

A patch-dynamic framework for food web metacommunities

Pradeep Pillai · Michel Loreau · Andrew Gonzalez

Received: 29 May 2009 / Accepted: 5 November 2009 / Published online: 5 December 2009
© Springer Science+Business Media B.V. 2009

Abstract The metacommunity concept has proved to be a valuable tool for studying how space can affect the properties and assembly of competitive communities. However, the concept has not been as extensively applied to the study of food webs or trophically structured communities. Here, we demonstrate how to develop a modelling framework that permits food webs to be considered from a spatial perspective. We do this by broadening the classic metapopulation patch-dynamic framework so that it can also account for trophic interactions between many species and patches. Unlike previous metacommunity models, we argue that this requires a system of equations to track the changing patch occupancy of the various species interactions, not the patch occupancy of individual species. We then suggest how this general theoretical framework can be used to study complex and spatially extended food web metacommunities.

Keywords Food webs · Metacommunities · Trophic interactions · Patch-dynamic models · Metapopulation theory · Predator–prey

Introduction

Metapopulation theory and patch-dynamic models were first introduced by Levins (1969) to explain the persistence of a single species in a spatially subdivided habitat. Since then, they have been used extensively as a spatially implicit

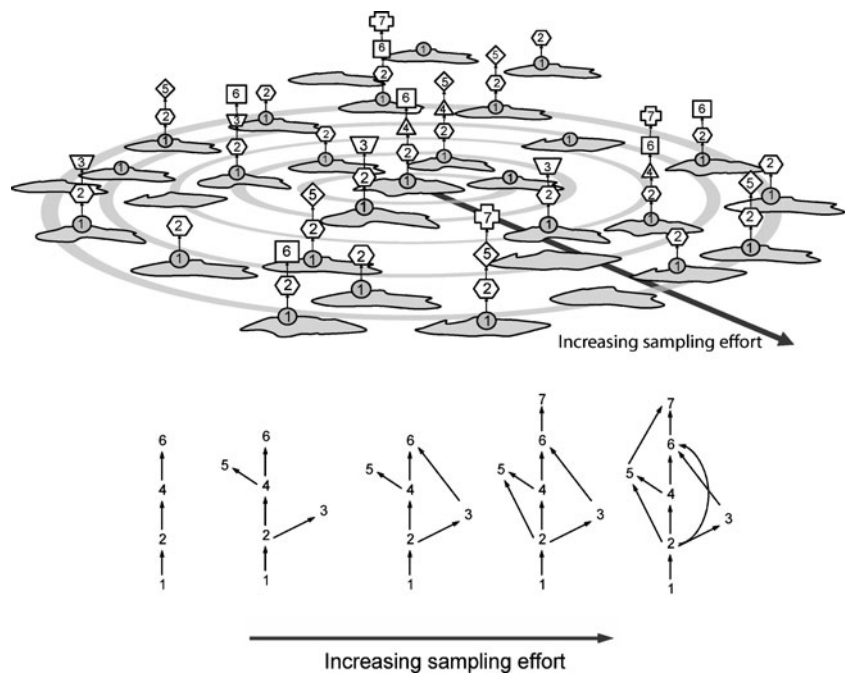
framework for studying how coexistence between a potentially unlimited number of competitors may arise at the regional scale despite competitive exclusion within local patches (Levins and Culver 1971; Hastings 1980; May and Nowak 1994; Tilman 1994). Despite the success of patch-dynamic models for competitive interactions, their application to trophic interactions has been more limited. Notable examples of the latter include Zeigler's (1977) and Crowley's (1979) studies of regional predator–prey persistence, May's (1994) study of the effects of habitat loss on predator and prey persistence, as well as similar studies on tritrophic chains by Holt (1997, 2002).

Incorporating trophic interactions into simple patch-dynamic metapopulation models can allow such models to serve as a metacommunity framework for investigating food webs, where local habitat patches no longer contain single *species* but local *food webs* linked to other patches through species dispersal. As such, the development of a patch-dynamic framework for food web metacommunities may provide a significant step towards broadening the scope of existing metacommunity theory (Leibold et al. 2004; Holyoak et al. 2005; Amarasekare 2008).

From a metacommunity perspective, food webs are comprised of numerous local food chains or subwebs connected by dispersal (Fig. 1). An approach that views food webs at large spatial scales as being the sum of numerous locally simple configurations may contribute to reconciling the contradiction between the complexity often observed in empirically compiled food webs and early theoretical expectations that food webs should be simple systems characterised by few interactions, short chain lengths and little or no looping (Gardner and Ashby 1970; Levins 1970; May 1972, 1973; Pimm and Lawton 1978; Lawton and Warren 1988). While several factors have been posited to explain this discrepancy between theoretical

P. Pillai (✉) · M. Loreau · A. Gonzalez
Department of Biology, McGill University,
1205 ave Docteur Penfield,
Montreal, QC H3A 1B1, Canada
e-mail: pradeep.pillay@mail.mcgill.ca

Fig. 1 Spatial food web model: a patch-dynamic approach allows a spatial perspective on food webs by viewing food webs as the regional aggregate of simpler, spatially distributed food chain configurations. The complexity of the full, spatially heterogeneous food web only emerges with increasing sampling effort at larger spatial scales



predictions and empirical observations (Pimm 1984; McCann et al. 1998; Loreau et al. 2002; Brose et al. 2006; Neutel et al. 2007; Otto et al. 2007; Allesina and Pascual 2008), the spatial structure of food webs is likely to be an important part of the explanation (Paine 1988; McCann et al. 2005).

Currently, most compiled food webs are aggregate representations of all possible feeding relationships over time and space. Although some meta-analyses (Schoenly and Cohen 1991) and theoretical studies (Michalski and Arditi 1995) have explicitly considered temporal variation, studies of spatial variation in food web architecture are relatively few (Warren 1989). Theoretical studies of the effects of space exist but are largely concerned with different spatial scales of predator and prey movement (McCann et al. 2005; Rooney et al. 2006). Despite the intense recent focus on the metacommunity concept, surprisingly, little theoretical attention has been paid to how food web structure may vary across a range of spatial scales in a metacommunity (Fig. 1). Here, we provide a general patch-dynamic framework for food web metacommunities.

From metapopulations to trophic metacommunities: extending the patch-dynamic framework

The underlying feature of all metacommunity models is the spatial subdivision of habitat into local patches and thus the division of a regional metacommunity into its local populations. Classic patch-dynamic metapopulation models

track the regional abundance of a species, measured as the fraction of patches occupied at the landscape level (Levins 1969). The basic differential equation for a single species mean-field metapopulation model is simply

$$\frac{dp}{dt} = cp(h - p) - ep, \quad (1)$$

where p is the regional abundance measured as the fraction of total habitat occupied ($0 \leq p \leq 1$), while c , e and h are, respectively, the colonisation rate, the extinction rate and the total fraction of patches that exist as suitable (non-destroyed) habitat ($0 \leq h \leq 1$; in the original Levins equation $h=1$). The first term gives the colonization rate of new patches due to the number of new colonisers that find available (unoccupied) habitat, while the second term gives the loss of occupied patches due to local extinction.

It has been relatively simple to extend the patch-dynamic approach to metacommunities governed by competitive interactions by simply adding an equation for each new competitor in the system and incorporating terms into each equation to account for the rate at which a species is competitively excluded from patches by superior competitors (Levins and Culver 1971; Hastings 1980; May and Nowak 1994; Tilman 1994). Attempts have been made to further extend the patch-dynamic formulation to encompass trophic interactions by similarly defining food webs using a system of differential equations to represent the rate of change in regional abundance of each species in the system: $\mathbf{dp}/dt = (\dot{p}_1, \dot{p}_2, \dots, \dot{p}_n)^T$, where $\dot{p}_i = dp_i/dt$ (Vandermeer 1973; Bascompte and Sole 1998; Swihart et al. 2001; Melian and Bascompte 2002). We argue that,

for trophically structured metacommunities, a system of equations tracking the changing patch occupancy of the various species will not work except in exceptional cases where each consumer species is either a specialist (i.e., has a single potential prey) or where the interactions between generalist consumers, and each of their resources are indistinguishable (all prey are interchangeable). We circumvent these limitations by presenting a framework that tracks the changing patch occupancies of various trophic interaction types, not species abundances.

A new framework based on the patch occupancy of interactions is required for two reasons. First, species within a local food web can be affected not only by the extinction of their immediate resource but also by all extinctions below it in the food chain. Keeping track of the rate of local extinctions for each species in the metacommunity requires determining the frequency of patch overlap between a given species and each of the species below it in the aggregate food web. Secondly, previous models (Vandermeer 1973; Swihart et al. 2001; Melian and Bascompte 2002) incorrectly determined the frequency of overlap between an interacting generalist predator and each of its resources by simply multiplying out each species’ density as though the densities represented independent probabilities, which will not be the case if the viability of either of the species involved in a consumer–resource interaction is in any way specially affected by the interaction itself.

Broadly speaking, there are two possible approaches to successfully incorporating trophic interactions into a patch-occupancy framework: One is to use a *state-transition model* (May 1994; Holt 1997, 2002) where the fraction of patches occupied by each possible trophic configuration, or community, is followed separately (in the simple case of a specialised predator–prey system, this would mean one equation to track the fraction of prey-only patches and another for the fraction of prey-plus-predator patches (May 1994)). The other is to follow the fraction of patches occupied by each feeding link or pairwise consumer–resource interaction, separately. This latter approach is the simplest possible and the one requiring the least number of equations to describe a metacommunity of trophic interactions. Below, we outline a general patch-dynamic model and then demonstrate its application to simple spatial food web modules.

A general metacommunity framework for food webs

A patch-dynamic approach views a food web as being partitioned into local trophic interactions and food chains, with the full complex food web only emerging as an aggregate of all local interactions at the metacommunity scale. The patch-dynamic approach thus offers one way of investigating

the emergence of complex food web networks within metacommunities composed of many patches.

We consider a food web showing all potential feeding links (Fig. 2) as a directed graph or a food web network, with the vertices of the graph representing species, and the directed edges, or arrows, representing the feeding links directed from the resource to the consumer. Each species vertex can be represented by a numerical index value, and each directed edge, or feeding link, by an ordered pair (i, j) indicating direction of feeding from i to j . The fraction of patches occupied by a given feeding link is thus $p_{(i, j)}$ (for the case of a basal species i subsisting or feeding in ‘empty’ habitat patches, h , the density of its feeding link is equivalent to the density of the basal species itself, i.e. $p_{(h, i)}=p_i$; see Fig. 2a, b). A food web graph represented by G can thus be defined by the expression $G=(V, E)$, where V is the set of all species vertices in the network, and E is the set of all directed feeding links.

The framework we introduce here focuses on a system of equations that follow patch occupancy of all pairwise interactions and not the various local food web configurations possible in the food web—as in a state-transition approach. The vertices in the corresponding food web graph thus represent *single species*. Although both approaches appear to represent two quite different perspectives, they both involve tracking the patch occupancy of the various *trophic interactions* and not the individual species in the network. As such, it is possible to combine the two approaches and move beyond tracking simple pairwise interactions in order to follow the patch occupancy of more complex trophic configurations.

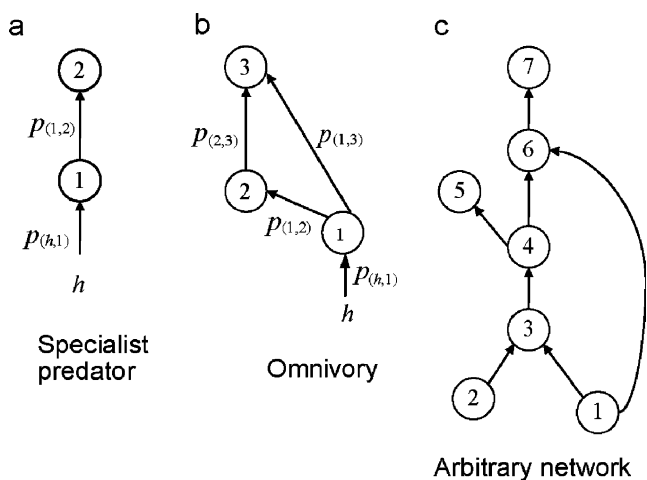


Fig. 2 Three simple trophic configurations. $p_{(i, j)}$ represents the regional density or patch occupancy of the pairwise feeding interaction (i is the resource and j the consumer); h represents available habitat. **a** Specialist predator–prey interaction. **b** Omnivory food web module with top predator able to persist in basal resource and intermediate consumer patches. **c** Example of an arbitrary trophic network

Formulating a general, yet reasonably workable metacommunity model requires certain simplifying assumptions. First, we assume that the food web graph is a directed acyclic graph, such that it exhibits no cannibalism (self-looping), mutual predation, or other non-transitive feeding loops (directed cycles of the form a ‘eats’ b , b ‘eats’ c , c ‘eats’ a) and such that the feeding links move from lower species indices to higher ones. Although empirically compiled food webs display numerous examples of cannibalism, mutual predation and looping, most such cases involve age-structured feeding interactions (e.g. feeding on juveniles by adults of the same or different species (Polis 1991)). We believe that our simplifying assumption is a reasonable starting point for our framework.

The types of food chain configurations possible within a local patch will be determined by the assumptions made regarding the mechanisms that allow for coexistence between consumers on a common resource. The basic model presented here assumes that habitat patches can contain only a single basal resource and that only one consumer can locally persist for each of the given resource species within a patch, as per the competitive exclusion principle. As a result, linear chains are the most complex configurations possible locally, though more complex topologies can emerge at the metacommunity scale. This is the simplest approach that would allow us to study the emergence of food web complexity at the metacommunity scale while making the fewest possible assumptions regarding specific local coexistence mechanisms. Adopting such a basic approach means that the trophic interactions that are tracked by the system of differential equations are simply the various pairwise trophic interactions between species.

Nevertheless, depending on the requirements of the food web system being modelled, the need to represent more complex *local* network topologies may arise due to the operation of mechanisms that are known to allow for more than one species to locally occupy and feed on a single resource species (e.g. resource partitioning, keystone predation, etc.). The basic model framework we introduce here can be extended to include such mechanisms, often by simply transforming the food web graph through the addition of new directed edges, and new consumer vertices representing local configurations of interacting species able to persist together on a single resource within a patch. As a result, additional differential equations will be required to track, not only the patch occupancy of pairwise interactions between species, but the patch occupancy of interactions between species and possible local configurations of coexisting species represented by the new vertices in the graph. Accounting for possible indirect effects between nonadjacent species (e.g. Holt 2002) similarly involves

extending our patch-dynamic framework to allow vertices to represent more than one interacting species at a time. The resulting differential equation system that arises by extending the model will still track pairwise interactions between *vertices* in the food web graph, but some of these vertices will now represent locally coexisting species instead of single species (Fig. 3).

However, the more the assumptions regarding strict competitive exclusion and the absence of indirect species interactions within patches are relaxed, and the more complex the local network configurations potentially become, the closer the modelling formulation will begin to resemble a state-transition approach, such that the trophic interactions tracked by the system of differential equations will now *primarily* involve pairwise interactions between local food web configurations rather than simple pairwise interactions between species. As the network complexity permitted within local patches increases maximally, the model formulation will eventually become indistinguishable from a state-transition model.

Below, we present our general model before moving on to demonstrate the approach for the simple food web configurations shown in Fig. 2. The overall approach of the model is to follow the rate of change in the density, or the patch occupancy, of the pairwise interactions between two trophically interacting species i and j , as represented by $dp_{(i,j)}/dt$. Changes in the patch occupancy of the (i,j) interaction results from a net balance between, on the one hand, the loss of the (i,j) interaction in patches due to the total number of local extinctions experienced by both i and j arising from patch extinctions, top-down predator effects and competitive displacement of either species and, on the other hand, the birth of new (i,j) interactions due to food chain reassembly following either local extinctions of other species or the colonisation of the i or j species into new patches. The basic form of the differential equation that follows the rate change in metacommunity abundance of the pairwise interaction between a given species j feeding on a species i can be represented by the following linear combination of terms

$$\frac{dp_{(i,j)}}{dt} = A - B - C + D + E - F - G - H. \quad (2)$$

Each of the terms in Eq. 2 represents an algebraic expression giving the rate of increase or decrease in the fraction of patches occupied by the (i,j) interaction due to various factors. All the algebraic expressions corresponding to each term in Eq. 2 are given in Table 1. The various model parameters and variables seen in Table 1 are defined in the description of the model below and are summarised again in Table 2.

Terms A and B are the most basic terms common to all single species mean-field patch-dynamic models. Term C

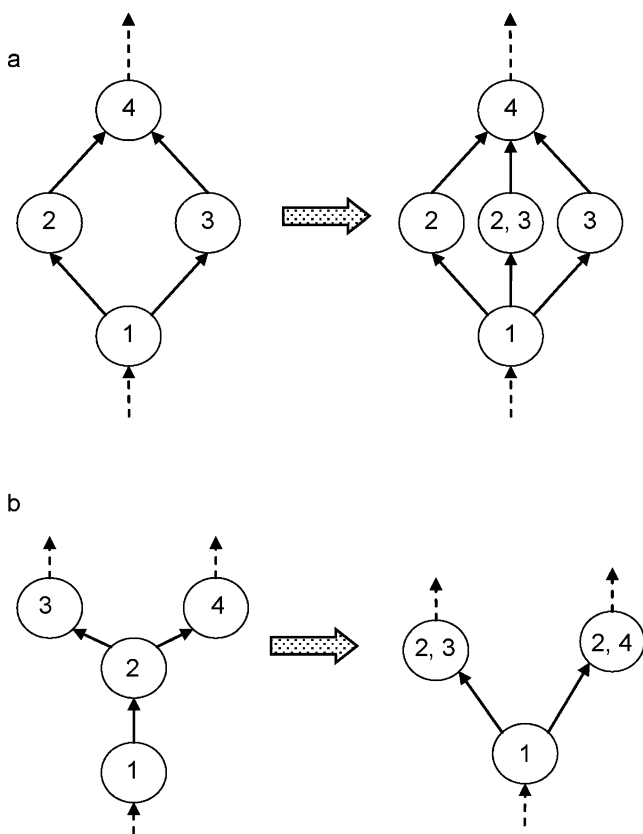


Fig. 3 Transforming food web graphs in order to allow vertices to represent more than one species at a time. **a** Example of coexistence of more than one consumer on a local resource. If species 2 and 3 can locally coexist together on a single resource 1 patch due to some form of resource partitioning, then the food web network on the left can be transformed by the addition of a new vertex and new directed feeding links to represent both the co-occurrence of 2 and 3, and the trophic interactions that the co-occurring species will have with common resources and potential consumers. The model’s differential equation system will still track the proportion of patches occupied by the pairwise interactions between vertices, though now some of these vertices will represent groups of co-existing species. **b** Example of indirect interactions between nonadjacent species in a food web. If the local interactions in a patch between species 1 and 2, shown in the network on the left, varies depending on whether consumer 3 or 4 is currently feeding on 2, then species 3 and 4 indirectly interact with species 1 [for example, by affecting the top-down predator induced extinction rate that 2 has on 1 (Holt 2002)] The model outlined in the text can be extended to account for these indirect interactions by simply transforming the food web graph on the left into the one on the right. The transformation is similar to that of creating a directed line graph and involves converting pairwise interactions between species in the graph on the left into new vertices. Again, the differential equation system of the model would still track the patch occupancy of pairwise interactions between vertices, but now, some of the vertices will represent trophically interacting pairs of species

extends the single species model to multiple competitor species (Levins and Culver 1971; Hastings 1980; May and Nowak 1994; Tilman 1994). Terms *D* to *H* include trophic interactions between multiple species, essentially transforming a mean-field metapopulation model into a meta-

community model. Of these latter terms, term *H* gives the added extinction rate experienced by a species due to the effects of top-down predation (Bascompte and Sole 1998), while terms *F* and *G* give the loss that a consumer species feeding on a particular resource experiences due to extinction of species further down the trophic chain. Terms *D* and *E* give the gain of patches containing the (*i*, *j*) interaction due to the reassembly of feeding links that follows species extinctions (term *D*) or competitive displacement (term *E*) in a trophic chain.

To understand the algebraic expressions given in Table 1, consider the graph of the food web network represented in Fig. 2c, where the set of all species vertices, *V*, and the set of all feeding links, *E*, are given by $V = \{1, 2, 3, \dots, 7\}$, and $E = \{(1, 3), (2, 3), \dots, (6, 7)\}$. For any species *i* in the network, we can let *C*(*i*) denote the set of all potential consumers of *i* (all the species at the terminal end of the links directed away from *i*). There is a competitive coefficient value $v_{j,i}$ associated with every element *j* in *C*(*i*), such that if $v_{j,i} > v_{k,i}$, then *j* is a better competitor for *i* than *k* is. It is possible that some of the directed paths in a network, like that depicted in Fig. 2c, will represent food chain sequences that cannot exist within a local patch. This arises in situations where a path from one species to another can be bypassed directly. For example, in Fig. 2c, the directed path 1, 3, 4, and 6 can be bypassed by the single link (1, 6). If species 6 is a better competitor for species 1 than 3 ($v_{6,1} > v_{3,1}$), then the chain sequence 1, 3, 4, and 6 cannot exist locally since 6 will always out compete 3. If, however, generalist consumers with higher indices are assumed to be inferior competitors for the prey further down in their food chains than other potential consumers with lower indices, then all the possible directed paths in the graph represent food chain sequences that are locally viable. To avoid the complications arising from non-permissible food chain sequences, we will adopt, for the time being, a working assumption that higher generalist consumers are less competitive or efficient at consuming species further down the food chain than lower level consumers. We show later how to apply our framework when this assumption is relaxed.

In the set of ordinary differential equations represented by Eq. 2 and described in Table 1, $c_{j,i}$ and $e_{j,i}$ are, respectively, the colonisation rate and the extinction rate that species *j* experiences in resource *i* patches, while $\mu_{j,i}$ gives the top-down effect of *j* on *i*, or the added rate of local extinction experienced by *i* due to consumption by *j*. We also represent the fraction of all *j* patches where the *j* consumer is feeding on resource *i* as

$$\rho(i, j), \text{ where } \rho(i, j) = \frac{P(i, j)}{\sum_{k \in R(j)} P(k, j)} = P(i, j) / p_j, \text{ such that } \sum_{k \in R(j)} \rho(k, j) = 1. \text{ Here, } R(j) \text{ is the set of all potential}$$

Table 1 Equation 2 details

Terms in Eq. 2	Description	Mathematical Expression
A	Increase in (i, j) interaction due to colonization of new i patches by j	$\sum_{k \in R(j)} c_{j,i} P(k,j) \left(\sum_{l \in R(i)} P(l,i) - \sum_{m \in C(i)} P(i,m) (1 - \zeta_i(j,m)) \right)$
B	Loss of (i, j) due to local extinctions of consumer j on i patches	$(e_{j,i} + \mu_{j,i}) P(i,j)$
C	Loss of (i, j) due to displacement of j by superior competitors	$P(i,j) \left(\sum_{k \in C(i)} \sum_{l \in R(k)} (c_{k,l} P(l,k) \zeta_i(k,j)) \right)$
D	Increase in (i, j) due to prey-switching by j onto i , from alternate resources, because of community reassembly following species extinctions	$\sum_{k \in R(j)} \left(P(k,j) \sum_{l \in C(i)} \sum_{m \in C(l)} \rho(l,m) (\mu_{m,l} + \rho(i,l) e_{l,i}) \Phi_{m,k}^i \right)$
E	Increase in (i, j) due to prey-switching by j onto i from alternate resources because of successful invasion of communities by i	$\sum_{k \in R(j)} \left(P(k,j) \sum_{q \in R(i)} \sum_{r \in C(q)} \sum_{l \in R(i)} c_{i,l} P(l,i) \zeta_q(i,r) \Phi_{r,k}^i \right)$
F	Decrease of (i, j) due to loss of resource i and other species further down trophic chain from extinction and top-down predator effects	$P(i,j) \sum_{s < i} \sum_{t \in C(s)} \left(\rho(s,t) (\mu_{t,s} + \sum_r \rho(r,s) e_{s,r}) \Phi'_{t,i} \right)$
G	Decrease in (i, j) due to loss of resource i , and other species further down trophic chain, from competitive displacement by superior competitors	$P(i,j) \sum_{t \leq i} \left(\sum_{s \in R(t)} \sum_{m \in C(s)} \sum_{q \in R(m)} c_{m,q} P(q,m) \zeta_s(m,t) \Phi_{t,i}^m \right)$
H	Loss of (i, j) due to extinctions caused by top-down effect of predators on consumer j	$P(i,j) \sum_{r \in C(j)} \mu_{r,j} P(j,r)$

resources of consumer j (i.e. the set of all species with links directed towards j). In other words, we can associate for every directed feeding link in the food web graph both a value for the proportion of patches occupied by that link, $p(i, j)$, and a value representing the fraction this link is of all other feeding links flowing into that consumer vertex, $\rho(i, j)$.

The large number of summations in the model, as formulated in Table 1, arises as a result of both the general and arbitrarily complex nature of the network being represented, as well as from the need to account for how extinctions further down each of the various possible food chains in the network can affect the viability of the (i, j) interaction. In order to be able to properly account for the effects that all extinctions below a given pairwise interaction in a food web will have on the overall abundance of that interaction, we will need to consider further our food web network graph, $G=(V, E)$. Imagine a directed path, or a sequence of directed feeding links $(s, s_1), (s_1, s_2), (s_2, s_3), \dots (s_m, t)$ in G , starting at species s and ending in species t . We can define $T_{s,t}$ as the *directed path* denoted by the sequence of species, $s, s_1, s_2, s_3, \dots, s_m, t$ along this feeding chain. The union of *all* possible directed paths along the feeding links in the food web between species s and t is $S_{s,t}$, i.e. $S_{s,t} = \bigcup_{i \in I} (T_{s,t})_i$ (here, I is an index set). $S_{s,t}$ is thus a subgraph of the food web G such that its set of feeding links, $E_{s,t}$, and species vertices, $V_{s,t}$, are subsets of E and V , ($V_{s,t} \subseteq V$ and $E_{s,t} \subseteq E$).

The *fraction* of all t -occupied patches containing the food chain sequence represented by $T_{s,t}$ can be represented by $f(T_{s,t})$. We can calculate the value of $f(T_{s,t})$ by multiplying all the ρ values corresponding to all the pairwise feeding links along the food chain, i.e. $f(T_{s,t}) = \prod_{(m,n) \in E_T} \rho(m,n)$. Thus, $f(S_{s,t})$ is the fraction of all t -occupied patches that have a food chain sequence starting at s and ending in t , giving us

$$f(S_{s,t}) = \sum_{T_{s,t} \subset S_{s,t}} \left(\prod_{(m,n) \in E_T} \rho(m,n) \right). \tag{3}$$

The density of patch overlap between any (i, j) interaction, and any given species k below it in the network is $p(i, j)f(S_{k,i})$. For convenience, we define $f(S_{k,k})=1$, and in the case where there exists no directed path between two species l and k , $f(S_{l, k})=0$.

It would appear that calculating the rate at which a species k 's extinction rate, further down in the food chain, will drive the (i, j) interaction locally extinct simply involves multiplying the rate at which k goes extinct with $p(i, j)f(S_{k,i})$. However, one must account for how possible food chain reassembly below the i species will prevent the (i, j) interaction from going extinct. This occurs when intermediate species between k and i switch their feeding to k 's resource l as k goes locally extinct. Therefore, measuring the effect of k 's extinction rate on i requires us to know the *net* fraction of patches where k and i overlap

Table 2 Summary of Eq. 2 parameters and food web network variables

Parameters and variables	Description
$P_{(i,j)}$	Proportion of patches containing the (i, j) interaction, i.e. species j feeding on species i
$c_{j,i}$	Rate of coloniser production by species j when on resource i patches
$e_{j,i}$	Rate of local extinctions experienced by species j when on resource i patches
$\mu_{j,i}$	Added local extinction rate experienced by species i due to effects of top-down predation of consumer j on resource i
$R(i)$	Set of all resource species that consumer j can locally persist on
$C(i)$	Set of all consumer species that can feed and locally persist on resource species i
$P_{(i,j)}$	Fraction of all j -occupied patches where j feeds on resource species i : $P_{(i,j)} = P_{(i,j)} / \sum_{k \in R(i)} P_{(k,j)}$
$\zeta_i(k, j)$	Competition function giving the probability that an invasive consumer k can displace consumer j from an i resource patch
$\Phi_{k,i}^l$	Fraction of patches where species k 's extinction on an l resource patch leads to extinction of species i further up food web. (see Eq. 4 and text for details)

yet where no intermediate species can switch its consumption towards k 's resource l after k goes locally extinct. This is represented in Eq. 4 by $\Phi_{k,i}^l$:

$$\Phi_{k,i}^l = f(S_{k,i}) - f\left(\bigcup_{m \in C(l)} (S_{k,m} \cup S_{m,i})\right). \tag{4}$$

Here, $\bigcup_{m \in C(l)} (S_{k,m} \cup S_{m,i})$ is a subgraph of $S_{k,i}$ representing all the directed paths between k and i that are also connected to k 's resource species l . Thus, by extension, $\Phi_{k,i}^l$ represents the largest subgraph between vertices k and i that is *not* directly connected (i.e. has no direct feeding links) to k 's resource l (see Appendix A for details).

Returning to Eq. 2, and to the expressions in Table 1, the A term, $\sum_{k \in R(j)} c_{j,i} P_{(k,j)} \left(\sum_{l \in R(i)} P_{(l,i)} - \sum_{m \in C(i)} P_{(i,m)} (1 - \zeta_i(j, m)) \right)$, gives the increase in (i, j) interactions due to successful colonisation of new i -occupied patches by j colonisers. The summed expression $\sum_{k \in R(j)} c_{j,k} P_{(k,j)}$ gives the total number of j colonisers produced by all the patches where j feeds on each of its possible resource k species. The expression acknowledges that local j populations feeding on different resource k species can produce different amounts of colonisers depending on the quality of the local resource species. The expression given in brackets in the A term describes the amount of resource i patches available for colonisation by j , which is equal to the total amount of resource i patches, $\sum_{l \in R(i)} P_{(l,i)}$, minus the density of i patches that are already being fed on by a superior competitor m species, $\sum_{m \in C(i)} P_{(i,m)} (1 - \zeta_i(j, m))$. The expression $\zeta_i(j, m)$ is a competition function determining the outcome of an attempt by an invasive j to displace a resident m from an i resource patch. Here, we assume the simple case where $\zeta_i(j, m)$ is a discrete step function, which is equal to 1 when invasive j is a superior competitor for i , able to successfully displace m and 0 when species m is the superior competitor, resistant to invasion by j :

$$\zeta_i(j, m) = \begin{cases} 1 & \text{if } v_{j,i} > v_{m,i} \\ 0 & \text{if } v_{j,i} \leq v_{m,i} \end{cases}$$

where $v_{j,i}$ is the competition coefficient of j for resource i . Although, here, $\zeta_i(j, m)$ is defined as a discrete function, it can also be defined to take on any value between 0 and 1 depending on the competition rules regarding site preemption (Calcagno et al. 2006).

The B term in Eq. 2, $(e_{j,i} + \mu_{j,i}) P_{(i,j)}$, gives the loss of (i, j) interactions due to the extinction rate j experiences on i , $e_{j,i}$ and the rate at which j drives resource i locally extinct, $\mu_{j,i}$.

The C term, $P_{(i,j)} \left(\sum_{k \in C(i)} \sum_{l \in R(k)} (c_{k,l} P_{(l,k)} \zeta_i(k, j)) \right)$, gives the

loss of (i, j) due competitive displacement of j from i patches by a superior competitor k [$\zeta_i(k, j)=1$]. This C term gives the total number of k colonists that are produced, $c_{k,l} P_{(l,k)}$, summed over all patches containing possible l resources of k that are currently occupied by the (l, k) interaction and further summed over all the possible k consumers that can feed on i .

D and E give the rate at which the consumer j switches local feeding from some other prey resource k to i because of local food chain reassembly following extinctions further down the food chain (term D) or competitive displacement of species further down the food chain by i colonisers (term E). Both terms are summed over all the relevant food chain densities given by $\Phi_{m,k}^i$. In the D term given

by $\sum_{k \in R(j)} \left(p_{(k,j)} \sum_{l \in C(i)} \sum_{m \in C(l)} \rho_{(l,m)} (\mu_{m,l} + \rho_{(i,l)} e_{l,i}) \Phi_{m,k}^i \right)$, the

expression $\rho_{(l,m)} (\mu_{m,l} + \rho_{(i,l)} e_{l,i}) \Phi_{m,k}^i$ gives the total frequency at which the extinction of a species l feeding on i below the (k, j) interaction in food web network will lead to j switching its feeding onto i because no other potential species between i and j is able to switch its feeding to i . This is summed over all the potential m consumers of l , which can drive l extinct through top-down effects, and all the possible l species that are currently consuming i . This total frequency is multiplied by the total fraction of patches where j is currently feeding on a resource k , $p_{(k, j)}$, summed for all k resources that have a higher index value than i . In the term E ,

given by $\sum_{k \in R(j)} \left(p_{(k,j)} \sum_{q \in R(i)} \sum_{r \in C(q)} \sum_{l \in R(i)} c_{i,l} p_{(l,i)} \zeta_q(i, r) \Phi_{r,k}^j \right)$,

the expression $c_{i,l} p_{(l,i)} \zeta_q(i, r) \Phi_{r,k}^j$ gives the rate at which i coloniser invasives displace, in the food web network below the (k, j) interaction, r consumers feeding on q resource patches and where no potential consumer between i and j can, as a result, switch their feeding towards i . The total i coloniser production is summed over all potential l resources, and $\zeta_q(i, r) \Phi_{r,k}^j$ is summed over all possible r and q .

The F and G terms give the rate at which extinction or displacement of species further down the food chain cause the loss of (i, j) (see Appendix A for example). The term $F = p_{(i,j)} \sum_{s < i} \sum_{t \in C(s)} \left(\rho_{(s,t)} (\mu_{t,s} + \sum_r \rho_{(r,s)} e_{s,r}) \Phi_{t,i}^s \right)$ gives the

extinction rate of the (i, j) interaction due to the frequency of extinctions experienced by each species s below (i, j) . The total extinction rate of an s species that will lead to extinction of (i, j) is given by $\rho_{(s,t)} (\mu_{t,s} + \sum_r \rho_{(r,s)} e_{s,r}) \Phi_{t,i}^s$. This expression is summed over all the possible t consumers of s that can potentially drive s extinct from top-down effects, and over all the possible s species below i in the network. The

term $G = p_{(i,j)} \sum_{l \leq i} \left(\sum_{s \in R(t)} \sum_{m \in C(s)} \sum_{q \in R(m)} c_{m,q} p_{(q,m)} \zeta_s(m, t) \Phi_{t,i}^m \right)$

gives the rate at which m colonists invade and competitively displace potential t species below the (i, j) interaction in the

network. The expression $c_{m,q} p_{(q,m)} \zeta_s(m, t) \Phi_{t,i}^m$ gives the frequency of patches where m colonists competitively displace t consumers but where no potential species exists between t and i that can switch its feeding towards m , thus resulting in extinction of the (i, j) interaction. This expression is summed over all q resources that allow m coloniser production and over all potential s resources that can sustain t and m consumers, as well as all t consumers where $t < i$.

Finally, the last term, $H = \rho_{(i,j)} \sum_{r \in C(j)} \mu_{r,j} p_{(j,r)}$, gives the loss of (i, j) suffered due to top-down effects of all r predators feeding on j . For simple food web networks, the system of differential equations can be defined by inspection of the corresponding food web graph (see Appendix B for a demonstration). For arbitrarily complex networks with numerous species, however, a computer algorithm would be required to define the system of differential equations. Both Appendices A and B provide a more detailed demonstration in applying the terms in Eq. 2 to examples of food web networks.

Relaxing the assumption regarding competitive ranking

If we relax the assumption of a competitive hierarchy based on species indices, we can no longer assume that the patch density of any particular food chain sequence can be calculated from the product of all the ρ values along the path defining that food chain. For example, in Fig. 2c, if species 6 is a better competitor for species 1 than 3, then the density of the chain defined by 1, 3, 4, and 6 will be 0, and not $p_{(4,6)} p_{(1,3)}$, as assumed in Eq. 3. Similarly, the density of the chains 2, 3, 4, and 6 will be $p_{(4,6)}$, and not $p_{(4,6)} p_{(2,3)}$. To simplify the calculations needed to determine the chain densities and patch overlap of species (particularly important in order to avoid an excessively large number of calculations during numerical simulations of the ordinary differential equation system), we can transform the food web graph so that no directed path will represent an a priori impossible food chain configuration. The transformation involves splitting existing paths and creating new vertices and edges. An example of an algorithm to carry out the transformation is given in Appendix C.

Exploring simple food web models

We demonstrate the application of the general patch-dynamic framework with examples of simple food web modules shown in Fig. 2. In the case of the specialised predator-prey system shown in Fig. 2a, the system of equations is

$$\frac{dp_1}{dt} = c_1 p_1 (h - p_1) - e_1 p_1 - \mu_{2,1} p_{(1,2)}, \tag{5a}$$

$$\frac{dp_{(1,2)}}{dt} = c_{2,1}p_{(1,2)}(p_1 - p_{(1,2)}) - e_{2,1}p_{(1,2)} - (e_1 + \mu_{2,1})p_{(1,2)}. \tag{5b}$$

[Note that, here, the densities of feeding links are interchangeable with the density of species, i.e. $\dot{p}_{(h,1)} = \dot{p}_1$ (prey) and $\dot{p}_{(1,2)} = \dot{p}_2$ (predator)]. This formulation is similar to the predator prey model of Bascompte and Sole (1998), where the predator as a resource specialist can only persist in patches that remain occupied by its prey; if a local prey population goes extinct in a predator-occupied patch, the local predator population is then expected to immediately go extinct. As a result, predator patches constitute a subset of total prey patches. However, Bascompte and Sole overlooked the effect that prey resource extinctions will have on predator extinction rates (third term in Eq. 5b). Not accounting for this added extinction rate means that predators can persist in patches without their prey.

The equilibrium densities of the prey \hat{p}_1 and predator \hat{p}_2 can be easily solved, giving us $\hat{p}_1 = 1/2(Z + \sqrt{Z^2 + 4\mu(e_1 + e_2 + \mu)/c_1c_2})$ and $\hat{p}_2 = \hat{p}_1 - (e_1 + e_2 + \mu_{2,1})/c_2$, where $Z = (h - e_1/c_1 - \mu_{2,1}/c_1)$. The behaviour of this specialist predator–prey system can be strikingly different from that expected of Bascompte and Sole’s (1998) formulation of the same system. The equilibrium abundances of both predator and prey for increasingly strong predator-induced extinction rates, μ , are shown for both formulations in Fig. 4a and b. Increasing μ values indicate an increasingly unstable and extinction prone local predator–prey interaction. For the original Bascompte and Sole (1998) formulation (Fig. 4a), both the equilibrium predator and prey abundances decrease in parallel as μ increases. For the corrected formulation given by Eq. 5a and 5b (Fig. 4b) equilibrium predator abundances drop rapidly towards regional extinction as the locally unstable nature of the predator–prey interaction increases, while equilibrium abundances for the prey only show a small decrease before returning to maximum patch occupancy at the regional scale. In short, despite driving both predator and prey locally extinct, strongly destabilising interactions are likely to have a disproportionately stronger metacommunity effect on the predator compared to the prey. This would imply that a specialist predator would be far more extinction prone than a prey species in the face of habitat loss and that specialist predators could potentially experience a stronger fitness advantage to dispersing more rapidly than their focal prey, which would experience little or no such fitness advantage.

We can compare the responses of a specialist predator to cases where the focal consumer–resource interaction is embedded in a more complex trophic network, such as when the predator can potentially survive in alternative

prey patches. Figure 4c and d shows the results of increasing μ values on focal predator and prey abundances when both are a part of the omnivorous module shown in Fig. 2b. The predator (species 3) is now a generalist predator able to subsist on focal prey species 2 and basal resource 1. This gives a four-equation system:

$$\frac{dp_1}{dt} = c_1p_1(h - p_1) - e_1p_1 - \mu_{2,1}p_{(1,2)} - \mu_{3,1}p_{(1,3)}, \tag{6a}$$

$$\begin{aligned} \frac{dp_{(1,2)}}{dt} &= c_2p_{(1,2)}(p_1 - p_{(1,2)}) - e_2p_{(1,2)} \\ &\quad - (e_1 + \mu_{2,1})p_{(1,2)} - \mu_{3,2}p_{(2,3)}, \end{aligned} \tag{6b}$$

$$\begin{aligned} \frac{dp_{(2,3)}}{dt} &= (c_{3,2}p_{(2,3)} + c_{3,1}p_{(1,3)}) \cdot (p_{(1,2)} - p_{(2,3)}) \\ &\quad + c_{2,1}p_{(1,2)}p_{(1,3)} - e_{3,2}p_{(2,3)} \\ &\quad - (e_1 + e_2 + \mu_{2,1} + \mu_{3,2})p_{(2,3)}, \end{aligned} \tag{6c}$$

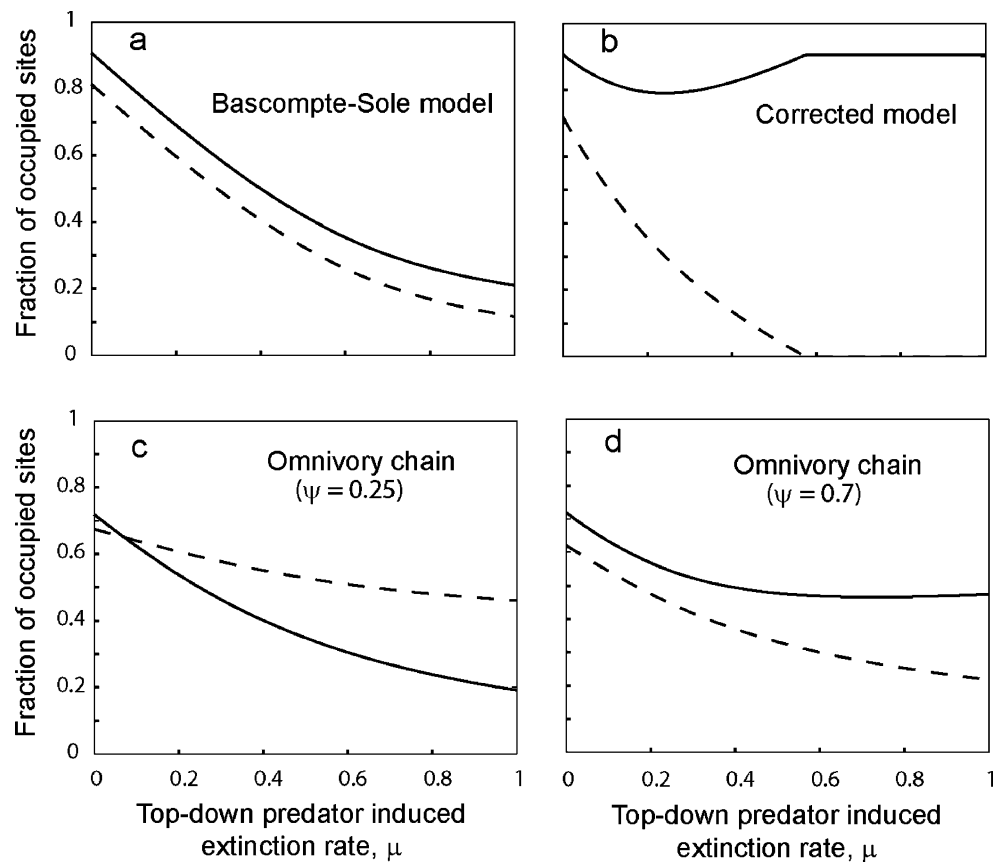
$$\begin{aligned} \frac{dp_{(1,3)}}{dt} &= (c_{3,2}p_{(2,3)} + c_{3,1}p_{(1,3)}) \cdot (p_1 - p_{(1,2)} - p_{(1,3)}) \\ &\quad + (e_2 + \mu_{3,2})p_{(2,3)} - e_{3,1}p_{(1,3)} \\ &\quad - (e_1 + \mu_{3,1})p_{(1,3)} - c_2p_{(1,2)}p_{(1,3)}. \end{aligned} \tag{6d}$$

For convenience, the density of basal resource 1 is given by p_1 instead of $p_{(h,1)}$, and the colonization and extinction rates of species 1 and 2 are given as c_1 and e_1 and c_2 and e_2 , respectively. The top–down extinction rate of resource i caused by consumer j is represented by $\mu_{j,i}$. Note that since predator 3 can subsist on two resource types, predator 3’s total colonization rate is the result of colonist production in both its resource patches (first terms in Eqs. 6c and 6d).

We assume in this module that predator 3 has a preference for prey 2, such that if a patch where 3 is feeding on basal resource 1 is invaded by the focal prey 2, then predator 3 will switch feeding towards 2 (second term in Eq. 6c and fifth term in Eq. 6d). Similarly, extinction of species 2 in patches with the (3, 2) interaction results in predator 3 switching its feeding towards basal resource 1 (second term in Eq. 6d). Thus, an occupied local patch can have one of four possible food chain configurations present: (1), (1, 2), (1, 2, 3), and (1, 3).

Following Swihart et al. (2001), we represent the extinction rate that predator 3 has on its alternate resource 1 as equalling the extinction rate it experiences on its preferred prey 2 ($e_{3,2} = e_3$), plus an added extinction rate, ψ , experienced due to feeding on a non-preferred resource: $e_{3,1} = e_3 + \psi$.

Fig. 4 Graphs showing predator and prey densities for increasing top-down or predator-induced extinction rates, μ . The *dashed line* represents the focal predator and *solid line* the focal prey. **a** Predator and prey densities for the original Bascompte and Sole (1998) formulation. **b** Predator and prey densities for corrected formulation (Eqs. 5a and 5b). **c** Densities shown for top predator and focal prey in omnivory module (Eqs. 6a, 6b, 6c, and 6d), when top predator is a strong generalist (low ψ value; $\psi=0.25$). **d** Densities shown for top predator and focal prey in omnivory module when top predator is a weak generalist (high ψ value; $\psi=0.7$). Parameter values for all graphs: $h=1$, $c_1=c_2=0.8$, $e_1=e_2=0.075$ and for the omnivory module $c_{3,2}=c_{3,1}=0.8$ and $e_{3,2}=e_{3,1}=0.075$



The responses of the focal predator and prey system to increasing instability and extinction rates (increasing $\mu_{3,2}$ values) in Fig. 4c and d shows how, with an alternative prey source, the predator at the metacommunity scale can avoid being driven to extinction by the locally strong interactions experienced with its focal prey. Now, the predator can exert a stronger effect on the regional abundance of its prey. The degree to which each focal species affects the other's metacommunity abundance and persistence depends upon the viability of the predator on its non-preferred, alternate resource, ψ : If ψ is small (predator very viable on the alternate resource), then locally strong interactions will have a greater regional effect on the prey than predator (stronger metacommunity top-down effect), while the opposite is the case if ψ is large (not viable on alternate resource).

Spatial subdivision of habitat and colonisation-extinction dynamics have long been suspected of allowing strong, extinction prone predator-prey interactions to persist at the landscape level despite frequent local extinctions of both predator and prey in individual patches (Huffaker 1958). We have demonstrated here, with a simple patch-dynamic formulation, how simple variation in the trophic structure connecting focal predators and prey to other species will translate that local effect into metacommunity level abundances and persistence.

By exploring two simple food web configurations, we were able to demonstrate the importance of properly accounting for both the distribution of species interactions and the rate of species extinctions within food webs when formulating a patch-dynamic model of food web metacommunities. The power of the approach introduced here, however, lies in its ability to provide a general framework that can be applied to arbitrarily complex food web configurations. The effects that the spatial subdivision of habitat and the spatial variability of trophic interactions can have on both the assembly and dynamics of large, highly reticulated food web metacommunities can now be tackled from a classic metapopulation perspective.

Discussion

Both the temporal and spatial scales assumed by ecological models can be deciding factors in their ability to explain or describe the mechanisms underlying the population and community-level dynamics observed in the field. Michalski and Arditi (1995) demonstrated how dynamic food webs that undergo changes in network configurations on their way to equilibrium can exhibit great temporal variation in terms of species diversity and connectivity. Sampling such a system over greater and greater time scales would result

in compiled webs of increasing complexity as a greater share of all the possible links and species become included in the web. Similarly, models that incorporate the effects of space are valuable for investigating how food webs assemble, and what properties emerge, when the trophic interactions are spatially distributed.

A metacommunity approach to modelling trophic interactions will be indispensable if theoretical studies are to start incorporating more realistic spatial aspects of natural food webs. The question of how a metacommunity model of trophic interactions should be formulated though will ultimately depend upon the assumptions made regarding species movement and interactions at large spatial scales. Relatively rare dispersal between patches implies that the dynamics within patches are fairly independent of each other. Under these circumstances, a modelling approach that focuses on colonisation–extinctions dynamics occurring within a metacommunity is a powerful simplification. A patch-dynamic framework is thus most appropriate to systems where habitat patches are sufficiently separated from each other by an intervening ‘inhospitable’ matrix, and dispersal and colonisation between patches is rare enough that it does not affect local dynamics, such as occurring at ‘larger’ spatial scales within fragmented landscapes or island systems.

The assumptions underlying a patch-dynamic approach make it particularly well-suited for metacommunity systems displaying strong *species sorting* behaviour, where regional dispersal is sufficient enough to allow species to track suitable habitat patches in a heterogeneous landscape, yet not strong enough to overwhelm the local, deterministic effects of species interactions and community assembly (Leibold et al. 2004). Conversely, we would expect the usefulness of the patch-dynamic approach to break down for those metacommunities where movement and colonisation *between* patches increases to the point where the dynamics occurring *within* patches become linked with one another (Keeling 2002). Relaxing the metapopulation assumption regarding patch movement necessitates a shift towards modelling frameworks that more explicitly consider how within patch dynamics are linked by the patch movement of one or more species (for example, Mouquet and Loreau 2002, 2003; Loreau et al. 2003; Guichard 2005; Koelle and Vandermeer 2005; McCann et al. 2005; Rooney et al. 2006; Gouhier et al., *in press*).

Evidence of species sorting has been observed for both natural and experimentally manipulated metacommunity systems. Van der Gucht et al. (2007), for example, found that local bacterial communities in a system of connected shallow lakes were largely determined by local environmental factors, as opposed to the metacommunity level effects of dispersal. In this case, it was believed that species sorting was facilitated by very fast local population growth

rates, which ensured that local bacterial population dynamics and metacommunity-level dispersal occurred at different temporal scales—the key assumption of most patch-dynamic models. Examples of zooplankton metacommunities inhabiting interconnected ponds (Cottenie and De Meester 2003, 2004; Cottenie et al. 2003) and inquiline food web communities inhabiting pitcher plants (Miller et al. 2002; Kneitel and Miller 2003) also support a species sorting perspective.

Although numerous models exist to describe food webs at the local community level, theoretical tools for studying food web assembly and dynamics at metacommunity scales are still sorely needed (Brose et al. 2005). One of the benefits of our framework is that it is now possible to investigate how food web complexity can emerge at large spatial scales. Just as the observed complexity of an empirical food web may arise when sampling occurs over large temporal scales, so a patch-dynamic approach may offer important insights into how complex trophic networks may emerge at large metacommunity scales through the aggregation of simpler local trophic interactions and modules. An example of such a food web metacommunity is given by the trophic interactions between the butterfly *Melitaea cinxia*, its host plants, and its interacting parasitoids and hyperparasitoids in the Finnish Aland Islands, as studied by van Nouhuys and Hanski (2005). In this metacommunity, many of the interacting species exhibit a metapopulation structure by virtue of the island landscape. As well, distinct and locally simple food web modules appear to be linked to each other across large geographic scales by the sharing of prey and predators (generalist predation).

Our patch-dynamic framework will also provide testable predictions. Once consumer–resource interactions are seen as being connected—through the sharing of common prey and predators—to other trophic interactions at the metacommunity scale, attempts at predicting the behaviour of any given consumer resource pair becomes possible. We demonstrated this by showing how the stabilising effects of space on a potentially strong, unstable predator–prey interaction varied depending on the ecological context provided by alternative prey. Increasingly strong interactions in a specialist predator–prey system can lead to rapid regional extinction of the predator with little or no regional effect on the prey, while both the availability and ability to survive on alternative prey resources can transform, even reverse, this outcome. The specialist predator–prey interaction can exhibit a type of ‘bottom-up’ effect at the metacommunity level, where predators appear to have little effect on their prey’s regional persistence and abundance, yet are strongly affected by their prey (Fig. 4b). The presence of alternative prey cannot only weaken this effect but can even lead to the opposite case of a metacommunity-level ‘top-down’ effect (Fig. 4c, d). The significance of

these simple results for conservation can be appreciated when one considers the ease with which a predator can be rapidly driven globally extinct—even in the absence of habitat loss—simply by the indirect effects that result from the extinction of an alternative, less preferred resource.

These results demonstrate how theoretical models of trophic interactions can provide the necessary framework for guiding empirical investigations since the focus of many empirical investigations—the abundance and persistence of consumer-resource interactions in the face of habitat loss—cannot be adequately studied in isolation without an appreciation of the larger food web interactions that focal predator–prey relations are embedded within. In fact, the lack of a guiding theoretical framework may explain the inability of recent empirical research to discern a clear pattern regarding the effects of habitat loss on predator–prey interactions (Ryall and Fahrig 2006). We hope that the framework we provide here will lead to a fuller integration of theory and experiment in the study of metacommunity food webs.

Acknowledgements We would like to thank M. Cherif, S. Leroux, Z. Long, C. de Mazancourt and F. Guichard for useful comments and discussions. A. Gonzalez and M. Loreau are supported by the Canada Research Chair program, NSERC Discovery grants, and an FQRNT team grant.

Appendix A

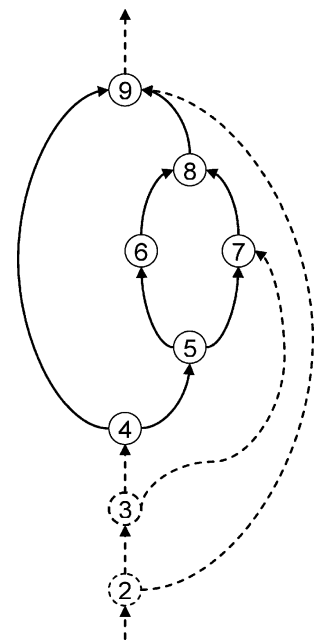
We can appreciate the motivation underlying Eq. 4 by considering the portion of a hypothetical food web shown in Fig. 5. The subgraph $S_{4,9}$ of the food web graph in Fig. 5 represents all the species and feeding links lying on a directed path between species 4 and species 9 (solid black lines). From Eq. 3, we know that $f(S_{4,9})$ gives the fraction of patches occupied by species 9 that are also occupied by species 4. In this case

$$f(S_{4,9}) = \left(\rho_{(4,5)} \cdot \rho_{(5,6)} \cdot \rho_{(6,8)} \cdot \rho_{(8,9)} \right) + \left(\rho_{(4,5)} \cdot \rho_{(5,7)} \cdot \rho_{(7,8)} \cdot \rho_{(8,9)} \right) + \rho_{(4,9)} \quad (7)$$

However, what we are actually interested in is the fraction of species 9-occupied patches where species 9 will be affected by extinctions of species 4. Looking at Fig. 5, we see that extinction of species 4 in patches containing the food chain sequence 4, 5, 7, 8, and 9 will not lead to the extinction of species 9, since an intermediate species 7 can switch predation to 4’s resource species 3, as indicated by the (3, 7) link (dashed line). As a result, a patch with the food chain sequence 3, 4, 5, 7, 8 and 9 will reassemble, after 4 goes extinct, into 3, 7, 8 and 9.

In order to know how the regional abundance of a species i is affected by the extinction rate of any particular

Fig. 5 An example of a sub-graph of a hypothetical food web network



species k below it, we need to know what fraction of patches containing species i also contains some intermediate species m capable of switching consumption to one of k ’s resources upon k ’s extinction. This is given by the second term in Eq. 4, $f\left(\bigcup_{m \in C(l)} (S_{k,m} \cup S_{m,i})\right)$. For the example given here,

$$f\left(\bigcup_{m \in C(l)} (S_{k,m} \cup S_{m,i})\right) = \rho_{(4,5)} \cdot \rho_{(5,7)} \cdot \rho_{(7,8)} \cdot \rho_{(8,9)} \quad (8)$$

Subtracting Eq. 8 from Eq. 7, as per Eq. 4 gives us the net fraction of patches occupied by 9, where 9 will go extinct upon 4 going extinct whenever 4 is consuming resource 3: $\Phi_{4,9}^3 = \left(\rho_{(4,5)} \cdot \rho_{(5,6)} \cdot \rho_{(6,8)} \cdot \rho_{(8,9)} \right) + \rho_{(4,9)}$.

Appendix B

We demonstrate here the application of Eq. 2 for the top two pairwise interactions in Fig. 2c (we assume $v_{5,4} > v_{6,4}$ and $v_{3,1} > v_{6,1}$).

For the (6, 7) interaction, the first term in Eq. 4 becomes $A = c_{7,6} p_{(6,7)} (p_{(1,6)} + p_{(4,6)} - p_{(6,7)})$. Here, the growth in the fractions of patches with the (6, 7) interactions is due to the total number of species 7 colonisers ($c_{7,6} p_{(6,7)}$) landing on available resource 6 patches, itself given by the total fractions of resource 6 patches ($p_{(1,6)} + p_{(4,6)}$), minus those already occupied by consumer 7 ($p_{(6,7)}$).

The second term given by $B = (e_{7,6} + \mu_{7,6}) p_{(6,7)}$ simply gives the extinction rate of the (6, 7) interaction due to the extinction rate of consumer 7 ($e_{7,6}$) and the rate that resource 6 is driven extinct due to predation by consumer 7, ($\mu_{7,6}$).

Since there are no competitors for resource 6 and no alternative resources for consumer 7 aside from 6, terms C , D and E are all equal to 0. However, a decrease in the (6, 7) interaction can occur due to extinctions of species further down the food web. The effect that species extinctions further down the food web has on the (6, 7) interaction will be determined by the degree of patch overlap between the (6, 7) interaction and the rate of extinction for each species below 6. In the F term, the extinction rates of all species interactions below (6, 7), multiplied by the fraction of the 7-occupied patches that will be affected by that extinction are summed (see Appendix A for an example). When this sum is multiplied by the density of (6, 7) patches, $p_{(6,7)}$,

$$\frac{dp_{(6,7)}}{dt} = c_{7,6}p_{(6,7)}(p_{(1,6)} + p_{(4,6)} - p_{(6,7)}) - (e_{7,6} + \mu_{7,6})p_{(6,7)} - p_{(6,7)} \left((e_{6,1}p_{(1,6)} + \rho_{(4,6)}((e_{6,4} + \mu_{6,4}) + (e_{4,3} + \mu_{4,3}) + \rho_{(2,3)}(e_{3,2} + \mu_{3,2}) + \rho_{(1,3)}(e_{3,1} + \mu_{3,1}))) - p_{(6,7)}(c_{5,4}p_{(4,5)}\rho_{(6,4)}) \right).$$

Similarly for the (4, 6) interaction, A gives growth of the interaction due to colonisation of available resource 4 patches by consumer 6. However, now, in order to determine the total number of species 6 colonisers produced, one must sum over all the resource patches occupied by 6 ($c_{6,4} p_{(4,6)} + c_{6,1} p_{(1,6)}$), giving us $A = (c_{6,4}p_{(4,6)} + c_{6,1}p_{(1,6)})(p_{(3,4)} - p_{(4,5)} - p_{(4,6)})$. B is defined similarly to the previous example.

$$\frac{dp_{(4,6)}}{dt} = (c_{6,4}p_{(4,6)} + c_{6,1}p_{(1,6)})(p_{(3,4)} - p_{(4,5)} - p_{(4,6)}) - (e_{6,4} + \mu_{6,4})p_{(4,6)} - c_{5,4}p_{(4,5)}(p_{(4,6)}) - p_{(4,6)} \left((e_{4,3} + \mu_{4,3}) + \rho_{(2,3)}(e_{3,2} + \mu_{3,2}) + \rho_{(1,3)}(e_{3,1} + \mu_{3,1}) \right) - \mu_{7,6}p_{(4,6)}.$$

we get $F = p_{(6,7)} \left((e_{6,1}p_{(1,6)} + \rho_{(4,6)}((e_{6,4} + \mu_{6,4}) + (e_{4,3} + \mu_{4,3}) + \rho_{(2,3)}(e_{3,2} + \mu_{3,2}) + \rho_{(1,3)}(e_{3,1} + \mu_{3,1}))) \right)$.

The (6, 7) interaction can also decrease due to competitive displacement of species further down the food web—in this case, species 5 displacing 6 from resource 4 patches. Thus, here, G is equal to the number of species 5 colonisers, $c_{5,4} p_{(4,5)}$, that successfully land on and displace consumer species 6 from resource 4 in food chains with the (6, 7) interaction, $\rho_{(6,4)} p_{(6,7)}$, giving us $G = p_{(6,7)}(c_{5,4} p_{(4,5)} \rho_{(6,4)})$. Finally, $H = 0$, since there is no predator species that can drive 7 extinct from top-down effects. The overall equation for the (6, 7) interaction is then

The (4, 6) interaction, unlike (6, 7), can decrease due to competitive displacement of the consumer species; in this case, 6 can be displaced from resource 4 by 5 giving us $C = c_{5,4} p_{(4,5)}(p_{(4,6)})$. Since there is no way 6 can directly switch from some alternative resource onto 4, both D and E are equal to 0. The F and H terms are determined similarly to the previous example, while $G = 0$, since there are no species below the interaction that can be displaced by superior competitors. The overall equation then for the (4, 6) interaction is

Appendix C

Algorithm for transforming a food web graph

Below, we outline an algorithm that can transform the food web graph so that no directed path in the graph will represent an a priori impossible food chain configuration. The algorithm required is relatively straightforward: (1) move up the vertex set until you come to a generalist species, t , with more than one incoming edge, at least one of which is a *bypass* link, which directly connects the consumer to a resource further down one of its other food chains. (2) Start at the resource vertex in one of the bypass links that has the lowest index value, and from there, start moving up the vertex set one index number at a time,

checking all the incoming edges for each vertex while doing so. If the current vertex, k , has more than one incoming edge, at least one of which is from a directed path rooted in one of the bypass resources and at least one of which is from a directed path *not* rooted in one of the bypass resources, and if at least one of vertex k 's outgoing edges is on a directed path towards t , then split vertex k into two parallel vertices, each with the same outgoing edge as before, but no incoming edges. (3) Attach to the original vertex, k , any incoming edges from directed paths that were *not* rooted in one of the bypass resources, and to the new vertex, k' , attach the incoming edges from paths that *are* rooted in the one of the bypass resources. (4) Continue this until you arrive at the consumer vertex t and then disconnect all incoming edges from t that are part of a

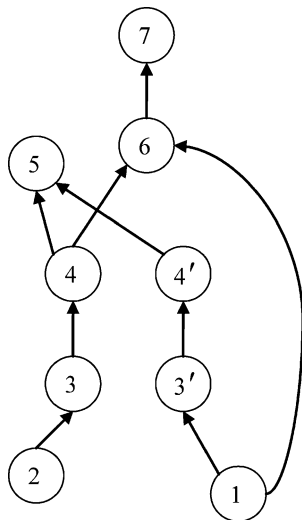


Fig. 6 The food web in Fig. 2c after being transformed by the algorithm described in Appendix C to ensure that all directed paths depicted in the food web graph are not a priori impossible food chains

directed path from one of the bypass species. (5) Start again at (1) moving up the food web looking for the next generalist predator with bypass loops in order to establish a new t , and then repeat (2)–(4).

This algorithm can be applied to the network before the system of differential equations is defined. A simple example of transformation can be observed for the graph in Fig. 2c, which becomes, by the above method, the graph shown in Fig. 6. In Fig. 6, the distribution of each consumer's feeding links among its prey can be considered independently of how the prey's own feeding links are distributed among its own resources and so on. As a result, the frequency of patch overlap between any two species in a directed path or food chain can be determined by multiplying the ρ values of the pairwise interactions along the path between them.

References

- Allesina S, Pascual M (2008) Network structure, predator–prey modules, and stability in large food webs. *Theor Ecol* 1:55–64
- Amarasekare P (2008) Spatial dynamics of keystone predation. *J Anim Ecol* 77:1306–1315
- Bascompte J, Sole RV (1998) Effects of habitat destruction in a prey–predator metapopulation model. *J Theor Biol* 195:383–393
- Brose U, Pavao-Zuckerman M, Eklof ABJ, Berg MP, Cousins SH, Mulder C, Verhoef HA, Wolters V (2005) Spatial aspects of food webs. In: de Ruiter P, Wolters V, Moore JC (eds) *Dynamic food webs: multispecies assemblages, ecosystem development and environmental change*. Academic, Burlington, pp 463–469
- Brose U, Williams RJ, Martinez ND (2006) Allometric scaling enhances stability in complex food webs. *Ecol Lett* 9:1228–1236

- Calcagno V, Mouquet N, Jarne P, David P (2006) Coexistence in a metacommunity: the competition–colonization trade-off is not dead. *Ecol Lett* 9:897–907
- Cottenie K, De Meester L (2003) Connectivity and cladoceran species richness in a metacommunity of shallow lakes. *Freshw Biol* 48:823–832
- Cottenie K, De Meester L (2004) Metacommunity structure: synergy of biotic interactions as selective agents and dispersal as fuel. *Ecology* 85:114–119
- Cottenie K, Michels E, Nuytten N, De Meester L (2003) Zooplankton metacommunity structure: regional vs. local processes in highly interconnected ponds. *Ecology* 84:991–1000
- Crowley PH (1979) Predator-mediated coexistence—equilibrium interpretation. *J Theor Biol* 80:129–144
- Gardner MR, Ashby WR (1970) Connectance of large dynamic (Cybernetic) systems—critical values for stability. *Nature* 228:784
- Gouhier T, Guichard F, Gonzalez A (2010) Synchrony and stability of food webs in metacommunities. *Am Nat* (in press)
- Guichard F (2005) Interaction strength and extinction risk in a metacommunity. *Proc R Soc Lond B Biol Sci* 272:1571–1576
- Hastings A (1980) Disturbance, coexistence, history, and competition for space. *Theor Popul Biol* 18:363–373
- Holt RD (1997) Community modules. In: Gange AC, Brown VK (eds) *Multitrophic interactions in terrestrial ecosystems*. Blackwell Science, Oxford, pp 333–349
- Holt RD (2002) Food webs in space: on the interplay of dynamic instability and spatial processes. *Ecol Res* 17:261–273
- Holyoak M, Leibold MA, Holt RD (eds) (2005) *Metacommunities: spatial dynamics and ecological communities*. University of Chicago Press, Chicago
- Huffaker CB (1958) Experimental studies on predation: dispersion factors and predator–prey oscillations. *Hilgardia* 27:343–383
- Keeling MJ (2002) Using individual-based simulations to test the Levins metapopulation paradigm. *J Anim Ecol* 71:270–279
- Kneitel JM, Miller TE (2003) Dispersal rates affect species composition in metacommunities of *Sarracenia purpurea* inquilines. *Am Nat* 162:165–171
- Koelle K, Vandermeer J (2005) Dispersal-induced desynchronization: from metapopulations to metacommunities. *Ecol Lett* 8:167–175
- Lawton JH, Warren PH (1988) Static and dynamic explanations for patterns in food webs. *Trends Ecol Evol* 3:242–245
- Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D, Loreau M, Gonzalez A (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecol Lett* 7:601–613
- Levins R (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull Entomol Soc Am* 15:237–240
- Levins R (1970) Complex systems. In: Waddington ECH (ed) *Towards a theoretical biology*. Edinburgh University Press, Edinburgh, pp 73–88
- Levins R, Culver D (1971) Regional coexistence of species and competition between rare species (mathematical model/habitable patches). *Proc Natl Acad Sci U S A* 68:1246
- Loreau M, Downing A, Emmerson M, Gonzalez A, Hughes J, Inchausti P, Joshi J, Norberg J, Sala O (2002) A new look at the relationship between diversity and stability. In: Loreau M, Naeem S, Inchausti P (eds) *Biodiversity and ecosystem functioning: synthesis and perspectives*. Oxford University Press, Oxford, pp 79–91
- Loreau M, Mouquet N, Gonzalez A (2003) Biodiversity as spatial insurance in heterogeneous landscapes. *Proc Natl Acad Sci U S A* 100:12765–12770
- May RM (1972) Will a large complex system be stable. *Nature* 238:413

- May RM (1973) *Stability and complexity in model ecosystems*. Princeton University Press, Princeton
- May RM (1994) The effects of spatial scale on ecological questions and answers. In: Edwards PJ, May RM, Webb RN (eds) *Large-scale ecology and conservation biology*. Blackwell Scientific Publications, Oxford, pp 1–17
- May RM, Nowak MA (1994) Superinfection, metapopulation dynamics, and the evolution of diversity. *J Theor Biol* 170:95–114
- McCann K, Hastings A, Huxel GR (1998) Weak trophic interactions and the balance of nature. *Nature* 395:794–798
- McCann KS, Rasmussen JB, Umbanhowar J (2005) The dynamics of spatially coupled food webs. *Ecol Lett* 8:513–523
- Melian CJ, Bascompte J (2002) Food web structure and habitat loss. *Ecol Lett* 5:37–46
- Michalski J, Arditi R (1995) Food-web structure at equilibrium and far from it—is it the same. *Proc R Soc Lond B Biol Sci* 259:217–222
- Miller TE, Kneitel JM, Burns JH (2002) Effect of community structure on invasion success and rate. *Ecology* 83:898–905
- Mouquet N, Loreau M (2002) Coexistence in metacommunities: the regional similarity hypothesis. *Am Nat* 159:420–426
- Mouquet N, Loreau M (2003) Community patterns in source-sink metacommunities. *Am Nat* 162:544–557
- Neutel AM, Heesterbeek JAP, van de Koppel J, Hoenderboom G, Vos A, Kaldeway C, Berendse F, de Ruiter PC (2007) Reconciling complexity with stability in naturally assembling food webs. *Nature* 449:599–U11
- Otto SB, Rall BC, Brose U (2007) Allometric degree distributions facilitate food-web stability. *Nature* 450:1226–U7
- Paine RT (1988) Food webs—road maps of interactions or grist for theoretical development. *Ecology* 69:1648–1654
- Pimm SL (1984) The complexity and stability of ecosystems. *Nature* 307:321–326
- Pimm SL, Lawton JH (1978) Feeding on more than one trophic level. *Nature* 275:542–544
- Polis GA (1991) Complex trophic interactions in deserts— an empirical critique of food-web theory. *Am Nat* 138:123–155
- Rooney N, McCann K, Gellner G, Moore JC (2006) Structural asymmetry and the stability of diverse food webs. *Nature* 442:265–269
- Ryall KL, Fahrig L (2006) Response of predators to loss and fragmentation of prey habitat: a review of theory. *Ecology* 87:1086–1093
- Schoenly K, Cohen JE (1991) Temporal variation in food web structure—16 empirical cases. *Ecol Monogr* 61:267–298
- Swihart RK, Feng ZL, Slade NA, Mason DM, Gehring TM (2001) Effects of habitat destruction and resource supplementation in a predator–prey metapopulation model. *J Theor Biol* 210:287–303
- Tilman D (1994) Competition and biodiversity in spatially structured habitats. *Ecology* 75:2–16
- Van der Gucht K, Cottenie K, Muylaert K, Vloemans N, Cousin S, Declerck S, Jeppesen E, Conde-Porcuna JM, Schwenk K, Zwart G, Degans H, Vyverman W, De Meester L (2007) The power of species sorting: local factors drive bacterial community composition over a wide range of spatial scales. *Proc Natl Acad Sci U S A* 104:20404–20409
- van Nouhuys S, Hanski I (2005) Metacommunities of butterflies, their host plants, and their parasitoids. In: Holyoak M, Leibold MA, Holt RD (eds) *Metacommunities: spatial dynamics and ecological communities*. University of Chicago Press, Chicago, pp 99–121
- Vandermeer J (1973) Regional stabilization of locally unstable predator-prey relationships. *J Theor Biol* 41:161–170
- Warren PH (1989) Spatial and temporal variation in the structure of a fresh-water food web. *Oikos* 55:299–311
- Zeigler BP (1977) Persistence and patchiness of predator–prey systems induced by discrete event population exchange mechanisms. *J Theor Biol* 67:687–713