

IDEA AND PERSPECTIVE

More than a meal... integrating non-feeding interactions into food webs

Sonia Kéfi,^{1,2*} Eric L. Berlow,^{3,4,5}
 Evie A. Wieters,^{6,7} Sergio A.
 Navarrete,⁶ Owen L. Petchey,^{8,9}
 Spencer A. Wood,¹⁰ Alice Boit,¹¹
 Lucas N. Joppa,¹² Kevin D.
 Lafferty,¹³ Richard J. Williams,¹²
 Neo D. Martinez,⁴ Bruce A.
 Menge,¹⁴ Carol A. Blanchette,¹⁵
 Alison C. Iles¹⁴ and Ulrich Brose¹

Abstract

Organisms eating each other are only one of many types of well documented and important interactions among species. Other such types include habitat modification, predator interference and facilitation. However, ecological network research has been typically limited to either pure food webs or to networks of only a few (<3) interaction types. The great diversity of non-trophic interactions observed in nature has been poorly addressed by ecologists and largely excluded from network theory. Herein, we propose a conceptual framework that organises this diversity into three main functional classes defined by how they modify specific parameters in a dynamic food web model. This approach provides a path forward for incorporating non-trophic interactions in traditional food web models and offers a new perspective on tackling ecological complexity that should stimulate both theoretical and empirical approaches to understanding the patterns and dynamics of diverse species interactions in nature.

Keywords

Ecological network, ecosystem engineering, facilitation, food web, interaction modification, non-trophic interactions, trophic interactions.

Ecology Letters (2012) 15: 291–300

INTRODUCTION

Trophic interactions have been one of the most productive ‘low hanging fruits’ of ecological complexity research (e.g. Pimm 1982; Berlow *et al.* 2004; Dunne 2006). Compilation and analysis of trophic networks – webs of feeding interactions – continue to provide insights into the simple rules responsible for their structure and dynamics (Pimm 1982; Williams & Martinez 2000; Brose *et al.* 2006). Yet trophic interactions are only one of many mechanisms by which one species can influence another. Although Darwin’s (1859) classic ‘entangled bank’ of species ‘dependent on each other in so complex a manner’ is often referred to in food web research, Darwin was referring to a wide variety of interactions in addition to feeding, e.g. bees pollinating flowers, shrubs providing shelter for other species and trees providing

nesting habitat for birds. Non-trophic interactions, like these, can drive species diversity and composition, community patterns and productivity, or even act as the foundation for community persistence (e.g. Bertness & Callaway 1994; Jones *et al.* 1994, 1997; Menge 1995; Odling-Smee *et al.* 1996; Hacker & Gaines 1997; Choler *et al.* 2001; Mulder *et al.* 2001; Stachowicz 2001; Baxter *et al.* 2004; Croll *et al.* 2005; Rixen & Mulder 2005; Eisenhauer *et al.* 2009).

Empirical ecological network studies have mostly considered particular interactions in isolation, trophic or non-trophic, e.g. pollination, seed dispersal (Ings *et al.* 2009). Studies of such ‘single interaction type’ networks suggest that they exhibit predictable structural regularities (Williams & Martinez 2000; Bascompte *et al.* 2003; Verdu & Valiente-Banuet 2008; Thébault & Fontaine 2010). Pioneering studies have recently explored networks simultaneously

¹J.F. Blumenbach Institute of Zoology and Anthropology, Georg-August-University Goettingen, Berliner Str. 28, 37073 Goettingen, Germany

²Institut des Sciences de l’Evolution, CNRS UMR 5554, Université de Montpellier II, Place Eugène Bataillon, CC 065, 34095 Montpellier Cedex 05, France

³Sierra Nevada Research Institute, University of California, Yosemite National Park, Yosemite Field Station, Merced, CA 95389, USA

⁴Pacific Ecoinformatics and Computational Ecology Laboratory, 1604 McGee Avenue, Berkeley, CA 94703, USA

⁵Western Ecological Research Center, U.S. Geological Survey, Yosemite Field Station, 40298 Junction Dr, Suite A, Oakhurst, CA 93644, USA

⁶Estación Costera de Investigaciones Marinas and Center for Advanced Studies in Ecology and Biodiversity, Depto. de Ecología, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

⁷Zoology Department, Rhodes University, Grahamstown, South Africa

⁸Department of Animal and Plant Sciences, University of Sheffield, Sheffield, S10 2TN, UK

⁹Institute of Evolutionary Biology and Environmental Studies, University of Zürich, CH-8057 Zürich, Switzerland

¹⁰The Natural Capital Project, Stanford University, 371 Serra Mall, Stanford, CA 94305, USA

¹¹Institute of Biochemistry and Biology, University of Potsdam, Am Neuen Palais 10, 14469 Potsdam, Germany

¹²Microsoft Research, Computational Ecology and Environmental Sciences, Cambridge, CB3 0FB, UK

¹³Western Ecological Research Center, U.S. Geological Survey, c/o Marine Science Institute, UC, Santa Barbara, CA 93106, USA

¹⁴Department of Zoology, Oregon State University, Cordley Hall 3029, Corvallis, OR 97331-2914, USA

¹⁵Marine Science Institute, University of California, Santa Barbara, CA 93105, USA

*Correspondence: E-mail: sonia.kefi@univ-montp2.fr

including different types of trophic interactions (predation and parasitism; Lafferty *et al.* 2006) or combined trophic and non-trophic mutualistic interactions in bipartite networks (Melián *et al.* 2009). In theoretical studies, non-trophic interactions have only recently been coupled with trophic interactions in model networks (Arditi *et al.* 2005; Goudard & Loreau 2008). Missing, however, are more comprehensive 'ecological networks' that include the multi-trophic architecture of natural food webs as well as the non-trophic interactions (Borer *et al.* 2002; Berlow *et al.* 2004; Ings *et al.* 2009; Olff *et al.* 2009; Fontaine *et al.* 2011). Assembling and analysing such 'inclusive networks' would allow, for example, the use of network analyses to more realistically address their complexity, perhaps elucidating simple rules for their complex structure.

There are many types of trophic interactions (e.g. predation, micropredation, parasitism, nectar feeding, frugivory, detritivory). The diversity of non-trophic interactions could be greater still, which creates a challenge for summarising non-trophic interactions so they can be expressed in a network. This challenge requires that the diversity of non-trophic interactions is organised into a reasonable number of functional classes. Proposing a functional typology of non-trophic interactions, and showing their importance, is the purpose of this article. Our goals are: (1) to present a conceptual framework that can organise the diversity of non-trophic interactions into a small number of functional classes based on how they modify specific parameters in a complex food web model, (2) to illustrate the applicability of this framework with an example of a food web model that integrates non-trophic interactions. We hope that this effort offers a new perspective on ecological complexity that encourages others to explore the patterns and dynamics of integrated trophic and non-trophic networks in models and natural systems.

ORGANISING THE DIVERSITY OF NON-TROPHIC INTERACTIONS

There is a great diversity of non-trophic interactions observed in nature (supporting information). Kelp forests provide habitat for the survival of many species (Dayton 1985), desert shrubs buffer environmental stress and facilitate the persistence of other plant species (Pugnaire *et al.* 1996) and many species engage in antagonistic interactions to defend their territories (Hixon & Brostoff 1983). Some non-trophic interactions are closely associated with feeding activities but affect species that are neither the trophic consumer nor the resource. For instance, whales, rays, sea otters, birds and many other large consumers dig, burrow, turn rocks or sieve sediment while feeding, negatively or positively affecting many other species (e.g. Oliver & Slattery 1985). Other interactions inherently involve a trophic and a non-trophic component between the same pair of species, such as pollination and frugivory. A functionally important class of non-trophic interactions is ecosystem engineering (by e.g. earthworms or beavers), which determines the structure and fate of entire communities (Jones *et al.* 1994, 1997; Odling-Smee *et al.* 1996; Bruno *et al.* 2003). The consequences of these non-trophic interactions are as diverse as affecting the ability and efficiency of feeding, survival, behaviour (with possible consequences for e.g. metabolism), recruitment success and reproduction.

Non-trophic interactions have often been classified based on the qualitative effect of the interaction on the fitness (or fitness components) of the two participants, for example, mutualism (++), commensalism (+0), antagonism (+-), neutralism (00), amensalism (-0) and competition (--). For example, mutualism may occur via

increased feeding efficiency or decreased mortality. Because the processes of feeding and mortality have different dynamic consequences, it is useful for a functional typology of non-trophic interactions to encode information about the processes and their bio-physiological rates, in addition to the sign of the effect. For the same reason, different types of trophic interactions (+-), e.g. predator-prey and host-parasite, can be functionally separated and described by different consumption equations (Lafferty *et al.* 2006).

Another organising approach is to classify non-trophic interactions by their natural history or ecological consequences. For example, one large class of non-trophic interactions, ecosystem engineering, refers to organisms which 'directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials' (Jones *et al.* 1994, 1997; Hastings *et al.* 2007).

However, these approaches to classifying non-trophic interactions fail to distinguish the mechanism by which effects are mediated (e.g. on growth, survival, feeding, or reproduction of the affected species). To organise the diversity of non-trophic interactions, we propose to classify them into a few functional classes that depend on the impact of the interaction on the affected species, rather than on the specific nature of the interaction. These functional classes can be guided by how non-trophic interactions can be expressed in model parameters that govern the dynamics of the target species in a network context.

An example of modelling approach

Consider the basic representation of an energy flow through a species (i.e. a 'node') in a food web in Fig. 1a:

$$\frac{dN_i}{dt} = \underbrace{\sum_k e_i \underbrace{f_{ki}(N_k)N_i}_{\text{consumption (i consumes k)}}}_{\text{growth/reproduction}} - \underbrace{m_i N_i}_{\text{metabolism/mortality}} - \underbrace{\sum_j \underbrace{f_{ji}(N_j)N_j}_{\text{consumption (j consumes i)}}}_{\text{mortality (by consumption)}} + \underbrace{I - E}_{\text{immigration/emigration}}$$

where N_i is the biomass density of species i , e_i is the conversion efficiency of the resource k into species i , m_i is the mortality/metabolism rate, f_{ki} is the functional response which describes how the intake rate of species i varies as a function of the density of prey k , I is the immigration rate and E is the emigration rate of species i in and out of the system (Yodzis & Innes 1992; Brose 2008). In the case of a closed-off infinite system, $I = E = 0$. Note that our general approach is not restricted to this particular mathematical formulation.

The general principle with which non-trophic interactions depicted in Fig. 1b,c can be added to such a model is that specific parameters of this energy flow become directly dependent on the biomass of other species in the web, the so-called 'non-trophic interactor' (n_m in Fig. 1b,c). More precisely, any parameter of eqn 1 can become a function of the biomass of non-trophic interactors. As shown in Table 1, this approach allowed us to synthesise all forms of non-trophic interactions according to the different types of parameters in trophic models that they can influence.

Let us take for example the mortality rate m_i which would be a constant in a classic food web model. Another species, a non-trophic

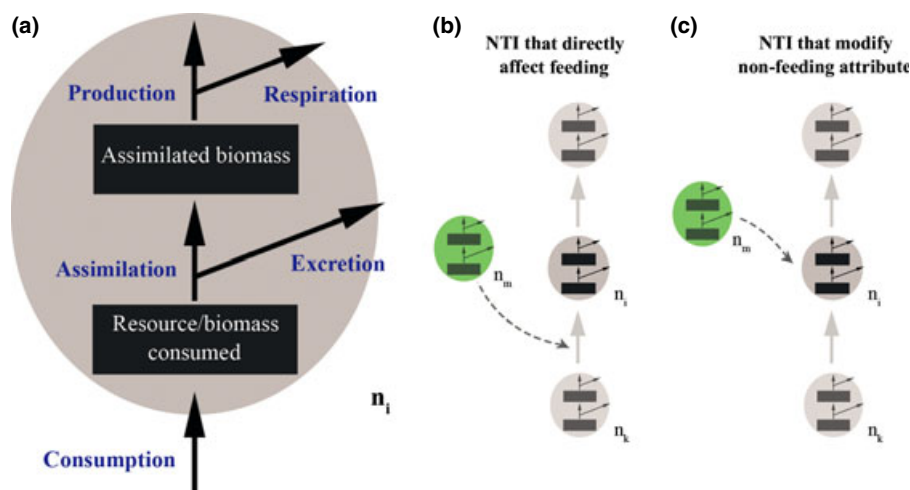


Figure 1 Illustration of the different ‘types’ of non-trophic interactions (NTI). (a) Schematic energy flow through a species (i.e. a ‘node’ in a network). (b and c) Basic modules within a network: nodes (circles) are species, plain grey arrows represent trophic interactions and dashed arrows represent non-trophic interactions. (b) Represents non-trophic interactions by a ‘non-trophic interactor’ (n_m) that affects feeding attributes of species n_i (dark dashed arrow). These types of non-trophic interactions affect attributes of the nodes in the network (e.g. attack rate, handling time), yet they can be visualised as affecting the trophic link between the two species n_i and n_k because they affect the feeding on species n_k . Such non-trophic interactions have been referred to as ‘interaction modifications’ when one focuses on the indirect consequence for n_k . Here, we define the non-trophic interactions as directly affecting feeding attributes of n_i . (c) Represents non-trophic interactions that affect an attribute of n_i which is unrelated to feeding. See Table 1 for the parameters that may be affected by non-trophic interactions along the energy flow diagram.

interactor, may affect the mortality rate of the focal species by buffering a physiological stress experienced by the focal species and thereby increasing its survival (Hay 1986; Bruno 2000; Cardinale *et al.* 2002). The parameter m_i is then a function of the biomass of the non-trophic interactor $m_i = f_{unc}(N_m)$, where f_{unc} is a function inversely relating the parameter m_i to the biomass density, N_m , of the non-trophic interactor. For example, the function f_{unc} could be a ‘rational function’ (using the terminology of Otto & Day 2007) such as:

$$m_i = f_{unc}(N_m) = \frac{m_{nti}N_m + m_oN_o}{N_m + N_o} \quad (2)$$

where N_m is the biomass density of the non-trophic interactor, N_o is a typical average biomass density of the non-trophic interactor, m_o is the mortality rate without non-trophic interaction, m_{nti} is the maximum mortality reached in the presence of non-trophic interactions. According to this function, the mortality of the focal species is m_o when there is no non-trophic interactor, and the mortality saturates at the value m_{nti} when non-trophic interactors are abundant. This function f_{unc} can be increasing or decreasing depending in the sign of $(m_{nti} - m_o)$ thereby allowing the description of both positive and negative effects of non-trophic interactors on mortality. Supporting information provides some general examples for these functions f_{unc} , but their exact shape will depend on the biology of the species. For trophic interactions, three types of functional responses have been defined (Holling 1959) – similar functions may be defined for non-trophic interactions but require observation.

A single non-trophic interactor may affect one or several parameters simultaneously. For example, mussel beds provide habitat for other species (e.g. crabs); this ‘habitat provisioning’ can increase establishment success and reduce physiological stress (decrease metabolism and/or increase survival) of crabs. In addition, crabs may benefit from reduced consumption by predators (e.g. birds), which in our approach would be encoded as a non-trophic effect of

mussels on bird consumption (e.g. decreasing the attack rate of birds on crabs).

Previous modelling approaches

The majority of theoretical studies that addressed non-trophic interactions have either studied several interaction types in systems with a few species or only one (or a few) interaction type(s) in multi-species systems (see Box 1 for details). To our knowledge, only two studies, Arditi *et al.* (2005) and Goudard & Loreau (2008), studied the role of non-trophic interactions in complex food web models. These two studies integrated non-trophic interactions as ‘modifications of trophic interactions’ or *rheagogies*, i.e. ‘a change in the direct interaction between two species due to the density of a third species’ (Arditi *et al.* 2005). They used linear functions to relate the biomass of the trophic interactor to the size of change in the strength of the trophic interaction (see details in Box 1). However, a number of non-trophic interactions cannot be summarised as modifications of trophic interactions (supporting information). Here, we build upon the approach of Arditi *et al.* (2005) and Goudard & Loreau (2008) to incorporate non-trophic interactions which modify non-linear trophic functional responses as well as non-trophic interactions that do not relate to feeding (Fig. 1c).

FUNCTIONAL CATEGORIES OF NON-TROPHIC INTERACTIONS

Non-trophic interactions that directly modify feeding

Organisms can affect how other organisms feed upon each other (e.g. associational defence, predation interference or escape responses; Hay 1986; Sih 1997). These non-trophic interactions induce changes in feeding and can be represented in the predator functional response (Arditi *et al.* 2005; Goudard & Loreau 2008). Here, we build on this approach based on linear functional responses by also including non-

Box 1 Previous Modelling Approaches of Non-Trophic Interactions

Although attention to non-trophic interactions in ecological networks has been sparse, these interactions have been included in several models of species interactions. Competition among organisms that use a common resource (termed 'exploitation competition'), for example, is probably one of the most studied interactions and has been considered to be a main factor shaping the structure and dynamics of ecological communities (Darwin 1859; MacArthur & Levins 1967; Tilman 1982). But competition for food is an indirect effect (Menge 1995) that is already incorporated into models of trophic interactions as consumer exploitation of shared prey.

In contrast to exploitation competition, interference competition for physical space or nutrients (sessile species or primary producers) or for refuges among territorial organisms is often not accounted for in network models because space, refuges or nutrients are not typically considered to be resource nodes in ecological networks. This is particularly problematic for basal species, which we know compete in natural ecosystems, but appear to have uncontested resources in most food web models. Competition among basal species in ecological networks can be accounted for by either explicitly specifying resource nodes (space, water, nutrients; see e.g. Brose 2008) or determining non-trophic interactions whose strength corresponds to niche overlap (Lafferty & Dunne 2010).

Direct competition among species (not occurring via a shared resource) has been included in different ways depending on whether it is inter or intraspecific. Interspecific competition was introduced early as a linear direct effect among species in simple mathematical models of population dynamics (Volterra 1926; Lotka 1932; Tilman 1982). Most often, intraspecific competition has been modelled by interference terms in the consumer functional response (DeAngelis *et al.* 1975), which implies that, in addition to search and handling times, consumers also spend time interfering non-trophically with each other.

A few studies have used extended Lotka–Volterra models of mutualism to address the functional consequences of the structure of mutualistic communities (e.g. Holland *et al.* 2002; Bascompte *et al.* 2006; Thébault & Fontaine 2010). Gross (2008) introduced positive interactions among resource competitors in a consumer–resource model and investigated their effect on species diversity.

To study the effect of non-trophic interactions that modify the environment, various studies have integrated ecological mechanisms such as ecosystem engineering and niche construction in theoretical models, usually by allowing certain species to affect the level of resource availability or of abiotic stress for others. Hastings *et al.* (2007) stressed the importance of incorporating the spatial and temporal scales of ecosystem engineering into ecological models. For example, Gurney & Lawton (1996) explicitly included time delays of the engineering effect, and Cuddington & Hastings (2004) proposed a spatially explicit model for engineers. Other models included more detailed interactions between the engineer and its habitat (van de Koppel *et al.* 2005; Kéfi *et al.* 2007; Kylafis & Loreau 2008; Diaz-Sierra *et al.* 2010). However, these studies are all based on one or a few species.

Arditi *et al.* (2005) and Goudard & Loreau (2008) studied the role of non-trophic interactions that affect feeding in complex food webs. In their model, the consumption of a prey by its predator increases linearly with the biomass of the prey, i.e. $f_{ki}(N_k) = c_{ki}N_k$ in eqn 1, where c_{ki} is the rate at which species i consumes k . In a pure food web model, c_{ki} is constant, but modifications of trophic interactions can be included by allowing the consumption rate c_{ki} to be a function of the biomass of non-trophic interaction interactors. Arditi *et al.* (2005) suggested to replace c_{ki} by the expression: $c_{ki}(1 + \sum_{j=1}^m a_{ikj}X_j)$, where a_{ikj} describes the influence of the non-trophic interactor, species j , on the trophic interaction between i and k . Note that a_{ikj} can be positive or negative but the expression should be bounded below by zero so that the flow of matter cannot be reversed in which case a prey would start eating its predator (Arditi *et al.* 2005).

trophic interactions that modify the shape of non-linear functional responses widely observed in nature (Skalski & Gilliam 2001).

Two parameters of the basic functional response can be affected by non-trophic interactions (see equations in supporting information) and become functions of the biomass of non-trophic interactors:

- (1) The asymptotic maximum consumption rate (c_{ki} in eqn 5 supporting information). This is the consumption rate reached when a further increase in prey density does not alter the per capita predator consumption anymore. This corresponds to situations where the speed of food processing is affected by a non-trophic interaction (e.g. some soil bacteria with external digestion facilitate the digestion of carbon resources for others; algae that erode the shell of bivalves and reduce handling time by shell crushing predators). In these cases, the per capita feeding rate at high (infinite) resource densities is increased by the non-trophic interaction, because the maximum resource processing rate is higher.
- (2) The half-saturation density (N_{kio} in eqn 5 supporting information). This is the density of prey at which the consumption rate is half the maximum. This corresponds to any non-trophic interaction that would increase or decrease the accessibility of

the resource (e.g. refuge provisioning, predator interference, associational defences). In these cases, the per capita feeding rate at high (infinite) resource density remains the same whereas feeding rates at lower resource densities are modified by non-trophic interactions.

Alternatively, the functional response can be formulated as a function of attack rates and handling times (which can easily be expressed as a function of the maximum consumption rate and the half-saturation density; supporting information). These non-trophic interactions that affect feeding do not only affect the parameters of the functional response, but also the shape of the functional response, i.e. the way the species interact. Predator interference, a non-trophic interaction that modifies feeding due to direct interactions among predator species of the same prey, was previously introduced in the functional response as an additive term in the denominator (proportional to the density of the species performing the non-trophic interaction; see supporting information for an example of equations). When the sign of this additive term is positive, the predator interferes with other predators of the same prey and its half-saturation density is increased (i.e. its attack rate is lowered), resulting in a negative non-trophic interaction.

Table 1 Summary of the categories of non-trophic interactions based on their direct effect on the focal species

Categories		Parameters that could be affected by non-trophic interactions	Examples
Non-trophic interactions that modify...			
...feeding parameters			
Parameters	half-saturation density/maximum consumption rate	N_{kio} c_{ki} (eqn 5 in Appendix) R_o C_{rb} (eqn 8 in Appendix)	Refuge from predation§ Escape responses§ Interspecific predator interference§ Plant substances attract enemies of their enemies§ Nitrogen fixing bacteria (on plants)*
...non-feeding parameters			
Parameters	Mortality/metabolism	m_i (eqn 1)	Whiplash effects (of algae on gastropods)§ Bulldozing effects (of gastropods on sessile species)§ Antagonistic interactions for territories§
	Conversion efficiency/reproduction	e_i (eqn 1)	Stress buffering (shading, rhizosphere oxidation, desiccation ...)§ Pollination§
	Access to pre-existing/available space (when space is modelled as a node: 'consumption' of space)	Establishment rate in space	Pre-emption of space (competition for space for sessile species)‡
	Total amount of space available (when space is modelled as a node)	Total amount of space available	3-D structures provided by kelps, coral reefs, tree litter Allelopathy‡
...flows across system boundaries			
Parameters	Immigration/emigration rates	I/E (eqn 1)	Alarm pheromones from aphids trigger escape behaviour§ Seed dispersal§ Recruitment facilitation§
	Supply/loss of detritus, nutrients and other abiotic resource	P/d (eqn 9 in Appendix)	Mussel faeces* Bird guano* Shading decreases evaporation of water*

Examples include cases where a non-trophic interaction affects a biotic resource (§), an abiotic resource (*) and space quality or availability (‡). Similarly to Fig. 1, subscript i refers to the focal species affected by non-trophic interactions, k to its prey, and j to its predator.

Any other species of the web could participate in this type of non-trophic interaction by 'interfering' with the functional response of a consumer, even in a passive manner. For example, in the presence of non-prey species, a predator may need to handle, evaluate and reject those individuals, thus reducing the amount of time available to search for and consume actual prey (van Veen *et al.* 2005).

Non-trophic interactions that modify non-feeding attributes of species

By modifying the level of abiotic stress experienced by others (e.g. by shading), species can directly alter life history attributes of other species independent of feeding. Such non-trophic interactions can affect the metabolic and mortality rates of the focal species (e.g. m_i in eqn 1) or the conversion efficiency (e.g. e_i , which can reflect growth and reproduction in the model of eqn 1).

Species can have direct effects on mortality, e.g. wave-induced whipping of barnacle recruits or gastropods on the rock surface by algae (Menge 1976; Ojeda & Santelices 1984), or killing of barnacles by gastropods which locally eliminate some non-prey sessile species by 'bulldozing' them off the rock while moving (Connell 1961; Dayton 1971). For these non-trophic interactions, the mortality parameter of the focal species is made a function of the biomass of the species causing the altered mortality.

In many cases, non-trophic interactions may have strong direct effects on reproduction. These include, for example, provisioning of nesting sites, pollination, and seed dispersal. Although some of these interactions have a trophic component (e.g. pollination), the effects

on the target species involve life history attributes rather than modified feeding. In models specifying reproductive traits (e.g. seed number or seed size for plants), non-trophic interactions would affect these reproductive traits. In our simple modelling framework (eqn 1), these effects could be included as a modification of the conversion efficiency.

Modelling non-trophic interactions that modify flows across system boundaries

One key constraint on non-trophic interactions is that they cannot alter the mass balance of an ecosystem that is modelled as a closed system (Arditi *et al.* 2005). However, if the system is 'open', non-trophic interactions can influence inflows and outflows of biomass and matter. One example of this is when species have 'open' populations with immigration and emigration. The immigration and emigration rates, I and E in eqn 1, may then become functions of the non-trophic interactor (e.g. facilitation of larval or spore settlement by structurally complex species, such as turf algae, mussel beds or barnacle beds in intertidal ecosystems; Wieters 2005; see also Hauzy *et al.* 2010). Non-trophic interactions may also modify the input or loss rate of an abiotic resource in the system. Typical examples are nitrogen fixation, shading (which decreases evaporative water loss) and substrate erosion or stabilisation.

When modelling a system, we impose artificial 'boundaries' (i.e. what is considered inside or outside the study system). Non-trophic interactions may affect the flows of material and biomass across these boundaries, or the partitioning of resources within the boundaries. For example, if the total nitrogen (N) in the ecosystem is

taken into account, nitrogen fixers only change the relative content of ammonia compared to nitrogen in the atmosphere (N_2), which makes nitrogen more accessible to their symbionts. However, if the boundary conditions of the model do not explicitly include this larger pool of nitrogen, facilitators may increase the total amount of nitrogen accessible to plants by modifying its flows in and/or out of the system, or they may increase the uptake rate of nitrogen by plants. Thus, in some cases, the definition of system boundaries and resource compartments (total nitrogen vs. N_2 and ammonium) of the model determine which attribute is affected by the non-trophic interaction: resource uptake rate parameters or total resources available.

The special cases of inorganic resources and of space

Inorganic, renewable resources

When an abiotic resource is modelled explicitly as a node in the model (e.g. Brose *et al.* 2005), non-trophic interactions may alter the parameters that govern the uptake efficiency or the amount of these abiotic resources (e.g. islands of fertility in dry lands; bird guano increases N available for algae in marine systems; see supporting information for an example of equations). Again, whether these non-trophic interactions alter access to resources or change the amount of resource in the system depends on how one defines the system boundaries. If the network does not explicitly track abiotic resources, competition among basal species for these resources can be determined by competition coefficients (Lotka 1932) or niche overlaps for inorganic resources (MacArthur & Levins 1967) among nodes (Lafferty & Dunne 2010). Including detritus, i.e. dead organic matter, as a node in the network (Moore *et al.* 2004) increases the number of possible non-trophic interactions that can occur because species' activities can then modify the amount and the kind of detritus available in the system.

Space, a limited resource

Space as a resource has been, to our knowledge, rarely modelled in a complex food web context (either explicitly or implicitly), but is commonly involved in non-trophic interactions. Space availability for establishment is one of the most important factors limiting population growth of sessile species. Mobile species also compete for space in the form of suitable sites and territories, e.g. for nesting or refuges from desiccation or solar radiation. In these cases, non-trophic interactors may modify how other species settle in, or 'consume', space.

One of the effects of structurally complex species or species assemblages (e.g. mussel beds) is to provide heterogeneity and surface area of attachment for smaller species, e.g. epiphytes and epibionts. These types of non-trophic interactions affect the total amount of space available for other species. In many cases, these same structurally complex species are also involved in other non-trophic interactions, such as refuge provisioning or stress buffering [e.g. structure provided by plants and trees (Franco & Nobel 1989); beavers (Jones *et al.* 1994), woody debris (Harmon *et al.* 1986) and coral reefs (Goreau *et al.* 1979)].

As a very first approximation, competition for space can be included by modelling space as a node in the network described by its own dynamic equation. Competition for space can also be incorporated as niche overlap between competing species (Lafferty & Dunne 2010). Finally, another approach consists of considering that food webs belong to patches which are connected to each other through

dispersal of organisms, i.e. metacommunities (McCann *et al.* 2005; Amarasekare 2008).

A refined definition of non-trophic interactions

Adding non-trophic interactions prompts important questions about what is included as a node in a network (e.g. nutrients, detritus, and space). Taking nutrients and detritus into account in food web models can improve our understanding of ecosystem functioning (e.g. Moore *et al.* 2004). Taking space into account might also be important, especially for sessile species that compete for space at the establishment stage, or for ecosystem engineers which can have large-scale spatial effects (Hastings *et al.* 2007). Adding these nodes allows a wider variety of non-trophic interactions to be integrated: species can affect the availability or access of any of these additional nodes for other species. We thus define a non-trophic interaction as: (1) a direct non-feeding effect of a species on another or (2) a direct non-feeding effect of a species on an abiotic node (e.g. nutrient, detritus or space), which indirectly affects one or more other species relying on that abiotic node.

A MODEL EXAMPLE

We consider a simple ecological network and we show how positive non-trophic interactions between plants and negative interference between predators can be included in these networks. This example is meant to illustrate the feasibility of the approach and not to study thoroughly or systematically the role of facilitation and interference in food webs.

Facilitation is particularly well documented for plant communities, where it may occur between species competing for the same resource (Callaway & Walker 1997). Herein, we consider a simple model of five plants consuming one common resource (e.g. such as eqns 8 and 9 in supporting information). We added facilitation in the functional response of the plants (other studies have added facilitation in the mortality term; Gross 2008). In other terms, the competitiveness of the facilitated species may depend on the biomass of the facilitating species. Following the same principle as previously explained in eqn 2, the half-saturation density of a plant consuming the resource, (i.e. R_{io} in eqn 8 in supporting information) becomes:

$$R_{io} = f_{inc}(N_m) = \frac{R_{nit}\alpha \sum_m N_m + R_o N_o}{\alpha \sum_m N_m + N_o} \quad (11)$$

where the index m refers to the plant species which is facilitating species i , N_m their biomass density and α a measure of the facilitation strength. When there is no facilitation (i.e. either when $\alpha = 0$ or when all the facilitating species are absent) the value of the half-saturation density is R_o , and the functional response is as formulated in eqn 8. In the presence of facilitating species, the R_{io} of the plant species decreases (i.e. competitiveness increases) when the N_m are more abundant or when α increases (and tends to its minimal value R_{nit}). The facilitative interactions between plants were set as follows. Plants were ordered by their competitive ability and superior competitors facilitated all the species that were less competitive than them (Verdu & Valiente-Banuet 2008). This very simple scenario was chosen for illustrative reasons.

To simulate a complete food web, on top of our five plant species we added 15 species (herbivores and carnivores) based on a niche model with connectance 0.1 (Williams & Martinez 2000). We used the

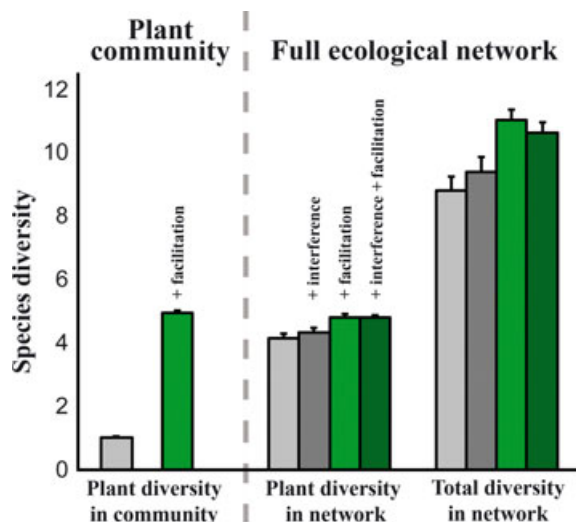


Figure 2 Effect of facilitation among plants and interference among predators on species diversity. Diversity is the number of species that survived in the community. Left of the grey dashed line: plant community starting with five plants. Middle and right of the grey dashed line: networks based on a niche model starting with 20 species including five plants. Middle: plant diversity in this network. Right: total diversity in this network (including plants). Light grey bars show simulation results in a trophic networks (no non-trophic interactions), dark grey bars correspond to simulations with interference among predators, light green bars to those with facilitation among plants and dark green bars to those with interference and facilitation. Each simulation was based on 100 repetitions with random variation in the food web structure. Error bars indicate the standard error of the mean. The parameter values and more details about the simulations are given in supporting information.

approach explained in Brose (2008) to build this multitrophic web (more details are given in supporting information).

Predator species hunting the same prey may interfere with each other. We included interference between all the predator species of a common prey following the equation of Guill & Drossel (2008) presented in supporting information (the interference term is added as the sum of all the predators of a given prey in the denominator of the functional response).

We ran simulations of the plant communities with and without facilitation among plants, and of the complete webs without non-trophic interactions (no facilitation, no interference), with facilitation only, with interference only and with both types of non-trophic interactions. When several plants consume the same resource, a well-known theoretical prediction is that the most competitive one (i.e. the one with the lowest R_{in}) will eventually take over and outcompete the other species (Tilman 1982). In plant communities, facilitation by competitively superior plants has a strong impact on diversity and all the five initial plants species survive in a plant community with facilitation (Fig. 2 left; Gross 2008; Diaz-Sierra *et al.* 2010).

When higher trophic levels are added on top of the plant community, almost all the five plant species can coexist in the complete web even without non-trophic interactions (Fig. 2 middle, light grey bar). As a consequence, the effect of facilitation on plant diversity still exists but is smaller. Interference also increases species diversity, but to a much lesser extent than facilitation, whereas the combination of facilitation and interference leads to an intermediate result between the case with facilitation only and the one with interference only. This small increase in diversity due to non-trophic

interactions still translates into an overall increase of diversity in the whole web, of 7% for interference alone and of 25% for facilitation alone (Fig. 2 right). This very simple example is meant to illustrate not only that it is feasible to integrate non-trophic interactions into complex food webs, but also that they can have important community level consequences for persistence and diversity.

PERSPECTIVES

Why have non-trophic interactions been largely ignored in ecological networks? Possible explanations are: (1) Non-trophic interactions appear so varied and context-specific that they seem intractably complex and idiosyncratic. Indeed, even their name only defines them by what they are not. (2) Empirically identifying the presence/absence of non-trophic interactions by necessity relies heavily on expert opinion, sometimes on disparate taxa, or experimental manipulations. (3) Two species may engage in multiple direct non-trophic interactions, making them difficult to functionally categorise and model. (4) A framework for incorporating such diverse interaction types into existing food web models has been lacking and is only starting to be developed (Arditi *et al.* 2005; Goudard & Loreau 2008). Fortunately, all these obstacles are interrelated, and the first three may be overcome by advancing the fourth.

One of the greatest challenges of environmental biology is to predict how human impacts propagate through the complex network of interactions among the organisms in natural communities. When considered together with feeding, the diverse interdependencies of trophic and non-trophic interactions determine how the extinction, invasion, and population dynamics of species affect other species within their community. Lack of their understanding may be a key source of many 'ecological surprises' (*sensu* Doak *et al.* 2008) that have been attributed to the overwhelming complexity of species interdependencies. Given the well documented functional importance of non-trophic interactions, it is essential that we begin integrating them with trophic interactions in one unified framework. We propose a systematic treatment of the high diversity of non-trophic interactions by classifying them based on how they affect key parameters in food web models. We show that non-trophic interactions can be organised into three main categories which modify feeding, non-feeding node attributes or flows of matter in and out of the system studied.

We see both empirical and theoretical perspectives to this work. First, it is essential to compile comprehensive ecological networks for a variety of ecosystems to search for general patterns in the relationship between trophic and non-trophic interactions, and in the distribution of different types of non-trophic interactions. Construction of comprehensive ecological networks including trophic and non-trophic interactions can be aided by the wealth of expert knowledge about non-trophic interactions that exists in many ecological communities. Many non-trophic interactions require experimental manipulation to fully quantify, but, as a first step, expert knowledge can be used to identify the set of interactions that are plausible over a specified spatial and temporal scale. Subsequent research on comprehensive ecological networks could help address a number of questions: How do the frequency, types and relative frequency of different types of non-trophic interactions vary across different classes of ecosystems? Where do non-trophic interactions occur within the web relative to each other and to trophic links? Pioneering studies on networks with two interaction types (antago-

nistic and mutualistic) have shown that the patterns observed in empirical data – a combination of topology (in particular the mutualism to antagonism ratio per plant) and distribution in interaction strength – increased species diversity in complex networks (Melián *et al.* 2009).

Second, beyond the description of non-trophic interactions in nature, we need to integrate the variety of non-trophic interactions into food web models to study their dynamical functional importance. Does the architecture of trophic and non-trophic links reflect dynamical constraints on ecological network structure? A critical next step is to develop a theoretical foundation for assigning the likely distribution of different types of non-trophic interactions within a typical food web – in other words, given the potential influence of non-trophic interactions on system-level dynamics, what types of effects are most likely and where are they most likely to occur? Lafferty & Dunne (2010) argue that, at the very least, networks should consider niche overlap (competition) among basal species. What are the dynamic consequences of non-trophic interactions in food webs? Previous studies suggest that non-trophic interactions could have very important and sometimes unexpected functional consequences. Initial studies combining trophic dynamics of complex food webs and explicit resource competition amongst basal species demonstrated that: (1) these non-trophic interactions change community dynamics (Brose *et al.* 2005), (2) consideration of competition among basal species reduces measures of network stability (Lafferty & Dunne 2010) and (3) trophic networks can lead to stable coexistence of basal species under asymmetric competition (Brose 2008). Interference competition can strongly stabilise consumer-resource and complex food web models (Rall *et al.* 2008). In the case of mutualistic networks, we know that their nested structure enhances their resilience (Bascompte *et al.* 2003; Thébault & Fontaine 2010). Various models addressing the role of habitat modification, ecosystem engineering and niche construction showed that non-trophic interactions can increase species diversity (Gross 2008), productivity (Kéfi *et al.* 2007), the spatial organisation of individuals (van de Koppel *et al.* 2005; Kéfi *et al.* 2007) and resilience to external disturbances (van de Koppel *et al.* 2005). Arditi *et al.* (2005) and then Goudard & Loreau (2008) showed that non-trophic interactions that are modifications of trophic interactions, can profoundly influence ecosystem properties such as species diversity, biomass and production. These results provide just a glimpse into the *potential* importance of non-trophic interactions in complex networks.

Our lack of knowledge of the functional role of non-trophic interactions in complex ecological communities reveals a serious gap in our understanding of how species interactions determine population and community dynamics. We anticipate that the conceptual framework of functional classes of non-trophic interactions initiated herein will facilitate future models integrating trophic and non-trophic interactions. Certainly, any successful integration will depend heavily on close collaborations between empiricists and modellers to determine quantitative functions of non-trophic interactions that can be incorporated into dynamic models (Bersier 2007). Similarly, the consequences of empirical uncertainty in functional forms can be explored theoretically to help better target where to devote empirical effort. In this vein, going further in the description and understanding of the role of non-trophic interactions will require a sense of their strength, and, therefore, of a currency that is comparable to trophic interactions. Incorporating non-trophic interactions into models of ecological communities will lead to additional complexity, but this

increased complexity may not make the system more complicated. The structure and dynamics of the ecosystems may be complex and also governed by simple rules (Berlow *et al.* 2009; Wood *et al.* 2010).

CONCLUSION

In ecosystems, the ‘entangled bank’ of species involves feeding as well as a myriad of non-trophic interactions which have long been recognised, but yet have hardly been studied in concert with trophic interactions in multi-species systems. Herein, we propose functional categories that might help in putting together ecological network datasets and integrating non-trophic interactions into food web models. There is considerable potential to improve our understanding of ecosystem functioning, dynamics, and resilience by studying different types of interactions together rather than in isolation.

ACKNOWLEDGEMENTS

Part of SK and ELB’s research was funded by a Humboldt fellowship from the Alexander von Humboldt foundation. A number of grants to SAN and EAW have allowed data collection and experimentation on Chilean rocky shores. Of these, a Fondap Fondecyt 15001-001 (CASEB) and Fondecyt #107335 to SAN and a Fondecyt #1100920 grant to EAW have been instrumental. This international collaboration would not have been possible without support from Rhodes University Fellowship to EAW, and a Fondecyt International Collaboration grant #7100021 to SAN and ELB. OLP received funding as a Royal Society University Research Fellow. UB is supported by the German Research Foundation (BR 2315/13-1). BAM has been supported by grants from NSF, and the AW Mellon, D & L Packard, G & B Moore and W & G Valley Foundations. ACI is supported by these and an NSERC Graduate Fellowship. This is publication #411 from PISCO (Partnership for Interdisciplinary Studies of Coastal Oceans) supported in part by the D & L Packard and G & B Moore Foundations. We would like to thank John McLaughlin and Erin Mordecai, five anonymous referees and the editor for very helpful comments on the manuscript.

AUTHORSHIP

All authors contributed to the conceptual development in a workshop at the Sierra Nevada Research Institute organised by ELB and CAB. SK was the lead on all writing and analysis, and all authors contributed substantially to revisions. EAW, SAN, SAW, BAM, KDL, CAB and ACI contributed substantially to the empirical perspectives on non-trophic interactions. EAW, SAN, SK, ELB, LNJ, OLP, AB, RJW, NDM and UB contributed substantially to the theoretical and conceptual perspectives on non-trophic interactions.

REFERENCES

- Amarasekare, P. (2008). Spatial dynamics of food webs. *Ann. Rev. Ecol. Evol. Syst.*, 39, 479–500.
- Arditi, R., Michalski, J. & Hirzel, A.H. (2005). Rheagogies: modelling non-trophic effects in food webs. *Ecol. Complex.*, 2, 249–258.
- Bascompte, J., Jordano, P., Melian, C.J. & Olesen, J.M. (2003). The nested assembly of plant-animal mutualistic networks. *Proc. Natl. Acad. Sci. USA*, 100, 9383–9387.
- Bascompte, J., Jordano, P. & Olesen, J.M. (2006). Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science*, 312, 431–433.

- Baxter, C.V., Fausch, K.D., Murakami, M. & Chapman, P.L. (2004). Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. *Ecology*, 85, 2656–2663.
- Berlow, E.L., Neutel, A.-M., Cohen, J.E., De Ruiter, P.C., Ebenman, B., Emmerman, M. *et al.* (2004). Interaction strengths in food webs: issues and opportunities. *J. Anim. Ecol.*, 73, 585–598.
- Berlow, E.L., Dunne, J.A., Martinez, N.D., Stark, P.B., Williams, R.J. & Brose, U. (2009). Simple prediction of interaction strengths in complex food webs. *Proc. Natl. Acad. Sci. USA*, 106, 187–191.
- Bersier, L.F. (2007). A history of the study of ecological networks. In: *Biological Networks* (ed. Kepes, F.). World Scientific, New Jersey, pp. 365–421.
- Bertness, M.D. & Callaway, R. (1994). Positive interactions in communities. *Trends Ecol. Evol.*, 9, 191–193.
- Borer, E.T., Anderson, K., Blanchette, C.A., Broitman, B., Cooper, S.D., Halpern, B.S. *et al.* (2002). Topological approaches to food web analyses: a few modifications may improve our insights. *Oikos*, 99, 397–401.
- Brose, U. (2008). Complex food webs prevent competitive exclusion among producer species. *Proc. R. Soc. London Ser. B*, 275, 2507–2514.
- Brose, U., Berlow, E.L. & Martinez, N.D. (2005). Scaling up keystone effects from simple to complex ecological networks. *Ecol. Lett.*, 8, 1317–1325.
- Brose, U., Jonsson, T., Berlow, E.L., Warren, P., Banasek-Richter, C., Bersier, L.F. *et al.* (2006). Consumer-resource body-size relationships in natural food webs. *Ecology*, 87, 2411–2417.
- Bruno, J.F. (2000). Facilitation of cobble beach plant communities through habitat modification by *Spartina alterniflora*. *Ecology*, 81, 1179–1192.
- Bruno, J.F., Stachowicz, J.J. & Bertness, M.D. (2003). Inclusion of facilitation into ecological theory. *Trends Ecol. Evol.*, 18, 119–125.
- Callaway, R.M. & Walker, L.R. (1997). Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology*, 78, 1958–1965.
- Cardinale, B.J., Palmer, M.A. & Collins, S.L. (2002). Species diversity increases ecosystem functioning through interspecific facilitation. *Nature*, 415, 426–429.
- Choler, P., Michalet, R. & Callaway, R.M. (2001). Facilitation and competition on gradients in alpine plant communities. *Ecology*, 82, 3295–3308.
- Connell, J.H. (1961). The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology*, 42, 710–723.
- Croll, D.A., Maron, J.L., Estes, J.A., Danner, E.M. & Byrd, G.V. (2005). Introduced predators transform subarctic islands from grassland to tundra. *Science*, 307, 1959–1961.
- Cuddington, K. & Hastings, A. (2004). Invasive engineers. *Ecol. Modell.*, 178, 335–347.
- Darwin, C. (1859). *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. John Murray, London.
- Dayton, P.K. (1971). Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.*, 41, 351–389.
- Dayton, P.K. (1985). Ecology of kelp communities. *Annu. Rev. Ecol. Syst.*, 16, 215–245.
- DeAngelis, D.L., Goldstein, R.A. & O'Neill, R.V. (1975). A model for trophic interaction. *Ecology*, 56, 881–892.
- Diaz-Sierra, R., Zaval, M.A. & Rietkerk, M. (2010). Positive interactions, discontinuous transitions and species coexistence in plant communities. *Theor. Popul. Biol.*, 77, 131–144.
- Doak, D.F., Estes, J.A., Halpern, B.S., Jacob, U., Lindberg, D.R., Lovvorn, J., Monson, D.H., Tinker, M.T., Williams, T.M., Wootton, J.T., Carroll, I., Emmerson, M., Micheli, F. & Novak, M. (2008). Understanding and predicting ecological dynamics: Are major surprises inevitable? *Ecology*, 89, 952–961.
- Dunne, J.A. (2006). The network structure of food webs. In: *Ecological Networks: Linking Structure to Dynamics in Food Webs* (eds Pascual, M. & Dunne, J.A.). Oxford University Press, New York, pp. 27–86.
- Eisenhauer, N., Milcu, A., Nitschke, N., Sabais, A.C.W., Scherber, C. & Scheu, S. (2009). Earthworm and belowground competition effects on plant productivity in a plant diversity gradient. *Oecologia*, 161, 291–301.
- Fontaine, C., Guimarães, P.R. Jr, Kéfi, S., Loeuille, N., Memmott, J., van der Putten, W.H. *et al.* (2011). The ecological and evolutionary implications of merging different types of networks. *Ecol. Lett.*, 14, 1170–1181.
- Franco, A.C. & Nobel, P.S. (1989). Effect of nurse plants on the microhabitat and growth of cacti. *J. Ecol.*, 77, 870–886.
- Goreau, T.F., Goreau, N.I. & Goreau, T.J. (1979). Corals and coral reefs. *Sci. Am.*, 241, 124–136.
- Goudard, A. & Loreau, M. (2008). Non-trophic interactions, biodiversity and ecosystem functioning: an interaction web model. *Am. Nat.*, 171, 91–106.
- Gross, K. (2008). Positive interactions among competitors can produce species-rich communities. *Ecol. Lett.*, 11, 929–936.
- Guill, C. & Drossel, B. (2008). Emergence of complexity in evolving niche-model food webs. *J. Theor. Biol.*, 251, 108–120.
- Gurney, W.S.C. & Lawton, J.H. (1996). The population dynamics of ecosystem engineers. *Oikos*, 76, 273–283.
- Hacker, S.D. & Gaines, S.D. (1997). Some implications of direct positive interactions for community species diversity. *Ecology*, 78, 1990–2003.
- Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D. *et al.* (1986). Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research*, 34, pp. 133–302.
- Hastings, A., Byers, J.E., Crooks, J.A., Cuddington, K., Jones, C.G., Lambrinos, J.G. *et al.* (2007). Ecosystem engineering in space and time. *Ecol. Lett.*, 10, 153–164.
- Hauzy, C., Gauduchon, M., Hulot, F.D. & Loreau, M. (2010). Density-dependent dispersal and relative dispersal affect the stability of predator-prey metacommunities. *J. Theor. Biol.*, 266, 458–469.
- Hay, M.E. (1986). Associational plant defenses and the maintenance of species diversity: turning competitors into accomplices. *Am. Nat.*, 128, 617–641.
- Hixon, M.A. & Brostoff, W.N. (1983). Damsel fish as keystone species in reverse: intermediate disturbance and diversity of reef algae. *Science*, 220, 511–513.
- Holland, J.N., DeAngelis, D.L. & Bronstein, J.L. (2002). Population dynamics and mutualism: functional responses of benefits and costs. *Am. Nat.*, 159, 231–244.
- Holling, C.S. (1959). Some characteristics of simple types of predation and parasitism. *Canad. Entomol.*, 91, 385–398.
- Ings, T.C., Montoya, J.M., Bascompte, J., Bluthgen, N., Brown, L., Dormann, C.F. *et al.* (2009). Ecological networks – beyond food webs. *J. Anim. Ecol.*, 78, 253–269.
- Jones, C., Lawton, J. & Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos*, 69, 373–386.
- Jones, C.G., Lawton, J.H. & Shachak, M. (1997). Positive and negative effects of organisms as physical ecosystem engineers. *Ecology*, 78, 1946–1957.
- Kéfi, S., Rietkerk, M., van Baalen, M. & Loreau, M. (2007). Local facilitation, bistability and transitions in arid ecosystems. *Theor. Popul. Biol.*, 71, 367–379.
- van de Koppel, J., Rietkerk, M., Dankers, N. & Herman, P.M.J. (2005). Scale-dependent feedback and regular spatial patterns in young mussel beds. *Am. Nat.*, 165, E66–E77.
- Kylafis, G. & Loreau, M. (2008). Ecological and evolutionary consequences of niche construction for its agent. *Ecol. Lett.*, 11, 1072–1081.
- Lafferty, K.D. & Dunne, J.A. (2010). Stochastic ecological network occupancy (SENO) models: a new tool for modeling ecological networks across spatial scales. *Theor. Ecol.*, 3, 123–135.
- Lafferty, K., Dobson, A.P. & Kuris, A.M. (2006). Parasites dominate food web links. *Proc. Natl. Acad. Sci. USA*, 103, 11211–11216.
- Lotka, A.J. (1932). The growth of mixed populations: two species competing for a common food supply. *J. Wash. Acad. Sci.*, 22, 461–469.
- MacArthur, R.H. & Levins, R. (1967). The limiting similarity, convergence and divergence of coexisting species. *Am. Nat.*, 101, 377–385.
- McCann, K.S., Rasmussen, J.B. & Umbanhowar, J. (2005). The dynamics of spatially coupled food webs. *Ecol. Lett.*, 8, 513–523.
- Melián, C.J., Bascompte, J., Jordano, P. & Křivan, V. (2009). Diversity in a complex ecological network with two interaction types. *Oikos*, 118, 122–130.
- Menge, B.A. (1976). Organization of the new england rocky intertidal community: role of predation, competition, and environmental heterogeneity. *Ecol. Monogr.*, 46, 355–393.
- Menge, B.A. (1995). Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecol. Monogr.*, 65, 21–74.
- Moore, J.C., Berlow, E.L., Coleman, D.C., de Ruiter, P.C., Dong, Q., Hastings, A. *et al.* (2004). Detritus, trophic dynamics and biodiversity. *Ecol. Lett.*, 7, 584–600.
- Mulder, C.P.H., Uliassi, D.D. & Doak, D.F. (2001). Physical stress and diversity-productivity relationships: the role of positive interactions. *Proc. Natl. Acad. Sci. USA*, 98, 6704–6708.
- Odling-Smee, F.J., Laland, K.N. & Feldman, M.W. (1996). Niche construction. *Am. Nat.*, 147, 641–648.

- Ojeda, F.P. & Santelices, B. (1984). Ecological dominance of *Lessonia nigrescens* (Phaeophyta) in central Chile. *Mar. Ecol. Prog. Ser.*, 19, 83–91.
- Olf, H., Alonso, D., Berg, M.P., Eriksson, B.K., Loreau, M., Piersma, T. *et al.* (2009). Parallel ecological networks in ecosystems. *Philos. Trans. R. Soc. London B*, 364, 1755–1779.
- Oliver, J.S. & Slattery, P.N. (1985). Destruction and opportunity on the sea floor: effects of gray whale feeding. *Ecology*, 66, 1965–1975.
- Otto, S.P. & Day, T. (2007). *A Biologist's Guide to Mathematical Modeling in Ecology and Evolution*. Princeton University press, Princeton and Oxford.
- Pimm, S.L. (1982). *Food Webs*. Chapman and Hall, London.
- Pugnaire, F.I., Haase, P. & Puigdefabregas, J. (1996). Facilitation between higher plant species in a semiarid environment. *Ecology*, 77, 1420–1426.
- Rall, B.C., Guill, C. & Brose, U. (2008). Food-web connectance and predator interference dampen the paradox of enrichment. *Oikos*, 117, 202–213.
- Rixen, C. & Mulder, C.P. (2005). Improved water retention links high species richness with increased productivity in arctic tundra moss communities. *Oecologia*, 146, 287–299.
- Sih, A. (1997). To hide or not to hide? Refuge use in a fluctuating environment. *Trends Ecol. Evol.*, 12, 375–376.
- Skalski, G.T. & Gilliam, J.F. (2001). Functional responses with predator interference: viable alternatives to the Holling Type II model. *Ecology*, 82, 3083–3092.
- Stachowicz, J.J. (2001). Mutualism, facilitation, and the structure of ecological communities. *Bioscience*, 51, 235–246.
- Thébault, E. & Fontaine, C. (2010). Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science*, 329, 853–856.
- Tilman, D. (1982). *Resource Competition and Community Structure*. Princeton University Press, Princeton.
- van Veen, F.J., van Holland, P.D. & Godfray, H.C.J. (2005). Stable coexistence in insect communities due to density- and trait-mediated indirect effects. *Ecology*, 86, 3182–3189.
- Verdu, M. & Valiente-Banuet, A. (2008). The nested assembly of plant facilitation networks prevents species extinctions. *Am. Nat.*, 172, 751–760.
- Volterra, V. (1926). Fluctuations in the abundance of a species considered mathematically. *Nature*, 118, 558–560.
- Wieters, E. (2005). Upwelling-control of positive interactions over mesoscales: A new path linking bottom-up and top-down processes. *Mar. Ecol. Prog. Ser.*, 30, 43–54.
- Williams, R.J. & Martinez, N.D. (2000). Simple rules yield complex food webs. *Nature*, 404, 180–183.
- Wood, S.A., Lilley, S.A., Schiel, D.R. & Shurin, J.B. (2010). Organismal traits are more important than environment for species interactions in the intertidal zone. *Ecol. Lett.*, 13, 1160–1171.
- Yodzis, P. & Innes, S. (1992). Body size and consumer resource dynamics. *Am. Nat.*, 139, 1151–1175.

SUPPORTING INFORMATION

Additional Supporting Information may be downloaded via the online version of this article at Wiley Online Library (www.ecologyletters.com).

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organised for online delivery, but are not copy edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

Editor, Wim van der Putten
 Manuscript received 15 June 2011
 First decision made 22 July 2011
 Second decision made 2 December 2011
 Manuscript accepted 14 December 2011