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

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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.

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 1993; Odling-Smeek et al. 1996; Hacker & Gaines 1997; Choler et al. 2001; Mulder et al. 2001; Stachowicz et al. 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

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including different types of trophic interactions (predation and parasitism; Lafferty et al. 2006) or combined trophic and non-trophic mutualistic interactions in bipartite networks (Melian 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; O’Neill et al. 2009; Oliff 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; Olff 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 (0 0), 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:

$$\frac{dN_i}{dt} = \sum_k e_{ki} f_{ki}(N_k)N_i - m_i N_i$$

where $N_i$ is the biomass density of species $i$, $e_{ki}$ 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 interactors’ ($n_{wi}$ 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...
Non-trophic interactions 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 $m_i = f_{\text{nti}}(N_m)$, where $f_{\text{nti}}$ is a function inversely relating the parameter $m_i$ to the biomass density, $N_m$, of the non-trophic interactor. For example, the function $f_{\text{nti}}$ could be a ‘rational function’ (using the terminology of Otto & Day 2007) such as:

$$m_i = f_{\text{nti}}(N_m) = \frac{m_{\text{nti}}N_m + m_{a}N_i}{N_m + N_i}$$

(2)

where $N_m$ is the biomass density of the non-trophic interactor, $N_i$ is a typical average biomass density of the non-trophic interactor, $m_{a}$ is the mortality rate without non-trophic interaction, $m_{\text{nti}}$ is the maximum mortality reached in the presence of non-trophic interactions. According to this function, the mortality of the focal species is $m_i$ when there is no non-trophic interactor, and the mortality saturates at the value $m_{\text{nti}}$ when non-trophic interactors are abundant. This function $f_{\text{nti}}$ can be increasing or decreasing depending in the sign of $(m_{\text{nti}} - m_{a})$ 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 $f_{\text{nti}}$ 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-
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) can be positive or negative but the expression should be bounded below by zero so that the the flow of matter cannot be reversed in which case a prey would start eating its predator. Arditi et al. (2005) suggested to replace \( c_{ki} \) by the expression: \( c_{ki}(1 + \sum_{j=1}^{n} a_{kj}X_{j}) \), where \( a_{kj} \) describes the influence of the non-trophic interactors, species \( j \), on the trophic interaction between \( i \) and \( k \). Note that \( a_{kj} \) 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).

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.

2. The half-saturation density \( N_{ki} \) (in eqn 5) can be positive or negative but the expression should be bounded below by zero so that the the flow of matter cannot be reversed in which case a prey would start eating its predator. Arditi et al. (2005) suggested to replace \( N_{ki} \) by the expression: \( N_{ki}(1 + \sum_{j=1}^{n} a_{kj}X_{j}) \), where \( a_{kj} \) describes the influence of the non-trophic interactors, species \( j \), on the trophic interaction between \( i \) and \( k \). Note that \( a_{kj} \) 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).
Table 1 Summary of the categories of non-trophic interactions based on their direct effect on the focal species

<table>
<thead>
<tr>
<th>Categories</th>
<th>Parameters that could be affected by non-trophic interactions</th>
<th>Examples</th>
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<tr>
<td><strong>Non-trophic interactions that modify...</strong></td>
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<td>Parameters</td>
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<td>Refuge from predation§</td>
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<td>c_{ijk} (eqn 5 in Appendix)</td>
<td>Escape responses§</td>
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<td>R_{i}</td>
<td>Interspecific predator interference§</td>
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<td>C_{jo} (eqn 8 in Appendix)</td>
<td>Plant substances attract enemies of their enemies§</td>
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<td>Nitrogen fixing bacteria (on plants)*</td>
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<td>Parameters</td>
<td>m_{i} (eqn 1)</td>
<td>Whiplash effects (of algae on gastropods)§</td>
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<td>е_{i} (eqn 1)</td>
<td>Bulldozing effects (of gastropods on sessile species)§</td>
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<td>Establishment rate in space</td>
<td>Antagonistic interactions for territories§</td>
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<td>Total amount of space available</td>
<td>Stress buffering (shading, rhizosphere oxidation, desiccation ...)§</td>
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<td>Pollination§</td>
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<td>Parameters</td>
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<td>Pre-emption of space (competition for space for sessile species)§</td>
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<td>P/d (eqn 9 in Appendix)</td>
<td>3-D structures provided by kelps, coral reefs, tree litter</td>
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<td>Allelopathy§</td>
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<td><strong>Non-trophic interactions that modify non-feeding attributes of species</strong></td>
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|      the study system). Non-trophic interactions may also modify 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 (N₂), 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. N₂ 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 interactions 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. \( R_o \) in eqn 8 in supporting information) becomes:

\[
R_o = \frac{f_{in}(N_w)}{\alpha} = \frac{R_{ao} \alpha \sum_{m} N_{wa} + R_N N_w}{\alpha \sum_{m} N_{wa} + N_w}
\]  

(11)

where the index \( m \) refers to the plant species which is facilitating species \( i \), \( N_w \) their biomass density and \( \alpha \) 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 \( R_o \) of the plant species decreases (i.e. competitiveness increases) when the \( N_w \) are more abundant or when \( \alpha \) increases (and tends to its minimal value \( R_{ao} \)). 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 & Valente-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
Parameter values and more details about the simulations are given in supporting facilitation. Each simulation was based on 100 repetitions with random variation in facilitation among plants and light green bars to those with interference and 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.

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 grey 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 $R_w$) 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; Díaz-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 (Melian 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; Thebault & 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 Gouard & 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 modelers 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.

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AUTHORSHIP

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