of multiple generations, the latter may be more prominent. In contrast, the movement-based food-web theory requires that different patches are spatially separated, and that consumers and predators should be able to move between them; thus, this theory may only be applicable at smaller spatial scales (Adler et al. 2001). In addition, adaptive movement and birth–death processes should be interactive under most spatial and temporal scale, as predicted by a number of community dynamics models. Yet, at the same time, interacting species might occupy different spatio-temporal scales. For example, predators at higher trophic level tend to be larger and, thus, their spatial

scale is also larger (Holt 1996; McCann et al. 2005). In comparison, parasitoids, which are usually smaller than their host, might have smaller movement ranges. Similarly, a time scale of multiple generations for a short-living species can be a time scale of behavioral movement for a long-living organism. This prey–predator mismatch in spatio-temporal scales may imply that the population dynamics of interacting species is driven by different mechanisms. In other words, while the population dynamics of one species is influenced by another species via the alternation of the birth–death process, the opposite effect arises from the induction of adaptive movement. The ecological consequence of this process and how the emerging pattern depends on the choice of spatio-temporal scale is an open future question that requires addressing to fully understand what drives community dynamics and what patterns should emerge in nature.

Appendix

I. Equilibrium state for the model with the birth–death process

(a)   Two-species model

The equilibrium is obtained by setting the right hand sides of Eq. 1a and b to zero and T to 0:

$$r - \alpha R^* C^* = 0 \tag{A1a}$$

$$e_C \alpha R^* C^* - d_C C^* = 0 \tag{A1b}$$

These equations are solved to give:

$$R^* = \frac{d_C}{e_C \alpha} \tag{A2a}$$

$$C^* = \frac{r e_C}{d_C} \tag{A2b}$$

(b)   Three-species model

Similarly, the equilibrium for three-species is obtained by solving:

$$r - \alpha R^* C^* = 0 \tag{A3a}$$

$$e_C \alpha R^* C^* - \beta C^* T^* - d_C C^* = 0 \tag{A3b}$$

$$e_T \beta C^* T^* - d_T T^* = 0 \tag{A3c}$$

as:

$$R^* = \frac{r e_T \beta}{\alpha d_T} \tag{A4a}$$

$$C^* = \frac{d_T}{e_T \beta} \tag{A4b}$$

$$T^* = \frac{r e_C e_T}{d_T} - \frac{d_C}{\beta} \tag{A4c}$$

Note, this system is always locally stable. Under equilibrium conditions, we obtain the Jacobian matrix, as follows:

$$J = \begin{pmatrix} -\dfrac{d_T \alpha}{e_T \beta} & -\dfrac{e_T r \beta}{d_T} & 0 \\ \dfrac{d_T e_C \alpha}{e_T \beta} & 0 & -\dfrac{d_T}{e_T} \\ 0 & \dfrac{e_T(e_C e_T r \beta - d_C d_T)}{d_T} & 0 \end{pmatrix} \tag{A5}$$

The characteristic equation, the solution of which is the eigenvalue, is given as:

$$\lambda^3 + w_1 \lambda^2 + w_2 \lambda + w_3 = 0, \tag{A6}$$

where:

$$w_1 = \frac{d_T \alpha}{e_T \beta}, \tag{A7a}$$

$$w_2 = e_C r(\alpha + e_T \beta) - d_C d_T, \tag{A7b}$$

$$w_3 = e_T \alpha \left(\frac{d_C d_T}{e_T \beta} - e_T r \right). \tag{A7c}$$

The equilibrium point is locally stable if w_1, $w_3 > 0$ and $w_1 w_2 > w_3$, according to the Routh-Hurwitz criteria. It is trivial that $w_1 > 0$ because all parameter values are positive. Inequality $w_3 > 0$ always holds, as long as the consumer has a positive equilibrium density. Hence, the stability condition reduces to $w_1 w_2 > w_3$. We find the last condition reduces to $r\alpha > 0$, which always holds.

II. Equilibrium state for the model with adaptive or non-adaptive movement

(a) Two-species model with non-adaptive consumer

The equilibrium is obtained by solving:

$$r_i - \alpha R_i^* C_i^* = 0 \tag{A8a}$$

$$0.5 m_C \{-C_1^* + C_2^*\} = 0 \tag{A8b}$$

as:

$$R_i^* = \frac{r_i}{\alpha C_i^*} \tag{A9a}$$

$$C_1^* = C_2^* \tag{A9b}$$

(b) Two-species model with an adaptive consumer

The following equations should hold at equilibrium:

$$r_i - \alpha R_i^* C_i^* = 0 \tag{A10a}$$

$$m_C \{-f_C C_1^* + (1-f_C)C_2^*\} = 0 \tag{A10b}$$

The two equations taken together give:

$$\frac{C_2^*}{C_1^*} = \frac{1}{f_C} - 1 = \exp\left[\theta_C \left(\frac{r_2}{C_2^*} - \frac{r_1}{C_1^*}\right)\right], \tag{A11}$$

Note, when $d(C_1+C_2)/dt=0$, it holds that $C_1+C_2=C_{\text{total}}$, where C_{total} is constant. Thus, Eq. A8 becomes:

$$\frac{C_{\text{const}}}{C_1^*} - 1 = \exp\left[\theta_C \left(\frac{r_2}{C_{\text{const}} - C_1^*} - \frac{r_1}{C_1^*}\right)\right]. \tag{A12}$$

The LHS of Eq. A12 is a monotonically decreasing function of C_1^* with its limits:

$$\lim_{C_1^* \to 0} \left(C_{\text{const}} / C_1^*\right) - 1 = \infty$$

and

$$\lim_{C_1^* \to C_{\text{const}}} \left(C_{\text{const}} / C_1^*\right) - 1 = 0.$$

The RHS of Eq. A12 is a monotonically increasing function of C_1^* with its limits:

$$\lim_{C_1^* \to 0} \exp\left[\theta_C \{r_2 / (C_{\text{const}} - C_1^*) - r_1 / C_1^*\}\right] = 0$$

and

$$\lim_{C_1^* \to C_{\text{const}}} \exp\left[\theta_C \{r_2 / (C_{\text{const}} - C_1^*) - r_1 / C_1^*\}\right] = \infty.$$

Taken together, there should be unique $\overrightarrow{C_1}$, which holds Eq. A12.

$\overrightarrow{C_1}$ should also be larger than $C_{\text{const}}/2$ as follows. The LHS of Eq. A12 is 1 for $C_i^* = C_{\text{const}}/2$, while the RHS is smaller than 1 for $C_1^* = C_{\text{const}}/2$ as:

$$\theta_C \{r_2 / (C_{\text{const}} - C_1^*) - r_1 / C_1^*\} < 0$$

suggesting that LHS should be larger than RHS for $C_1^*=C_{\text{const}}/2$. Given that the LHS and LHS of Eq. A12 are decreasing and increasing functions of C_1^*, respectively, the solution, $\overline{C_1}$, should be larger than $C_{\text{const}}/2$. Thus, it follows that $C_2^*>C_1^*$ as:

$$\overline{C_2^*} = C_{\text{const}} - \overline{C_1^*} < C_{\text{const}} - C_{\text{const}}\Big/2 = C_{\text{const}}\Big/2 < C_1^*.$$

Note, when $\left(C_{\text{const}}\big/\overline{C_1}\right)-1 < 1$, it should follow that:

$$\exp\left[\theta_C\left\{r_2\Big/\left(C_{\text{const}}-C_1^*\right)-r_1\Big/C_1^*\right\}\right] < 1$$

suggesting that $r_2/C_2^*-r_1/C_1^*<0$ and, thus, $R_1^*>R_2^*$.

(c) Three-species model with a non-adaptive consumer and non-adaptive top predator

The following equations should hold at equilibrium:

$$r_i - \alpha R_i^* C_i^* = 0 \tag{A13a}$$
$$0.5m_C\left\{-C_1^* + C_2^*\right\} = 0 \tag{A13b}$$
$$0.5m_T\left\{-T_1^* + T_2^*\right\} = 0 \tag{A13c}$$

These three equations taken together give:

$$R_i^* = \frac{r_i}{\alpha C^*} \tag{A14a}$$
$$C_1^* = C_2^* = C^* \tag{A14b}$$
$$T_1^* = T_2^* = T^* \tag{A14c}$$

It should hold that $R_1^*>R_2^*$ as $r_1>r_2$.

(d) Three-species model with a non-adaptive consumer and adaptive top predator

The following equations should hold at equilibrium:

$$r_i - \alpha R_i^* C_i^* = 0 \tag{A15a}$$
$$0.5m_C\left\{-C_1^* + C_2^*\right\} = 0 \tag{A15b}$$
$$m_T\left\{-f_T T_1^* + (1-f_T)T_2^*\right\} = 0 \tag{A15c}$$

Equations A15a and A15b give:

$$R_i^* = \frac{r_i}{\alpha C^*} \tag{A16a}$$
$$C_1^* = C_2^* = C^* \tag{A16b}$$

Further, note, when $f_T = \frac{1}{1+e^{\theta_T(\beta C^*-\beta C^*)}} = 0.5$, it follows that:

$$T_1^* = T_2^* = T^* \tag{A16c}$$

It should hold that $R_1^*>R_2^*$ as $r_1>r_2$.

(e) Three-species model with an adaptive consumer and non-adaptive top predator

The following equations should hold at equilibrium:

$$r_i - \alpha R_i^* C_i^* = 0 \tag{A17a}$$
$$m_C\left\{-f_C C_1^* + (1-f_C)C_2^*\right\} = 0 \tag{A17b}$$
$$0.5m_C\left\{-T_1^* + T_2^*\right\} = 0 \tag{A17c}$$

Equation A17c gives:

$$T_1^* = T_2^* = T^* \tag{A18}$$

Using this equation with Eq. A17b, we get:

$$\begin{aligned}
f_C &= \frac{1}{1 + e^{\theta_C\left\{\left(\alpha R_i^* - \beta T^*\right) - \left(\alpha R_j^* - \beta T^*\right)\right\}}} \\
&= \frac{1}{1 + e^{\theta_C \alpha\left(R_i^* - R_j^*\right)}}
\end{aligned} \tag{A19}$$

Given this, Eqs. A17a and A17b are identical to A10a and A10b. Thus, $R_1^*>R_2^*$ and $C_1^*>C_2^*$.

(f) Three-species model with an adaptive consumer and adaptive top predator

At equilibrium, it should hold that:

$$r_i - \alpha R_i^* C_i^* = 0 \tag{A20a}$$
$$m_C\left\{-f_C C_1^* + (1-f_C)C_2^*\right\} = 0 \tag{A20b}$$
$$m_T\left\{-f_T T_1^* + (1-f_T)T_2^*\right\} = 0 \tag{A20c}$$

Using Eq. A13a, Eqs. A13b and A13c are transformed to:

$$\begin{aligned}
\frac{C_2^*}{C_1^*} &= \frac{1}{f_C}-1 \\
&= \exp\left[\theta_C\left\{\alpha\left(\frac{r_2}{C_2^*}-\frac{r_1}{C_1^*}\right) + \beta\left(T_1^*-T_2^*\right)\right\}\right]
\end{aligned} \tag{A21a}$$

$$\frac{T_2^*}{T_1^*} = \frac{1}{f_T}-1 = \exp\left[\theta_T\left\{\alpha\left(C_2^*-C_1^*\right)\right\}\right], \tag{A21b}$$

respectively. Note, when $d(C_1+C_2)/dt=0$ and $d(T_1+T_2)/dt=0$, it should hold that $C_1+C_2=C_{\text{const}}$ and that $T_1+T_2=T_{\text{const}}$,

where C_{const} and T_{const} are constants. Using these equations, Eqs. A13c and A14a taken together give:

$$\frac{C_{const}}{C_1^*}-1 = \exp\left[\theta_C\left\{\alpha\left(\frac{r_2}{C_{const}-C_1^*}-\frac{r_1}{C_1^*}\right) + \beta\left(\frac{2T_{const}}{\exp\left[\theta_T\alpha\left(C_{const}-2C_1^*\right)\right]+1}-T_{const}\right)\right\}\right], \quad (A22)$$

LHS of Eq. A14b is a decreasing function of C_1^* with its limits, $\infty(C_1^*\to 0)$ and $0(C_1^*\to C_{const})$; RHS of Eq. A14b is an increasing function of C_1^* with its limits, $0(C_1^*\to 0)$ and $\infty(C_1^*\to C_{const})$. Therefore, there should exist a unique solution, C_1^*, for Eq. A14b.

It should generally hold that $T_1^*>T_2^*$ and, consequently, it should also hold that $C_1^*>C_2^*$ and that $R_1^*>R_2^*$ ($r_1/C_1^*>r_2/C_2^*$). This is proved as follows. First, assume that $T_1^*<T_2^*$. Then, using Eq. A14b, it should follow that $C_1^*<C_2^*$. However, if both $T_1^*<T_2^*$ and $C_1^*<C_2^*$ hold, then Eq. A14a never holds, suggesting that it should not hold that $T_1^*<T_2^*$. Next, assume that $T_1^*=T_2^*$. Then, using Eq. A14b, it should follow that $C_1^*=C_2^*$. However, if both $T_1^*=T_2^*$ and $C_1^*=C_2^*$ hold, then Eq. A14a should never hold, suggesting that it should not hold that $T_1^*=T_2^*$. Consequently, it is proven that $R_1^*>R_2^*$, $C_1^*>C_2^*$ and $T_1^*>T_2^*$ always hold.

References

Abrams PA (1993) Effects of increased productivity on the abundances of trophic levels. Am Nat 141:351–371

Abrams P (1995) Monotonic or unimodal diversity-productivity gradients: what does competition theory predict? Ecology 76:2019–2027

Abrams PA (2007) Habitat choice in predator–prey systems: spatial instability due to interacting adaptive movements. Am Nat 169:581–594

Abrams PA, Roth J (1994) The responses of unstable food chains to enrichment. Evol Ecol 8:150–171

Adler PB, Raff DA, Lauenroth WK (2001) The effect of grazing on the spatial heterogeneity of vegetation. Oecologia 128:465–479

Allesina S, Tang S (2012) Stability criteria for complex ecosystems. Nature 483:205–208

Alonzo SH (2002) State-dependent habitat selection games between predators and prey: the importance of behavioural interactions and expected lifetime reproductive success. Evol Ecol Res 4:759–778

Arditi R, Ginzburg LR (1989) Coupling in predator–prey dynamics: ratio-dependence. J Theor Biol 139:311–326

Bastolla U, Fortuna MA, Pascual-García A, Ferrera A, Luque B, Bascompte J (2009) The architecture of mutualistic networks minimizes competition and increases biodiversity. Nature 458:1018–1020

Bolker B, Holyoak M, Krivan V, Rowe L, Schmitz O (2003) Connecting theoretical and empirical studies of trait-mediated interactions. Ecology 84:1101–1114

Briggs CJ, Hoopes MF (2004) Stabilizing effects in spatial parasitoid–host and predator–prey models: a review. Theor Popul Biol 65:299–315

Cowie RJ, Krebs JR (1979) Optimal foraging in patchy environments. In: Anderson RM, Turner BD, Taylor RL (eds) Population dynamics. Blackwell Scientific Publications, Oxford, pp 183–205

Cressman R, Garay J (2009) A predator–prey refuge system: evolutionary stability in ecological systems. Theor Popul Biol 76:248–257

Cressman R, Křivan V, Garay J (2008) Ideal free distributions, evolutionary games, and population dynamics in multiple- species environments. Am Nat 164:473–489

DeAngelis DL, Persson L, Rosemond AD (1995) Interaction of productivity and consumption. In: Polis G, Winemiller KO (eds) Food Webs. Kluwer, Dordrecht, pp 109–112

deRuiter P, Wolters V and Moore J (2005) Dynamic food webs. Elsevier, Burlington

Fretwell SD, Lucas HL (1969) On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheor 19:16–36

Fretwell SD (1972) Populations in a seasonal environment. Princeton University Press, Princeton

Hairstone NG, Smith FE and Slobodkin LB (1960) Community structure, population control, and competition. Am Nat 94:421–425

Holt RD (1984) Spatial heterogeneity, indirect interactions, and the coexistence of prey species. Am Nat 124:377–406

Holt RD (1985) Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. Theor Popul Biol 28:181–208

Holt RD (1996) Food webs in space: an island biogeographic perspective. In: Polis G, Winemiller KO (eds) Food Webs. Kluwer, Dordrecht, pp 313–323

Hugie DM, Dill LM (1994) Fish and game: a game theoretic approach to habitat selection by predators and prey. J Fish Biol 45(Supplement sA):151–169

Iwasa Y (1982) Vertical migration of zooplankton: a game between predator and prey. Am Nat 120:171–180

Jackson AL, Ranta E, Lundberg P, Kaitala V, Ruxton GD (2004) Consumer-resource matching in a food chain when both predators and prey are free to move. Oikos 106:445–450

Johnson AR, Wiens JA, Milne BT, Crist TO (1992) Animal movements and population dynamics in heterogeneous landscapes. Landsc Ecol 7:63–75

Kacelnik A, Krebs JR, Bernstein C (1992) The ideal free distribution and predator–prey populations. Trends Ecol Evol 7:50–55

Kagata H, Ohgushi T (2006) Bottom-up trophic cascades and material transfer in terrestrial food webs. Eco Res 21:26–34

Křivan V (1997) Dynamic ideal free distribution: effects of optimal patch choice on predator–prey dynamics. Am Nat 149:164–178

Křivan V, Cressman R (2009) On evolutionary stability in predator–prey models with fast behavioural dynamics. Evol Ecol Res 11:227–251

Křivan V, Cressman R, Schneider C (2008) The ideal free distribution: a review and synthesis of the game-theoretic perspective. Theor Popul Biol 73:403–425

Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68:619–640

Lima SL (2002) Putting predators back into behavioral predator–prey interactions. Trends Ecol Evol 17:70–75

Lotka AJ (1925) Elements of physical biology. Williams and Wilkins Company, Baltimore

McCann KS, Rasmussen JB, Umbanhowar J (2005) The dynamics of spatially coupled food webs. Ecol Lett 8:513–523

McCann KS, Rooney N (2009) The more food webs change, the more they stay the same. Philos Trans R Soc B Bio Sci 364:1789–1801

Mittelbach GG, Osenberg CW, Leibold MA (1988) Trophic relations and ontogenetic niche shifts in aquatic ecosystems. In: Ebenman B, Persson L (eds) Size-structured populations. Springer, Berlin, pp 219–235

Morales JM, Moorcroft PR, Matthiopoulos J, Frair JL, Kie JG, Powell RA, Merrill EH, Haydon DT (2010) Building the bridge between animal movement and population dynamics. Philos Trans R Soc B 365:2289–2301

Mougi A, Kondoh M (2012) Diversity of interaction types and ecological community stability. Science 337:349–351

Mougi A, Kondoh M (2014) Stabilizing effect of competition-antagonism-mutualism hybrid community and the role of community network structure. J Theor Biol 360:54–58

Oksanen L, Fretwell SD, Arruda J, Niemelä P (1981) Exploitation ecosystems in gradients of primary productivity. Am Nat 118:240–261

Oksanen L (1990a) Exploitation ecosystems in seasonal environment. Oikos 57:14–24

Oksanen T (1990b) Exploitation ecosystems in heterogeneous habitat complexes. Evol Ecol 4:220–234

Persson L, Bengtsson J, Menge BA, Power ME (1996) Productivity and consumer regulation - concepts, patterns, and mechanisms. In: Polis G, Winemiller KO (eds) Food Webs. Kluwer, Dordrecht, p 396–434

Polis G, Winemiller KO (1995) Food webs. Kluwer, Dordrecht

Power M (1992) Top-down and bottom-up forces in food webs: do plants have primacy? Ecology 73:733–746

Rosenzweig ML (1971) Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. Science 171:385–387

Schmitz OJ, Hambäck PA, Beckerman AP (2000) Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. Am Nat 155:141–153

Sih A (1984) The behavioral response race between predator and prey. Am Nat 123:143–150

Strong DR (1992) Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. Ecology 73:747–754

Thébault E, Fontaine C (2010) Stability of ecological communities and the architecture of mutualistic and trophic networks. Science 329:853–856

van Baalen M, Sabelis MW (1999) Nonequilibrium population dynamics of "ideal and free" prey and predators. Am Nat 154:69–88

Volterra V (1926) Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. Mem R Accad Naz dei Lincei 2:31–113

Wang W, Takeuchi Y (2009) Adaptation of prey and predators between patches. J Theor Biol 258:603–613

Yodzis P (1984) Energy flow and the vertical structure of real ecosystems. Oecologia 65:86–88

Yodzis P, Innes S (1992) Body size and consumer-resource dynamics. Am Nat 139:1151–1175