

Spatial trophic cascades in communities connected by dispersal and foraging

DAVID GARCÍA-CALLEJAS,^{1,7} ROBERTO MOLOWNY-HORAS,² MIGUEL B. ARAÚJO,^{3,4,5} AND DOMINIQUE GRAVEL⁶

¹Estación Biológica de Doñana, CSIC, Calle Américo Vespucio 26, 41092 Sevilla, Spain

²CREAF, Cerdanyola del Vallès 08193 Spain

³Departamento de Biogeografía y Cambio Global, Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas (CSIC), Calle de José Gutiérrez Abascal 2, Madrid 28006 Spain

⁴InBiol/Centro de Investigação em Biodiversidade e Recursos Genéticos (CIBIO), Largo dos Colegiais, Universidade de Évora, Évora 7000 Portugal

⁵Center for Macroecology, Evolution and Climate (CMEC), Natural History Museum of Denmark, University of Copenhagen, Copenhagen 2100 Denmark

⁶Département de Biologie, Université de Sherbrooke, Sherbrooke, Québec, Canada

Citation: García-Callejas, D., R. Molowny-Horas, M. B. Araújo, and D. Gravel. 2019. Spatial trophic cascades in communities connected by dispersal and foraging. *Ecology* 100(11):e02820. 10.1002/ecy.2820

Abstract. Pairwise interactions between species have both direct and indirect consequences that reverberate throughout the whole ecosystem. In particular, interaction effects may propagate in a spatial dimension, to localities connected by organismal movement. Here we study the propagation of interaction effects with a spatially explicit metacommunity model, where local sites are connected by dispersal, foraging, or by both types of movement. We show that indirect pairwise effects are, in most cases, of the same sign as direct effects if localities are connected by dispersing species. However, if foraging is prevalent, this correspondence is broken, and indirect effects between species often have a different sign than direct effects. This highlights the importance of indirect interactions across space and their inherent unpredictability in complex settings with species foraging across local patches. Further, the effect of a species over another in a local patch does not necessarily correspond to its effect at the metacommunity scale; this correspondence is again mediated by the type of movement across localities. Every species, despite their trophic position or spatial range, displays a non-zero net effect over every other species in our model metacommunities. Thus we show that local dynamics and local interactions between species can trigger indirect effects all across the set of connected patches, and these effects have a distinct signature depending on whether the prevalent connection between patches is via dispersal or via foraging. However, the magnitude of this effect between any two species strongly decays with the distance between them. These theoretical results strengthen the importance of considering indirect effects across species at both the community and metacommunity levels, highlight the differences between types of movement across locations, and thus open novel avenues for the study of interaction effects in spatially explicit settings.

Key words: dispersal; foraging; indirect effects; interaction networks; metacommunity; spatial cascades; trophic cascades.

INTRODUCTION

Ecological communities are complex systems in which species interact with each other through a multitude of pathways. The effect of a species on the rest of the ecosystem is generally difficult to predict and quantify. This effect likely depends on a variety of factors, such as the topology of the community network (Polis 1994), or the strength of the interactions in which the species engages (Zhao et al. 2016). Trophic cascades are striking

examples of interaction effects propagating through food chains: changes in the occurrence, strength or outcome of a certain trophic interaction often have a significant top-down influence on the rest of the community (Schmitz et al. 2000).

Just as the spreading of disease (Balcan et al. 2009) or information (Barthélemy 2011) in other types of complex networks, the propagation of interaction effects across ecological networks has a spatial dimension, as interaction cascades often link organisms that are occurring at different locations. Thus, we may define a *spatial cascade* as a set of indirect interactions that propagate in a spatial dimension, potentially linking disconnected species. Spatial cascades are ubiquitous in nature: migratory animals couple the dynamics of different regions

Manuscript received 12 December 2018; revised 23 April 2019; accepted 17 June 2019. Corresponding Editor: José Ponciano.

⁷E-mail: david.garcia.callejas@gmail.com

(Springer et al. 2018) or, on a more local scale, mobile individuals connect spatially separated communities (Leibold et al. 2004). Spatial cascades may occur between different locations of a single habitat type. For example, predator species may consume bird eggs from nests of different forest patches (Chalfoun et al. 2002), with potential feedbacks for the bird populations and associated resources. The importance of nutrient and organism transfer across habitat types has also been well established theoretically (Loreau et al. 2003, Gounand et al. 2018) and empirically (Polis et al. 1997, Estes et al. 1998, Knight et al. 2005). However, despite the growing number of studies documenting spatial propagation of interaction effects, the concept of spatial cascades has not yet been rigorously explored and generalized. For example, there are currently no theoretical hypotheses on the decay of the magnitude of interaction effects with spatial distance, or on whether different modes of movement propagate interaction effects similarly.

Pairwise interactions trigger direct effects on the interacting species and also indirect effects among them and with the rest of the community. We consider here, as an estimate of how interaction effects propagate across space, the pairwise net interaction effect (Novak et al. 2016). The net interaction effect between any two species is, conceptually, the sum of their direct effects from pairwise interactions and indirect effects mediated by other species or entities (Abrams 1987). The direct effects of a species over another can be formulated in several ways (Berlow et al. 2004), but generally involves the effects over some property of interest at the population level, such as short-term growth rate (Abrams 1987). Indirect effects, in turn, involve all effects between two species that do not occur via direct interactions. These indirect effects may occur between species that interact directly or not, via the propagation of effects over the ecological network. These effects have been classified as being triggered by changes in the abundance of the intermediary species (*density-mediated indirect interactions*) or by these intermediary species modifying the context of a direct interaction (see, e.g., Wootton 2002 for further definitions and examples). It has been shown that indirect effects may be as strong, or even stronger than, direct effects, up to the point of switching interaction net effects from positive to negative or vice versa (e.g., Menge 1995).

The metacommunity concept (i.e., a set of local communities linked by the movement of potentially interacting species; Leibold and Chase 2018) provides a comprehensive theoretical framework for studying the propagation of interaction net effects in a spatially explicit setting. In virtually all metacommunity studies we are aware of, it is assumed that species connect the local communities via dispersal, i.e., the permanent establishment of individuals on a different territory from their birthplace. Dispersal, however, is not the only process by which species can link spatially disconnected patches. Foraging, the active search for food of a mobile

individual, may link the trophic community of its reproductive area with other, potentially disconnected communities in which the individual acquires varying fractions of its diet (McCann et al. 2005). If foraging species are based on a central site, for example, their reproductive area, their foraging effort and associated effects on local communities generally decay with distance. This concept is termed *central-place foraging*, (Orians and Pearson 1979). It has been postulated that dispersal and foraging modes of connecting spatially isolated patches have clearly distinct dynamics and ecosystem-level consequences (Amarasekare 2008, Massol et al. 2011, Gounand et al. 2018). Therefore, as a first approximation, we may expect spatial cascades triggered by each movement type to display different properties and effects on the connected local communities (Fig. 1). For example, in two simple food chains connected by a dispersing species, the net flow of individuals from one community to the other will benefit the local predators of the dispersing species, and in turn, adversely affect its prey. On the other hand, if the same species connects the two food chains by foraging sporadically on the second location, it will trigger a negative effect up the trophic chain of that location, and will benefit species on which the preyed species feeds. These differences in effect propagation can be analyzed quantitatively with the interaction matrices associated to the metacommunity. In particular, the variability in sign structure of the direct and net effect matrices (Fig. 1) is informative of whether the overall effect of one species over any other can be predicted from their pairwise direct effects. High ratios of sign switch point, in general, to a disproportionately high influence of indirect effects on species dynamics (Menge 1995, Montoya et al. 2009). Furthermore, network structural properties can be obtained from the interaction matrices, to understand the potential differences between direct and net effects of the different movement types. Connectance, for example, is expected to increase from direct to net effect matrices, as shown in Fig. 1, with a subsequent decrease in modularity. It is, however, unclear whether different movement types will trigger differences in these or other structural properties.

Here we study how net effects are propagated in space when local food webs are connected by dispersal, foraging, or a combination of both movement types, using model multi-trophic metacommunities. In particular, we ask the following questions: (1) What is the distribution of signs and magnitudes of net effects in communities connected by dispersal, foraging, or a mixture of both? (2) What is the distribution of direct and net effects across the metacommunity? (3) Does the magnitude of the net effects between any two species decay with increasing distance between them?

METHODS

We developed a spatially explicit metacommunity model in which local trophic communities are

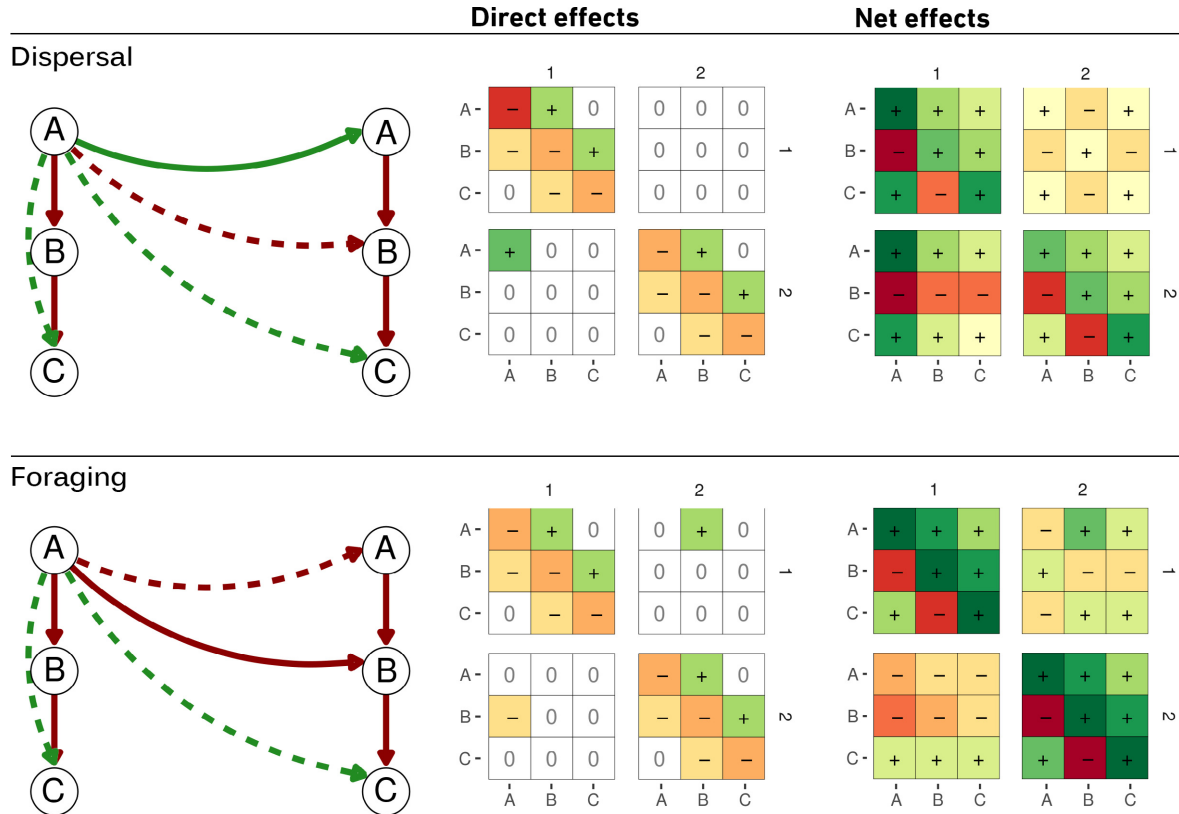


FIG. 1. Spatially explicit interaction matrices and net effect matrices for two simple configurations. In both cases, a linear food chain is represented at two locations (1 and 2). Each matrix is divided into four blocks, representing the effects of species in location 1 over themselves (upper left), location 1 over location 2 (lower left), location 2 over location 1 (upper right), and location 2 over themselves (lower right). In the dispersal configuration, species *A* disperses from the first location to the second. In the second configuration, species *A* preys on species *B* on both locations. Green links represent positive effects, red negative. Solid arrows represent direct effects; dashed arrows expected indirect effects. For clarity, in the food chains we display only the indirect effects arising directly from species *A* at location 1. Darker shades in the matrices indicate stronger effects. The matrices can be read as with the following example: in the foraging configuration, the direct effect of *A* in location 1 over *B* in location 2 is given by locating the column that indicates species *A* at location 1 (the first column of the matrix), and the row indicating species *B* at location 2 (fifth row).

connected through (1) dispersal, (2) foraging, or (3) both. The dynamics of the system are given by a general Lotka–Volterra implementation, following Gravel et al. (2016). For each configuration we ran numerical simulations and recorded both the direct effect and the net effect between each pair of species in the metacommunity, as well as a set of network metrics for characterizing potential differences in metacommunity structure.

Quantification of direct and net effects

In theoretical analyses of ecological networks, the Jacobian matrix of a system (also called *community matrix*) is widely used to describe the direct effects between each pair of species at equilibrium. In its most common implementation, it represents the effect on one species' growth rate in response to small changes in another species' abundance (Berlow et al. 2004, Novak et al. 2016). Consider a general population dynamics

model of S species in which the population density of species i over time is given by

$$\frac{dN_i}{dt} = N_i f_i(N_1, \dots, N_S) \quad (1)$$

where N_i is the density of species i , and $f_i(N_1, \dots, N_S)$ is its growth rate, potentially influenced by any other species. In this general case, the elements of the Jacobian matrix C are

$$c_{ij} = \frac{\partial(\frac{dN_i}{dt})}{\partial N_j} = \frac{\partial[N_i f_i(N_1, \dots, N_S)]}{\partial N_j} \quad (2)$$

The net effect of species j over species i , in turn, is the sum of its direct effects and all indirect effects between the two species (Bender et al. 1984, Montoya et al. 2009, Novak et al. 2016). The net effect matrix of a community is defined as the negative of the inverse Jacobian matrix, that is, $-C^{-1}$, and its coefficients represent the

net effect of an increase in species j 's population growth rate on the density of species i , when all species respond to direct effects (Novak et al. 2016).

The model

The dynamics of the community are modelled with a general Lotka–Volterra implementation, following Gravel et al. (2016). Considering a set of S species present at n locations, the dynamics of species i at location x is given by:

$$\frac{dN_{ix}}{dt} = N_{ix} \left(m_{ix} + \sum_{y \in n} \sum_{j \in S} b_{ix,jy} N_{jy} \right) + \Delta N_{ix} \quad (3)$$

where m_{ix} is the intrinsic growth rate of species i at location x , N_{ix} its population density, ΔN_{ix} is the net migration balance (see Eq. 5), and $b_{ix,jy}$ is the per capita effect of species j at location y on species i at location x . The parameter $b_{ix,jy}$ encapsulates the effect of foraging to/from other locations, and represents a basic situation in which species i moves out of its reproductive area x to feed at location y on species j . Specifically, we assume that a foraging species allocates a fraction f of its foraging effort to communities outside its reproductive location, which implies that the effort allocated to feeding in its local community is $1-f$. We incorporate this in our model as follows:

$$b_{ix,jy} = \begin{cases} (1-f)\alpha_{ix,jy} & \text{if } x = y \\ \frac{f}{|n_{ix}|} \alpha_{ix,jy} & \text{if } x \neq y, \alpha_{ix,jy} > 0 \\ \frac{f}{|n_{jy}|} \alpha_{ix,jy} & \text{otherwise} \end{cases} \quad (4)$$

The first situation corresponds to the effect of predation from the same location, in which case the interspecific interaction coefficient $\alpha_{ix,jy}$ is weighted by the relative effort dedicated to foraging within its home location $(1-f)$. The second situation represents foraging of species i at location x on species j at location y . The net foraging effort f is equally divided among all locations reachable by species i from location x (the set given by n_{ix} , which has a cardinality of $|n_{ix}|$). The last situation is the opposite, where species i at location x is preyed upon by species j at location y . In this case, f is divided among all locations reachable by species j from location y . Note that this situation represents an equal division of foraging effort among all reachable locations.

Dispersal among different locations, in turn, is represented simply by the net variation in species densities between reachable locations, modelled by passive diffusion with coefficient d (Gravel et al. 2016):

$$\Delta N_{ix} = \sum_{y \in n_{ix}} \frac{d_{ixy}}{|n_{ix}|} (N_{ix} - N_{iy}) \quad (5)$$

Thus, as is the case with foraging, dispersal effort d is divided equally among all patches reachable by species i on location x .

Parameterization and simulations

We considered predator–prey interactions, but the approach could easily be generalized to other types of interactions. The structure of local communities, that is, who interacts with whom, is determined according to the niche model (Williams and Martinez 2000), ensuring a realistic topology and that there are no disconnected species. We further assumed that the niche axis obtained from the niche model is linearly correlated with the foraging and dispersal distance of the different species, such that the species with lowest niche values could only forage or disperse to adjacent communities (Jacquet et al. 2017). Interaction coefficients α for the metacommunity are drawn from a normal distribution $N(0.25, 0.1)$ (in order to be consistent with Gravel et al. 2016), with the sign structure given by the niche model. We introduced a small amount of spatial heterogeneity by drawing local coefficients from a normal distribution with mean centered on the corresponding metacommunity coefficients and standard deviation of 0.1. This unstructured spatial heterogeneity was introduced to capture the behaviour of the system in the presence of small stochastic perturbations, not to simulate environmental gradients explicitly.

Local communities were placed along a single dimension space, the ends of which were connected together in order to maximize distances between non-connected communities, and prevent edge effects of communities at the end of the linear chain. We fixed the maximum dispersal and foraging distances to two communities away from the species' home location in order to avoid excessive parameterization and allow for better comparison of the net effects of the different movement types.

We implemented the model in R 3.4.4 (R Development Core Team 2018; see Appendix S1: Section S1 for further details of the implementation). We simulated the dynamics of 15 species at 10 local communities (preliminary analyses showed that the results were robust to variations in species richness or number of local communities). The number of species and size of the landscape correspond to a meta-adjacency matrix of $15 \times 10 = 150$ rows. This size was chosen in order for the numerical calculation of the Jacobian matrices to be computationally feasible. Although this represents a relatively small species richness and number of patches, it allowed us to obtain spatial distances and path lengths between species from zero to over five units.

We generated three sets of metacommunity configurations: only dispersal, in which we set the dispersal coefficient $d = 0.5$, and the foraging coefficient $f = 0$ for every species; only foraging, with $d = 0$ and $f = 0.5$; and dispersal and foraging, with $d = 0.5$ and $f = 0.5$. These values were chosen heuristically, in the range of those evaluated by Gravel et al. 2016; see Appendix S1: Table S1 for the complete parameterization). We ran sensitivity analyses to check the robustness of the results to variations of both dispersal and foraging rates (Appendix S1: Section S2).

We generated 1,000 food web topologies for each configuration. On each replicate, we obtained numerically the direct and net interaction coefficients between each pair of populations in the metacommunity. These could then be (1) qualitatively compared and (2) analyzed with regards to the distance between the interacting populations. We also computed basic quantitative descriptors of the direct and net effects networks at equilibrium. These networks represent either the direct links among all populations in the metacommunity, or the links representing the net effect between each population. First, we obtained the *connectance* of the metacommunity networks, defined as the ratio of realized links with respect to the potential number of links of a fully connected network. We calculated connectances of sets of species interacting in a given patch (intra-patch), and also connectances of the whole metacommunity networks (inter-patch). We also obtained the *average path length* between any two populations, i.e. the average of the shortest path lengths between them in the metacommunity. This metric was obtained with the function “distances” from the R package igraph (Csardi and Nepusz 2006). Lastly, we calculated the *modularity* of the metacommunity network, which measures the tendency for nodes to be grouped into distinct modules (Newman 2006). We calculated a weighted version of modularity that considers both positive and negative link weights, as implemented in the R igraph package (Csardi and Nepusz 2006). We evaluate all our results qualitatively, because statistical significance tests are not appropriate for simulation-based studies (White et al. 2014).

RESULTS

What is the distribution of signs and magnitudes of net effects in communities connected by dispersal, foraging, or a mixture of both?

Net effects are mainly of equal sign to direct effects when local communities are connected by dispersal (Table 1), whereas sign switches occur in around 50% of pairwise interactions with foraging or a mixture of movement types. The ratio of positive to negative net effects is maintained at values close to 1, meaning a similar number of positive and negative net effects for all configurations.

The two types of movement and their combination displayed distinctly different net effects on interactions occurring both within the same location (intra-patch) and across different locations (inter-patch; Fig. 2). Intraspecific effects across locations are generally positive with dispersal (blue points on panel A of Fig. 2). Intraspecific effects are, however, more variable and have a higher frequency of negative magnitudes with foraging and mixed movement modes (panels B and C of Fig. 2). Interspecific net effects are also generally of the same sign in local patches and across patches when communities are connected by dispersal (orange points

TABLE 1. Summary metrics of the simulations performed. For each simulation, we group the results by location, that is, whether the interaction occurs between species of the same (intra-) or different (inter-) patch. We show the ratio of positive to negative net effects, and the relative frequency of pairwise interactions that switch sign from direct to net effect.

Movement mode	Location	+/- ratio	Sign switches	
			+ to -	- to +
Dispersal	Intrapatch	0.95	0.07	0.33
	Interpatch	1.03	0.002	0
Foraging	Intrapatch	1.02	0.51	0.47
	Interpatch	0.97	0.42	0.41
Dispersal and foraging	Intrapatch	1.02	0.52	0.57
	Interpatch	1.02	0.48	0.49

on panel A of Fig. 2). Again, this trend is diluted in the foraging and mixed configurations. In these cases, interspecific effects display any combination of positive and negative signs, with no clear trend. Although here we analyze the results for $d = 0.5$ and $f = 0.5$, the distinctiveness of the effects of dispersal and foraging is maintained across a range of parameters (Appendix S1: Section S2).

What is the distribution of direct and net effects across the metacommunity?

All pairs of species interact indirectly, as evidenced by net effect networks having connectances and path lengths of 1 in all cases (Fig. 3). In contrast, direct effect networks are not fully connected, displaying intra-patch connectances at steady state of 0.38 on average and inter-patch connectances between 0.01 (dispersal only) and 0.1 (dispersal and foraging). Weighted modularity is also much higher in the direct effects networks than in the net effects ones, as expected. However, the modularity of the net effects networks also shows a decreasing trend from dispersal-only networks to dispersal and foraging ones (Fig. 3).

Does the magnitude of the net effects between any two species decay with increasing distance between them?

The magnitude of the net effect between any two species decays sharply with the length of the interaction chain connecting them (panel A of Fig. 4). This result is observed with the two movement types and their combination, although the decay rate is generally highest with foraging. The trend is also robust to variations on dispersal and foraging rates (Appendix S1: Section S2). The trend is also observed, albeit weaker, when the distance metric considered is the spatial distance between species pairs (i.e., the distance between their home locations, assuming that connected locations are at distance 1 from each other; panel B of Fig. 4).

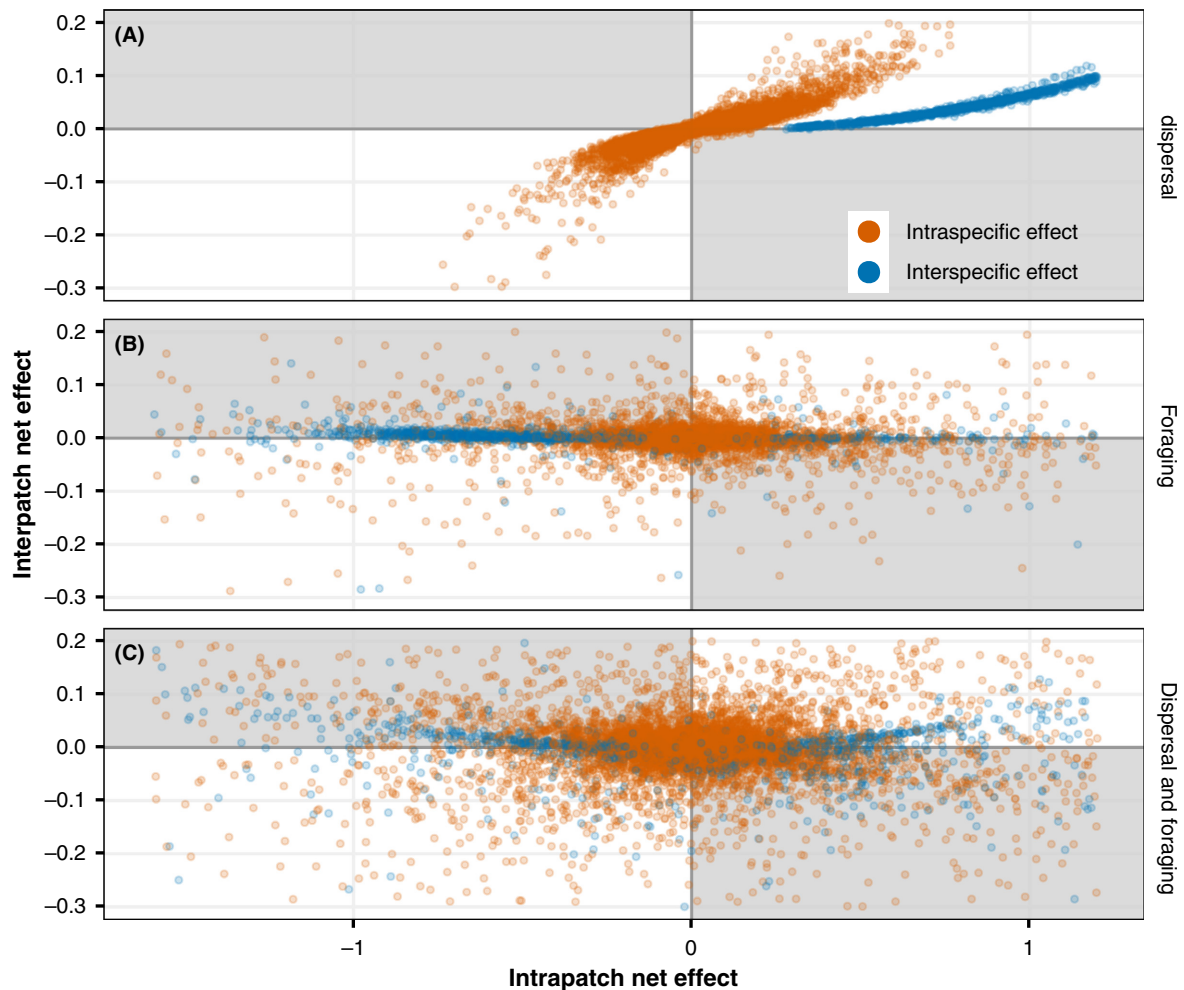


FIG. 2. Distribution of intra- and inter-patch net effects in the three configurations. Shaded quadrants are those where a sign switch occurs between intra- and inter-patch effects.

DISCUSSION

The importance of indirect effects, including trophic cascades, in driving ecosystem dynamics and structure is well established in theory (Abrams 1992, Wootton 2002, Gravel et al. 2010, Mayfield and Stouffer 2017) and empirically (Menge 1995, Peacor and Werner 1997, Moya-Laraño and Wise 2007, Barbosa et al. 2017, Trussell et al. 2017). The propagation of these effects across space has, however, not been studied systematically, despite many scattered observations of spatially explicit trophic cascades (Polis et al. 1997, Estes et al. 1998, Knight et al. 2005, Casini et al. 2012, Springer et al. 2018). Here we show that the sign and magnitude of spatial interaction effects are strongly influenced by the prevalent type of species movement (dispersal, foraging, or a mixture of both). In particular, model metacommunities with populations connected by dispersal and foraging differ on (1) the proportion of pairwise interactions that switch sign between their direct and net

effects (Table 1), and (2) the sign and magnitudes of net effects on the local patch and across patches (Fig. 2). Furthermore, the networks of net effects are markedly different from the direct effect ones, in all cases (Fig. 3). Lastly, we observed that, in most cases, the magnitude of net effects between any two populations decays significantly with the distance between the two populations (Fig. 4). In particular, the strongest decay occurs when distance is measured as the number of spatial connections necessary for linking the two populations.

Indirect effects may generate unexpected net interaction outcomes between pairs of species. For example, Montoya et al. (2009) analyzed a set of well-resolved empirical food webs and showed that the influence of indirect effects induced a switch in interaction signs from direct to net effect for approximately 40% of species pairs. Using a similar approach, we show that net effects between populations of spatially disconnected communities may also be primarily driven by indirect feedbacks, as for example, cases in which a species foraging on a

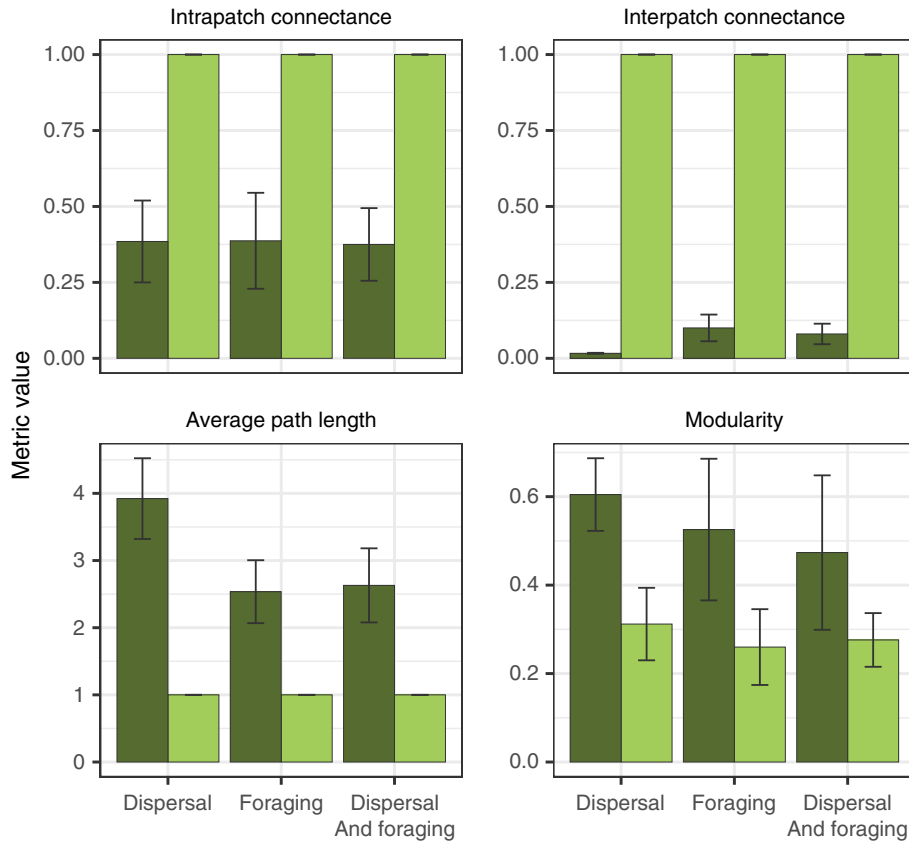


FIG. 3. Network metrics of the metacommunities at equilibrium. Dark shades represent networks of direct effects, light shades networks of net effects, and error bars intervals of one standard deviation around the mean.

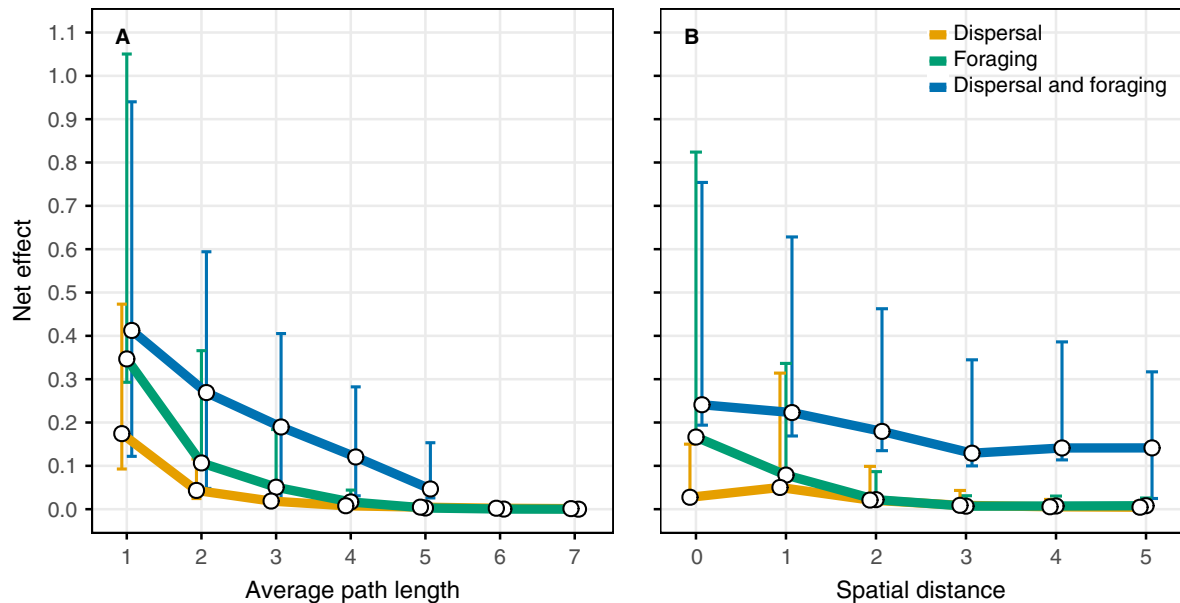


FIG. 4. Net effect between species pairs as a function of (A) average path length between species, (B) spatial distance between patches. Values are averaged over all replicates, and error bars represent 95% confidence intervals around the mean.

secondary location indirectly benefits its prey on this second location by altering the dynamics of the whole food web. This theoretical possibility has, to our knowledge, not been tested in empirical systems.

The “signatures” of net effects produced by dispersal, foraging, or mixed types of movement across localities are clearly different from each other (Amarasekare 2008). This occurs even though we imposed equal maximum dispersal and foraging distances, and after accounting for different values of dispersal and foraging rates (Appendix S1: Section S2). In the dispersal scenario, the almost complete concordance between the sign of intra- and inter-patch net effects points to a relatively homogeneous role of species at local and regional scales. Therefore, in natural systems with the same species pool connected mainly by dispersal, a local evaluation of the influence of the dispersing species may offer insights for the whole metacommunity. In the foraging or mixed modes, however, net effects between any two species are often of different sign at the local (within a given patch) and regional (across patches) scales. Therefore, within the assumptions of our model, when foraging is a prevalent mode of movement across locations, interspecific effects between any two species cannot be extrapolated from the local to the regional scale. In other words, a consumer that decreases a prey locally may have a positive effect on the same prey at the regional scale. Note, however, that our parameterizations represent communities within an homogeneous habitat, the same species pool in all locations, with no density-dependent movement modes, and no active prey or habitat selection. Furthermore, we deliberately chose dispersal and foraging modes of movement with identical maximum distances and temporal dynamics, in order to highlight their intrinsic differences. In reality, of course, both dispersal and foraging have extremely variable spatiotemporal scales. Foraging, in general, happens much faster than local demographic dynamics, which has led to characterise its effects as *spatial coupling* of local communities (Massol et al. 2011). This spatial coupling is thought to dampen population oscillations at lower trophic levels (McCann et al. 2005). The effects of dispersal, on the other hand, occur on temporal scales comparable to those of local dynamics, favouring different types of coexistence relationships, such as source–sink dynamics. The relative scales of foraging and dispersal are very heterogeneous, so that the spatial signal of interaction cascades will likely be correlated, in general, with these movement-related traits. In our model, we restricted the maximum dispersal and foraging rates to two cells away from the local community, and different values will presumably alter the net effect decay with spatial distance (Fig. 4, right panel). Interestingly, the decay of net effects with path length (Fig. 4, left panel) did not vary strongly with increases in maximum movement rates in our model (d and f , see Appendix S1: Fig. S4 and Fig. S5). This result suggests that indirect effects may dampen the propagation of strong

interactions across space, at least in environments with similar habitats and species pools. We have similarly shown that the variability in foraging net effects is usually much higher than that of net effects driven by dispersal (note the scatter of values in panels B and C of Fig. 2, and the error bars in Fig. 4). This likely occurs because foraging effects depend on the population sizes of the two species involved, whereas dispersal effects are mediated only by the size of the dispersing population. In that vein, although it is out of the scope of our first-principles study, our methodology makes it possible to evaluate the relative importance of direct and indirect effects for metacommunity dynamics, for example, by using variance partitioning techniques.

Networks of net effects are fully connected (Fig. 3), meaning that every species has a non-zero influence on every other species of the metacommunity through direct and/or indirect pathways. The magnitude of this effect, however, decays consistently with the distance and number of connections between species (Fig. 4). At the scale of local communities, Williams et al. (2002) reported that the majority of species in empirical food webs are separated by no more than two trophic links. We have shown that in small metacommunities, this distance increases only slightly, to no more than four links on average (average path lengths of Fig. 3). The number of connections between local communities increases from dispersal to foraging and mixed modes. This is reflected in the weighted modularity of the net effects networks, which tends to decrease along that axis. In the simple metacommunities modelled here, however, these structural patterns of the net effect networks are mostly confirmatory. In particular, net effect networks of dispersal and foraging modes are structurally similar, because in our model configuration, all species are able to disperse or, except for basal ones, forage outside their local community. Thus, the values of the metrics presented here represent upper bounds for metacommunities of the size and richness modeled.

Most empirical studies on ecological subsidies are focused on organismal movement or transfers between different habitats, which usually involve very specialized interactions (e.g., the consumption of Pacific salmon by grizzly bears, Naiman et al. 2002, Levi et al. 2012) or species with life stages in different habitats, such as arthropods with aquatic larval stages that, in their adult form, switch to a predator role in terrestrial habitats (Knight et al. 2005). We, in turn, modelled communities with the same pool of species and interactions on each patch. In general, we expect interactions connecting different habitats to be more specialized and have greater indirect effects than the foraging interactions modelled here (in what has been called *keystone interactions*, Helfield and Naiman 2006). This specificity is likely to alter both the structure of the overall meta-network (Fig. 3) and the distance decay curves observed in our model system (Fig. 4). For example, Knight et al. (2005) showed how predatory fish could have strong net effects

on terrestrial plants through a series of specialized interactions, even though the number of links separating these species is four (fish–dragonfly, larvae–dragonfly, adults–insect, pollinators–plants). More generally, insights from optimal foraging theory can be discussed under the same light. Directed foraging based on prey availability, distance, or other relevant parameters will increase the variability in the magnitude of direct effects, e.g., making some interactions stronger and other weaker, and thus coupling more strongly the dynamics of certain localities. Whether this expected stronger direct coupling will result in stronger indirect effects across the landscape is dependent on specific properties of the system under study, as, for example the centrality (in a network sense) of the species involved, and the spatial centrality of the localities with stronger coupling.

Spatial distributions of net effects can also vary from our expectations depending on the distances covered by the foraging or dispersing species. Intercontinental migrations are an extreme example of this, where strong coupled effects occur between species separated by thousands of kilometers (Alerstam and Bäckman 2018). Further, such migratory movements connect localities at different moments in time, rather than continuously. The effect of such temporal decoupling may provoke strong oscillatory dynamics between systems (Springer et al. 2018). So far, however, the stability dynamics associated with migrations have received little attention to date. Overall, the interplay between the rates and distances of dispersal and foraging, and their relationship to the spatial decay of net effects, clearly need more attention in theoretical models and empirical studies. For example, experimental mesocosms allowing spatial movement of certain species among them may be used to test the differential influence of foraging and dispersal on local dynamics.

CONCLUSIONS

We have provided a theoretical basis to the study of spatial propagation of indirect effects across ecosystems. We have shown that the net effect patterns generated by dispersal and foraging movements are clearly different: dispersal-driven metacommunities display patterns of direct and net effects consistent with each other, whereas foraging introduces a strong degree of variability on the distribution of net effects between species. Furthermore, the structure of the metacommunity networks is markedly different depending on whether one considers direct interactions or net effects between species. The decay of net effect magnitude with distance, in our model, is the only result common to all simulations performed. These results may shed light on the spread of interaction effects in patches of the same habitat type, such as forest patches inserted in agricultural or urban areas. Furthermore, they represent a baseline case for developing more complex scenarios, such as the effects of interaction spread (1) across different habitat types and species pools, or (2) considering long-distance species movements.

ACKNOWLEDGMENTS

We are grateful to three anonymous reviewers for their constructive suggestions. DGC was funded by the Spanish Ministry of Education (FPU fellowship reference 2013/02147). MBA acknowledges support from AAG-MAA/3764/2014 and CGL2015-68438-P projects.

LITERATURE CITED

- Abrams, P. A. 1987. On classifying interactions between populations. *Oecologia* 73:272–281.
- Abrams, P. A. 1992. Predators that benefit prey and prey that harm predators: unusual effects of interacting foraging adaptation. *American Naturalist* 140:573–600.
- Alerstam, T., and J. Bäckman. 2018. Ecology of animal migration. *Current Biology* 28:R968–R972.
- Amarasekare, P. 2008. Spatial dynamics of foodwebs. *Annual Review of Ecology, Evolution, and Systematics* 39: 479–500.
- Balcan, D., V. Colizza, B. Gonçalves, H. Hu, J. J. Ramasco, and A. Vespignani. 2009. Multiscale mobility networks and the spatial spreading of infectious diseases. *Proceedings of the National Academy of Sciences* 106:21484–21489.
- Barbosa, M., G. W. Fernandes, O. T. Lewis, and R. J. Morris. 2017. Experimentally reducing species abundance indirectly affects food web structure and robustness. *Journal of Animal Ecology* 86:327–336.
- Barthélemy, M. 2011. Spatial networks. *Physics Reports* 499:1–101.
- Bender, E. A., T. J. Case, and M. E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. *Ecology* 65:1–13.
- Berlow, E. L., et al. 2004. Interaction strengths in food webs: issues and opportunities. *Journal of Animal Ecology* 73:585–598.
- Casini, M., T. Blenckner, C. Möllmann, A. Gårdmark, M. Lindgren, M. Llope, G. Kornilovs, M. Plikshs, and N. C. Stenseth. 2012. Predator transitory spillover induces trophic cascades in ecological sinks. *Proceedings of the National Academy of Sciences* 109:8185–8189.
- Chalfoun, A. D., F. R. Thompson, and M. J. Ratnaswamy. 2002. Nest predators and fragmentation: a review and meta-analysis. *Conservation Biology* 16:306–318.
- Csardi, G., and T. Nepusz. 2006. The Igraph software package for complex network research. *InterJournal Complex Systems*:1695.
- Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak. 1998. Killer Whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282:473–476.
- Gounand, I., E. Harvey, C. J. Little, and F. Altermatt. 2018. Meta-ecosystems 2.0: rooting the theory into the field. *Trends in Ecology and Evolution* 33:36–46.
- Gravel, D., F. Guichard, M. Loreau, and N. Mouquet. 2010. Source and sink dynamics in meta-ecosystems. *Ecology* 91:2172–2184.
- Gravel, D., F. Massol, and M. A. Leibold. 2016. Stability and complexity in model meta-ecosystems. *Nature communications* 7:12457.
- Helfield, J. M., and R. J. Naiman. 2006. Keystone interactions: salmon and bear in riparian forests of Alaska. *Ecosystems* 9:167–180.
- Jaquet, C., D. Mouillot, M. Kulbicki, and D. Gravel. 2017. Extensions of island biogeography theory predict the scaling of functional trait composition with habitat area and isolation. *Ecology Letters* 20:135–146.

- Knight, T. M., M. W. McCoy, J. M. Chase, K. A. McCoy, and R. D. Holt. 2005. Trophic cascades across ecosystems. *Nature* 437:nature03962.
- Leibold, M. A., and J. M. Chase. 2018. Metacommunity ecology. Number 59 in *Monographs in population biology*. Princeton University Press, Princeton, New Jersey, USA.
- Leibold, M. A., et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7:601–613.
- Levi, T., C. T. Darimont, M. MacDuffee, M. Mangel, P. Paquet, and C. C. Wilmers. 2012. Using grizzly bears to assess harvest-ecosystem tradeoffs in salmon fisheries. *PLOS Biology* 10:e1001303.
- Loreau, M., N. Mouquet, and R. D. Holt. 2003. Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. *Ecology Letters* 6:673–679.
- Massol, F., D. Gravel, N. Mouquet, M. W. Cadotte, T. Fukami, and M. A. Leibold. 2011. Linking community and ecosystem dynamics through spatial ecology. *Ecology Letters* 14:313–323.
- Mayfield, M. M., and D. B. Stouffer. 2017. Higher-order interactions capture unexplained complexity in diverse communities. *Nature Ecology and Evolution* 1:0062.
- McCann, K. S., J. B. Rasmussen, and J. Umbanhowar. 2005. The dynamics of spatially coupled food webs. *Ecology Letters* 8:513–523.
- Menge, B. A. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecological Monographs* 65:21–74.
- Montoya, J. M., G. Woodward, M. C. Emmerson, and R. V. Solé. 2009. Press perturbations and indirect effects in real food webs. *Ecology* 90:2426–2433.
- Moya-Laraño, J., and D. H. Wise. 2007. Direct and indirect effects of ants on a forest-floor food web. *Ecology* 88:1454–1465.
- Naiman, R. J., R. E. Bilby, D. E. Schindler, and J. M. Helfield. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. *Ecosystems* 5:399–417.
- Newman, M. E. J. 2006. Modularity and community structure in networks. *Proceedings of the National Academy of Sciences* 103:8577–8582.
- Novak, M., J. D. Yeakel, A. E. Noble, D. F. Doak, M. Emmerson, J. A. Estes, U. Jacob, M. T. Tinker, and J. T. Wootton. 2016. Characterizing species interactions to understand press perturbations: What is the community matrix? *Annual Review of Ecology, Evolution, and Systematics* 47:409–432.
- Orians, G. H., and N. E. Pearson. 1979. On the theory of “central place foraging”. Pages 155–177. in J. Horn, G. R. Stairs, and R. D. Mitchell, editors. *Analysis of ecological systems*. Ohio State Press, Columbus, Ohio, USA.
- Peacor, S. D., and E. E. Werner. 1997. Trait-mediated indirect interactions in a simple aquatic food web. *Ecology* 78:1146–1156.
- Polis, G. A. 1994. Food webs, trophic cascades and community structure. *Australian Journal of Ecology* 19:121–136.
- Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28:289–316.
- R Development Core Team. 2018. R: a language and environment for statistical computing, Vienna, Austria. www.r-project.net.
- Schmitz, O. J., P. A. Hambäck, and A. P. Beckerman. 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *American Naturalist* 155:141–153.
- Springer, A. M., G. B. van Vliet, N. Bool, M. Crowley, P. Fullagar, M.-A. Lea, R. Monash, C. Price, C. Vertigan, and E. J. Woehler. 2018. Transhemispheric ecosystem disservices of pink salmon in a Pacific Ocean macrosystem. *Proceedings of the National Academy of Sciences* 115:E5038–E5045.
- Trussell, G. C., C. M. Matassa, and P. J. Ewanchuk. 2017. Moving beyond linear food chains: trait-mediated indirect interactions in a rocky intertidal food web. *Proceedings of the Royal Society B: Biological Sciences* 284:20162590.
- White, J. W., A. Rassweiler, J. F. Samhouri, A. C. Stier, and C. White. 2014. Ecologists should not use statistical significance tests to interpret simulation model results. *Oikos* 123:385–388.
- Williams, R. J., and N. D. Martinez. 2000. Simple rules yield complex food webs. *Nature* 404:180–183.
- Williams, R. J., E. L. Berlow, J. A. Dunne, A.-L. Barabási, and N. D. Martinez. 2002. Two degrees of separation in complex food webs. *Proceedings of the National Academy of Sciences* 99:12913–12916.
- Wootton, J. T. 2002. Indirect effects in complex ecosystems: recent progress and future challenges. *Journal of Sea Research* 48:157–172.
- Zhao, L., H. Zhang, E. J. O’Gorman, W. Tian, A. Ma, J. C. Moore, S. R. Borrett, and G. Woodward. 2016. Weighting and indirect effects identify keystone species in food webs. *Ecology Letters* 19:1032–1040.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.2820/supinfo>

CODE AND DATA AVAILABILITY

The R code used to generate the data and results is publicly available at <https://doi.org/10.5281/zenodo.1489992>